The behavioural ecology of burbot, *Lota lota*: Diel migrations, spatial behavioural syndromes, and behavioural thermoregulation in a reservoir resident.

by

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A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Doctor of Philosophy

in

Biology

Waterloo, Ontario, Canada, 2015

Authors Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

Chapter 2: Diel vertical migration of adult burbot: A dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain. Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Leake, A., Cooke, S.J. & Power, M.

While the research was my own, all authors provided valuable contributions to the research. PMH conducted the fieldwork, analysed the data and wrote the paper. Assistance in the field was provided by LFGG, EGM, DAP, and SJC. The idea for the study was a collaborative effort involving PMH, LFGG and MP. Study design was a collaborative effort between all authors. Oversight and assistance in the data-analysis was provided by EGM. All authors provided valuable edits to the final document. The chapter was published as:

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

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Abstract

While the impacts of hydropower development on diadromous and riverine fish species have received considerable attention, the ecology and behaviour of fish species residing in hydropower reservoirs is not well understood. As a winter-specialist species, commonly found in hydropower impoundments in North America, burbot, *Lota lota,* provide a useful model species to test hypotheses regarding reservoir resident ecology and behaviour. In this thesis, 3 empirical studies were used to investigate the behavioural ecology of burbot residing in Kinbasket Reservoir, British Columbia, Canada. Hypotheses regarding diel differences in depth use, individual differences in space use, and seasonal and diel differences in thermal habitat selection, were tested using biotelemetry and mixed effects modelling frameworks.

In Chapter 2, results indicated adult burbot performed a diel migration into shallow water at night. Further, the size structured nightly depth distributions, seasonal diel differences in thermal habitat use, and elevated nightly activity observed, suggested the adaptive significance of this migration was best explained by a trade-off among foraging opportunity, bionenergetics advantage, and predation avoidance. In Chapter 3, burbot spatial behavioural traits were identified as personality dependent, with significant repeatability detected in home range, movement, site-fidelity, rate of vertical movement and dispersal from release. Further, home range, movement and site fidelity were correlated at the between individual level, indicating a spatial behavioural syndrome. In Chapter 4, results showed nightly selection by burbot for 8-10°C during the pre-spawn period, 0-2°C during the spawning period, and for 12-14°C during the summer, indicating that selection occurs outside the summer period and differs between seasons and diel periods.

The results of the three data chapters provided the first empirical documentation of several interesting species-specific behavioural patterns, including; diel migrations, spatial behavioural syndromes, and seasonal and diel shifts in thermal habitat selection, in adult burbot. Further at broader ecological scales, these data chapters provided: a significant contribution to the general understanding of the ultimate causes of diel migrations, important advances in the understanding of the role of animal personality in shaping spatial ecology, and considerable progress towards an improved understanding of the temporal dynamics of thermal habitat selection. Combined, these findings emphasise the importance of conservation of benthic diel migrating species for lake and reservoir ecosystem integrity, suggest that conservation policy based on mean measures of space use may not adequately capture the space use requirements of populations, and highlight the vulnerability of winter specialist species to increased winter temperatures.

In North America, hydropower has been hypothesised as contributing to the decline of burbot populations and a need for a broad synthesis of existing knowledge regarding burbot and hydropower, was identified. Accordingly, a review of scientific literature regarding the benefits and threats of hydropower to burbot populations, was undertaken in Chapter 5. The synthesis provided important clarity regarding the relationship between burbot and hydropower, suggesting that while winter discharge routines may threaten downstream burbot populations, reservoir habitats can provide suitable thermal and trophic niches for the stenothermic, predatory burbot. Furthermore, while turbine entrainment has been hypothesised as a possible factor in burbot declines, the synthesis and traits based approach used, indicated overall population level risk from entrainment was low and resulted in a recommendation for research into the ability of juvenile entrained fish to contribute to downstream recruitment.

Together, the findings of this thesis have made an important contribution to knowledge regarding: the behavioural ecology of burbot, the relationship between hydropower and burbot ecology and the behavioural ecology of fish in general. Furthermore, this thesis has provided a detailed account of the relevance of these findings to both burbot-specific and wider conservation management and policy. Finally, this thesis has identified several interesting topics for future research which include: the role of animal personality in partial diel migrations, the ability of physiological and behavioural correlates to predict spatial behavioural syndromes *a priori*, the fitness consequences of thermal habitat selection, and the impacts of hydropower on population connectivity of a fascinating winter-specialist diel-migrating species.

Acknowledgements

Thanks to my excellent supervisors Mike Power and Steve Cooke for providing such a great opportunity, and for mentoring and encouraging me throughout my PhD program, particularly in light of my growing family situation. Special thanks also go to my fantastic collaborators, Eduardo Martins and Lee Gutowsky for their many contributions to publications, discussions, and ideas. Thanks also to David Patterson for field support, editing, and manuscript contributions. Thanks to my biology committee members Brian Dixon and William Taylor. Thanks to Jamie Tippe of Grizzly Country Marine, Sean Landsman, Jeff Nitichoruk, Juan Molina, Mark Taylor, Glenn Crossin, Jason Thiem, Jamie Hills, Taylor Nettles, and Lisa Donaldson for field assistance. Thanks to Alf Leake, Karen Bray, and the late Paul Higgins and all at BC hydro and the Mica Camp for logistical support. Thanks to Valemount, British Columbia, RCMP for contributions to a safe fieldwork environment. Thanks to all Power lab members past and present, with particular thanks to Wendy Michaud for sharing ideas and homebrew. Thanks to Horst and Antoinette Vogel and Chris and Richard Harrison for their kindness, encouragement and support. Thanks most of all to my partner Margaret-Rose, without whom none of this would be possible. Thank you for sacrificing so much to ensure that our daughters were well looked after during the completion of this PhD, and for counting worms for me, so I could pursue my dreams.

Funding was provided by 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. 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.

Dedication

This thesis is dedicated to my wonderful partner Margaret-Rose for her continued support, encouragement and patience during the PhD process.

This thesis is also dedicated to my family: To Chris and Richard Harrison, for being brilliant parents and for the interest in ecology they inspired in me, through their passion for orchids and butterflies; to my brother Neil, for first taking me fishing and igniting my interest in all things about fish, and providing an excellent academic role model. Finally to my daughters Malila-Jane and Josephine-Rose, in the hope that my passion for burbot might one day inspire something in you.

Table Of Contents

List of Figures

List of Tables

1 General Introduction

Hydropower accounts for around 60% of electricity generation in Canada, demand is growing rapidly, and capacity is expected to double in the next 15 years (Smokorowski *et al.* 2011). Hydropower changes natural river and lake systems to regulated rivers and reservoirs, and this change often has large scale environmental impacts (Rosenberg *et al.* 1997; Rosenberg *et al.* 2000). While the effects of hydropower on anadromous and riverine fish species below hydropower infrastructure, have received considerable attention in the literature (Poff *et al.* 1997; Lytle and Poff 2004; Poff and Zimmerman 2010), much less is known about the ecology and behaviour of fish species that reside in hydropower reservoirs (Martins *et al.* 2013).

Study Species: burbot *Lota lota*

As a species commonly occurring across a wide northern circumpolar distribution and often found in reservoir systems (Stapanian *et al.* 2010), burbot provide a useful and interesting model species to test hypotheses regarding hydropower effects on reservoir resident fish behaviour and ecology. Burbot are a large bodied, benthic species (Stapanian *et al.* 2010), often acting as the top predator (Cott *et al.* 2011). As the lone freshwater member of the gadoids, burbot are thought to have invaded from the marine system fairly recently, in evolutionary terms (Van Houdt *et al.* 2003; Van Houdt *et al.* 2005). It is the evolution in the marine system that is thought to account for the adoption of a winter active phenology (Hölker *et al.* 2004; Hardewig *et al.* 2004), that is commonly observed in North Atlantic marine species, but rare in temperate freshwater species

(Pörtner 2006; Shuter *et al.* 2012). Burbot feed extensively during winter and spawn in late winter/early spring (Cott *et al.* 2013) and as an *R* strategist, burbot have high fecundity, producing up to 3 million small eggs per female on an annual basis (Roach and Evenson 1993). While spawning is thought to be broadcast and involve large groups of burbot, spawning habitat requirements are not well documented (McPhail and Paragamian 2000). Burbot are found both in lakes and rivers and display a variety of life history strategies in lakes, including adfluvial, and lake spawning (Jude *et al.* 2013). Burbot are not consistently valued within their range (Stapanian *et al.* 2010), and historically little was known about their biology, behaviour or ecology (McPhail and Paragamian 2000). However in recent years, scientific interest in the species has grown, in part due to the existence of four recent burbot specific symposia (Paragamian and Willis 2000; Paragamian and Bennett 2008; Paragamian and Stapanian 2011; Stapanian and Madenjian 2013). Nonetheless, considerable knowledge gaps regarding the behaviour and ecology of burbot exist, both in hydropower and natural systems (Stapanian and Madenjian 2013).

Study Site: Kinbasket Reservoir

The Columbia River is heavily impacted by hydroelectric generation, with a total 194 large dams in the catchment (Revenga *et al.* 1998) and only 70km of free flowing water in the ~2000km long mainstem river (McCully 2001). Historically, burbot were abundant in the Columbia River (Prince 2001). Today, while burbot populations are found in several Columbia River reservoirs (for example the Duncan Lakes and Arrow Lakes B.C (Spence and Neufeld 2002; Ardnt and Baxter 2006), and Lake Kookanusa, Montana (Dunnigan and Sinclair 2008)), burbot population status in many Columbia River reservoirs are unknown (Cope 2008), and riverine populations appear to be in decline (see for example (Hardy and Paragamian 2013)). The study site for this thesis, Kinbasket Reservoir (52°08’N, 118°27’W, Figure 2.1), is situated on the upper reaches of the Columbia River, in British Columbia, Canada, and is the fourth largest reservoir in British Columbia, and the 2nd largest on the Columbia River System. The reservoir is a large (43, 200 ha), deep (up to 190m), montane reservoir situated in the Kootenay-Rocky Mountain ranges, operated for storage and for hydroelectric generation, with a current generation capacity of 1805MW and a head height of 243 meters (Bray 2011). The dam was constructed in 1972, a few kilometers downstream of the historical confluence of the Canoe and Columbia Rivers, which, along with the Bush River, now form the three main tributary arms of the reservoir (Figure 2.1). The reservoir is fed by glacial run off and snow melt, and is operated on a winter drawdown regime, with a large seasonal difference in reservoir elevation (for example in 2011, the reservoir reached low pool (722m) on 21st of April 2011 and was filled maximum elevation (754m) on 4th November 2011). Burbot are thought to have been abundant in the area before construction of the Dam (Prince 2001). Little was known about the burbot population in Kinbasket Reservoir, prior to our study. Nonetheless, anecdotal evidence suggested that burbot populations were large enough to warrant concern about possible entrainment vulnerability (see (Martins *et al.* 2013)), and sufficient to enable the capture of a suitable number of fish for a large telemetry project. Additional fish species confirmed in the reservoir include: bull trout *Salvelinus confluentus*, rainbow trout *Onchorynchus mykiss*, and northern pikeminnow *Ptychocheilus oregonensis,* kokanee *Oncorhynchus nerka,* mountain whitefish *Prosopium williamsoni,* longnose sucker *Catostomus catostomus,* largescale sucker *Catostomus macrochelius,* redshide shiner *Richardsonius balteatu,* and slimy sculpin *Cottus cognate* (Westslope 2005).

Knowledge Gaps

While burbot are known to be benthic (Fischer 1999; McPhail and Paragamian 2000; Fischer 2000a; Fischer 2000b; Cott *et al.* 2015), adult burbot depth distribution, both in reservoirs and lakes, has not been extensively researched, and seasonal and diel patterns of depth use are an important knowledge gap in our understanding of reservoir fish ecology. Diel migrations (DMs), where organisms migrate between habitats on a diel basis (Scheuerell and Schindler 2003), have been observed in a wide range of organisms (Lampert 1989) including pelagic species in reservoirs (for example kokannee (Bevelhimer and Adams 1993), and bull trout (Gutowsky *et al.* 2013)). While DM direction is often vertical (DVMs) in pelagic species, horizontal diel migrations (DHMs) have been observed in stream dwelling salmonids (Armstrong *et al.* 2013), and profundal-littoral diel migrations known as diel bank migrations (DBMs) have been noted in several benthic species (Gorman *et al.* 2012a; Gorman *et al.* 2012b). Pelagic stage juvenile burbot are known to perform DVMs in lacustrine systems (Probst and Eckmann 2009; Donner and Eckmann 2011). However, diel patterns of vertical distribution of adult burbot have rarely been studied, and although DMs have been hypothesised, evidence to date remains anecdotal (see for example (Carl 1995)). The proximate cause of DMs for most species, are known to be the change in light conditions between diel periods (Ringelberg and Van Gool 2003). The ultimate causes of DVM, that is the long term evolutionary benefits associated with the behaviour, may differ between species and are a matter of some debate (Mehner 2012). DM ultimate hypotheses include: improved feeding opportunity (Janssen and Brandt 1980), predation avoidance (Hrabik *et al.* 2006; Gjelland *et al.* 2009), and bioenergetics advantage i.e. fitness advantages gained from exploiting thermal heterogeneity (Sims *et al.* 2006). Multi-factor hypotheses, such as “the anti-predation window” (Scheuerell and Schindler 2003), are increasingly being recognized for their ability to explain DMs (Mehner 2012). In juvenile burbot, DVM was attributed to multiple factor trade-offs (Donner and Eckmann 2011), however, hypotheses for diel migratory behaviour in adult burbot have not previously been explored.

Along with depth distributions, the spatial ecology and movement of burbot in both natural lake and reservoir systems, are important knowledge gaps. While home range sizes of burbot were estimated in Kookanusa Reservoir, Montana (Dunnigan and Sinclair 2008) and movement patterns of burbot have been explored in the Kootenai River/Lake system below Libby Dam (Paragamian and Wakkinen 2008), these radio-tracking studies were hampered by the small numbers of tagged individuals and infrequent detections. Nonetheless, in both studies, anecdotal evidence was presented to suggest inter-individual differences in spatial behaviours occurred. When behavioural differences between individuals are consistent over time and between contexts (i.e. repeatable), they are known as animal personality (Gosling and John 1999; Sih *et al.* 2004; Stamps and Groothuis 2010). Personality traits (PTs) have been detected in many different behaviours and organisms, with personality typically accounting for ~35% of the variance in most behavioural traits (see (Bell *et al.* 2009) for a meta-analysis). While traditional ecologists have often considered these individual differences to be noise around the mean (Careau *et al.* 2008), behavioural ecologists are now recognizing that individual differences have many implications for species' ecology, evolution and conservation (see (Wolf and Weissing 2012) for a review). Spatial personality traits have been observed in several animal species (for example Western Bluebirds *Sialia mexicana* (Duckworth and Badyaev 2007; Duckworth 2008)), however, previous work has tended to focus on metrics of dispersal, and few authors have investigated the role of personality in alternative important spatial metrics, such as home-range, movement and site fidelity. Furthermore movement heterogeneity is commonly found in spatial ecology datasets (Taylor and Cooke 2012; Radinger and Wolter 2013), yet explanations have tended to focus on environmental cues, with few authors considering the role of animal personality (see (Taylor and Cooke 2014) for an exception). When PTs are correlated at the between-individual level, i.e. the ranking of individuals are consistent among two or more traits, they are known as behavioural syndromes (Dingemanse *et al.* 2012; Sih *et al.* 2012; Dingemanse and Dochtermann 2013). Spatial behavioural syndromes involving dispersal and other traits that might benefit invasion have received considerable attention in invasive species (see (Clobert *et al.* 2009; Cote *et al.* 2010) for reviews). In contrast, few authors have investigated the relationship between dispersal and other key spatial metrics.

Given the importance of temperature for the physiology and behaviour of ectotherms (Huey and Stevenson 1979; Huey 1991; Hertz *et al.* 1993), and the thermal habitat changes that occur as a result of reservoir construction (Baxter 1977), a more thorough understanding of the thermal ecology of fish in reservoirs represents a key knowledge gap for reservoir resident species. Temperature is often competed for and thus is considered a niche resource (Magnuson *et al.* 1979; Attrill and Power 2002; Attrill and Power 2004). Thermal resource selection, also known as behavioural thermoregulation (BT), is an important tactic used by ectotherms to optimise thermal experience for physiological processes (Huey 1991). However, while BT has often been investigated during summertime periods of high thermal heterogeneity, few authors have considered how BT might change on a seasonal and diel basis in response to differing physiological requirements. Furthermore, while BT is often hypothesised as factor in the evolutionary significance of DMs (for example (Sims *et al.*, 2008)), few authors have taken a quantitative approach to model thermal habitat selection at a diel scale. As a cold water stenotherm (McPhail and Paragamian 2000), burbot may be particularly sensitive to changes in thermal habitat availability. Although lab based thermal preferences have been established (Pääkkönen and Lyytikäinen 2000), field based thermal selection has not been quantitatively investigated, and potential diel and seasonal shifts in temperatures have not been explored.

Burbot are threatened and endangered towards the southern end of the North American range and hydropower has been hypothesised as contributing to the decline (Stapanian *et al.* 2010). Yet few authors have attempted to synthesise and collate existing scientific information regarding the relationship between burbot and hydropower infrastructure. Indeed, despite considerable research effort involving burbot residing above and below hydropower systems (see for example (Hardy *et al.* 2013)), few authors have attempted to summarise the associated threats and benefits. Given the proliferation of hydropower construction within the North American range of burbot, a greater understanding of the impacts of hydropower on burbot populations, and an identification of key research needed to mitigate current hydropower impacts will likely be important for the conservation of the species.

Methodological Opportunities

Passive acoustic biotelemetry has led to considerable advances in our understanding of the spatial (Welch *et al.* 2002), behavioural (Altmann and Altmann 2003), and thermal (Martins *et al.* 2011) ecology of fishes. Given the ability of biotelemetry to provide frequent measures of depth, spatial location and body temperature (Donaldson *et al.* 2014), application of the technology presents an excellent opportunity to gather a detailed picture of the ecology and behaviour of reservoir resident fishes (Cooke *et al.* 2004). Telemetry provides time-stamped data, over long periods, and through seasons and conditions when direct field work are challenging. Thus telemetry facilitates investigation of long and short term temporal (for example yearly, seasonal and diel) patterns of behaviour (Donaldson *et al.* 2014). Furthermore, the ability of passive telemetry to simultaneous collect data from multiple individuals, allows for inference at both the individual and population level that is often not possible with active methods (Heupel *et al.* 2006). Passive telemetry data have proved useful for the estimation of many important spatial metrics (for example; short-term center of activity estimates (Simpfendorfer *et al.* 2002), home range estimates (Heupel *et al.* 2004), site-fidelity measures (Heupel *et al.* 2006), and movement metrics (Campbell *et al.* 2012). When combined with environmental data, passive telemetry provides an excellent opportunity to define habitat use, selection and preference at a resolution and scale not previously possible (Johnson *et al.* 2008; Aarts *et al.* 2008), and can provide valuable insight into the role of abiotic factors in governing behavioural and ecological metrics (Cagnacci *et al.* 2010; Donaldson *et al.* 2014). In addition, given that telemetry detections are individually coded, correlations with internal measures such as sex and body size can easily be modelled (Cooke *et al.* 2004). Finally, the availability of multiple repeated measures of individuals, provides data well suited to the study of animal personality in the wild (Miriam *et al.* 2013; Harrison *et al.* 2014).

While telemetry provides unique opportunities for field ecology, telemetry data also present some intrinsic statistical analytical challenges. Chief among these challenges is the repeated measures nature of telemetry data, where multiple measures on the same individual violate the assumption of independence required of many statistical methods (Rogers and White 2007). Use of mixed effects models, that allow relaxation of the independence assumption by incorporating separate intercepts and/or slopes for individuals, is becoming increasingly common in ecology (see (Bolker *et al.* 2009; Zuur *et al.* 2009) for in-depth guides). Mixed effects statistical software (for example, the R package *nlme* http://cran.r-project.org/web/packages/nlme/index.html) is now widely available that accounts for the individual level correlations and explicitly incorporates the temporal and spatial correlation between detections from the same individual, that can bias results, if not accounted for appropriately (Rooney *et al.* 1998). Mixed effects models are also increasingly being recognized for their utility in modelling resource selection data collected by telemetry (Gillies *et al.* 2006; Hebblewhite and Merrill 2008). Further, non-normal response distributions, which are commonly encountered in ecological studies, are now accessible to ecologists in a mixed effect framework (Zuur *et al.* 2012). Finally, Bayesian mixed effects models are increasingly being recognized by behavioural ecologists as important tools for the study of animal personality and behavioural syndromes, for their ability to distinguish between individual, residual, and environmental driven variances (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013; Brommer 2013a).

Thesis Objectives

Given the identified gaps in our understanding of the behavioural ecology of reservoir resident fish and burbot in particular, and the combined potential of biotelemetry methods and mixed effects frameworks to provide a detailed long term and potentially rich account of the spatial, thermal and migratory behavioural ecology of burbot in reservoir settings, the primary objective of this thesis was; **to improve understanding of the behavioural ecology of burbot in the Kinbasket Reservoir, British Columbia, Canada, utilising passive acoustic biotelemetry methods and a mixed effects modelling framework.** In that regard, data analytical chapters as described below were completed to explore aspects of burbot spatial and behavioural ecology.

Chapter 2: Diel vertical migration of adult burbot: A dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain.

In this study, acoustic telemetry was used to record the depth use and thermal experience of 47 adult burbot in Kinbasket Reservoir, British Columbia, Canada over a two year period. Mixed effects models were used to investigate the influence of season, diel period, and body size on the depth distribution, vertical activity, probability of migration, and thermal experience. Hypotheses related to diel differences in burbot depth use, thermal experience, diel differences in vertical activity, and the consistency of individual DVMs were tested. Finally, burbot DVM was explored in the context of a number of possible explanatory hypotheses, including: bioenergetics optimisation, anti-predation response, foraging opportunity optimisation, and multi-factor explanations. Results of the study were published in the manuscript:

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

Chapter 3: Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (Lota lota)

In this study, the spatial behaviour of 44 wild, free-swimming burbot in Kinbasket Reservoir, British Columbia, was monitored over two years using acoustic telemetry. Bayesian mixed effects modelling frameworks were used to test whether burbot home range, horizontal movement, vertical activity, site-fidelity and dispersal from release met personality dependent behaviour criteria. Finally, collected data were used to test for between-individual correlations among spatial behaviours, indicative of a spatial behavioural syndrome. Results of the study were published the manuscript:

Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Cooke, S.J. & Power, M. (2014) Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (Lota lota). Behavioural Ecology , 26 (2): 483-492

Chapter 4: Thermal habitat selection is temporally plastic in the diel-migrating winter-specialist species

In this study, animal-borne thermal biotelemetry, thermal habitat logging and zero-inflated mixed-effects resource selection index models were used to investigate thermal resource use, selection and avoidance in 18 burbot, tracked for 1 year, in Kinbasket reservoir. Obtained data were used to test the hypotheses that: behavioural thermoregulation occurs throughout the year and temperatures selected for by burbot differ on a diel and seasonal basis. Results of this study were submitted to The Journal of Fish Biology on July 2nd 2015 and the manuscript is currently under review (Manuscript number: MS 15-397).

Given the identified need to synthesis and collate scientific information regarding the relationships between burbot and hydropower infrastructure, a secondary aim of the thesis was: ***to synthesise existing knowledge regarding burbot and hydropower to define the overall probable impacts on populations of hydropower operations and identify key remaining research needs.*** The objective was achieved through the completion of a literature review as described below.

Chapter 5: Burbot Lota lota and large hydropower in North America: Benefits, threats, and research needs for mitigation

In this paper, a traits-based assessment approach (Rubach *et al.* 2011; Cada and Schweizer 2012) was used to review the threats and benefits of hydropower to burbot populations. The effects of flow alterations, thermal habitat changes and disruption of downstream connectivity for riverine burbot below hydropower structure were discussed, and the consequences for burbot of turbine entrainment, reservoir drawdown, trophic depression and upstream connectivity were investigated. A synthesis of knowledge was presented and used to assess and compare relative impacts to burbot populations with the aim of identifying potential conservation issues. Finally, the review concluded with an outline of key research needed to conserve riverine burbot below hydropower and better understand and manage burbot in reservoirs. This review manuscript was submitted to the journal: Fisheries Management and Ecology on May 27th 2015 and is currently under review (Manuscript number: FME-15-082).

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

Overview

Diel vertical migration (DVM) in pelagic organisms is typically attributed to bioenergetic gain, foraging opportunity, predator avoidance, and multi-factor hypotheses. While a number of benthic species perform nightly migrations into shallower waters, the function of these DVMs have largely been ignored in benthic fishes. We used depth and temperature sensing telemetry to investigate DVM function in a freshwater benthic piscivore, adult burbot (*Lota lota*). We modelled the influence of season, diel period, and body-size on the depth, vertical activity, migration probability and thermal experience of 47 adult burbot over two years in a reservoir in BC, 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 a nocturnal predator, constrained by predation/cannibalism threat in smaller individuals. The thermal experience patterns observed, suggest DVM may also provide a seasonal bioenergetic advantage. Our detection of within-individual plasticity in migration strategy, are indicative of a partial migration. Taken together, our results suggest a multi-factor DVM hypothesis; a dynamic trade-off between bioenergetic advantage, foraging opportunity, and predation threat.

Introduction

Diel vertical migrations (DVMs) are common among a range of aquatic organisms (Blaxter 1974; Lampert 1989), however 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.* 2012b), however 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 between the light and dark cycles (Mehner 2012). In pelagic organisms, the ultimate function of DVM is thought to be a function of bioenergetic gain, predation avoidance, foraging opportunity optimisation, and multi-factor 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 have rarely been studied.

The decision to migrate among habitats can be seen as an optimisation of the mortality rate to foraging gain ratio (μ/f) (Werner and Gilliam 1984; Gilliam and Fraser 1987). Inter-specific, inter-population, 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 DVM that compromise <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 bioenergetic driven scenario, DVMs cease during periods when no thermal advantage is apparent (Sims *et al.* 2006). While solely bioenergetic driven DVMs have been described in benthic sharks (Sims *et al.* 2006), no similar empirical evidence have 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, 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 optimisation 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).

Multi-factor DVM explanations, where DVMs are a function of a combinations of factors, are increasingly being recognised for their ability to better explain DVM than simplistic single hypotheses (Stockwell and Johnson 1999; Mehner 2012). The most common multi-factor explanation is the ‘anti-predation window’ strategy (Clark and Levy

1988), where differences in the visual range of predators and prey, allow animals to remain undetected by predators, while still foraging in the upper water column at night (Scheuerell and Schindler 2003).

As a benthic species (Stapanian *et al.* 2010), burbot (*Lota lota*) provide an interesting model species in which to explore the function of DVM outside of the traditional pelagic species focus. Burbot, have been shown to exhibit a 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 which anecdotally observed an adult burbot DVM (Bergersen *et al.* 1993; Carl 1995). Given that lentic burbot are known to benthic (Fischer 2000a; Fischer 2000b), and often found in profundal/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 thermal experience. We tested the hypothesis that burbot depth distribution and activity differs between day and night, and investigated whether DVMs were consistently performed by all individuals. We then explored burbot DVM in the context of number of possible explanatory hypotheses, including: bioenergetics, thermal experience, anti-predation response, foraging opportunity optimisation, and multi-factor explanations.

Materials and Methods

Data for the study were collected from May 2010 to May 2012 in Kinbasket Reservoir, a deep (~190m maximum depth, 57m average depth), steep-sided, oligotrophic, 410km^2 hydroelectric storage reservoir (Bray 2011). The reservoir is situated 147km north of Revelstoke, in British Columbia, Canada (52°08′N 118°27′W ;Figure 2.1). 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 30m 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 15m, with surface waters varying between 2 and 13°C. Over the summer this broad thermocline increased to a maximum depth of 64m 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), largescale sucker (*Catostomus macrochelius*), redshide shiner (*Richardsonius balteatu*), and slimy sculpin (*Cottus cognate*) (Westslope 2005).

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 ^{o}C), which have been shown to reduce capture stress and maximise capture rates (Bernard *et al.* 1991). Minimum size for tagging (300g) was established by using the 2% tag mass in water rule (Brown *et al.* 1999). Captured burbot were anaesthetized in a 90ppm 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 45mm X 13mm, 6g in water, signal transmission rate 60-180 seconds, average 120 seconds, 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 20mm incisions made approximately 30-50mm anterior to the vent, slightly off-set from the mid-ventral line. The post spawn timing of the sampling period generally precluded sexing of fish. Throughout the surgery, re-circulating 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).

Telemetry Array

Forty two independent omni-directional 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 (Figure 2.1). Average receiver range was ~750m radius, yielding acoustic coverage of approximately 8% (35km^2) reservoir (Figure 2.1). Receivers were deployed at minimum reservoir drawdown in late April 2010, and 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 5 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; Fischer 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 post 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 pre-analysis 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 <1m shallower than mean daytime depths in a given 24h 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. pre-spawn & spawn (November to January), post-spawn (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 centered in order to facilitate model convergence. All four models (prior to backwards 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 auto-regressive 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 auto-regressive component uses a linear regressing co-efficient at order p, and the moving average component uses an un-weighted moving average co-efficient 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 LMM (Zuur *et al.* 2009) and log likelihood tests for GLMMs (Zuur *et al.* 2009). Normality assumptions for LMMs were checked graphically using Q-Q plots and histograms of standardised 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 61.0cm 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 migration was investigated using the probability of migration model (Model 4). The bioenergetics efficiency strategy explanation was explored using post hoc comparisons of mean thermal experience between night and day from the temperature model (Model3), with the expectation that under a solely bioenergetics DVM scenario, DVM would only 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 bioenergetics advantage (Sims et al. 2006; Andrews et al 2009). Evidence of 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 night-time depth distribution or migration probability would be expected to be indirect evidence of predation avoidance (Busch *et al.* 2011). The foraging optimisation strategy DVM explanation was explored using post hoc comparison of daytime and night time activity rates from our ROVM model (Model 2), with the expectation that increased night-time 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 post filter burbot sensor detections were recorded comprising 481,337 depth detections and 448,945 temperature detections. Burbot were detected at 37 of our 42 receivers (Figure 2.1).More than 95% of detections were recorded at receivers in the confluence area (Figure 2.1*a*). Detections were recorded between April 29, 2010 and April 26, 2012 (i.e., over a period of 727 days). Total length of tagged burbot ranged from 44.8to 74.1cm. Observed post-surgical mortality was limited to one individual (0.75%).

Depth (Model 1)

A total of 7,893 mean depths, per diel period, per fish, response variable observations were calculated from a total of 481,337 post-filter depth detections. Overall mean depth ± SE was 37.09 ± 1.30m during the day and 25.9 ± 1.52m at night. A variety of DVM amplitudes and behaviours were observed; four individual burbot DVM behaviours are shown in Figure 2.2. In the reduced depth model, significant effects were found for the season x diel period x year, and the season x diel period x total length interactions (see Table 2.1 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 test, all *P* = <0.01, Figure 2.3). Back transformed model predictions at median total length (54.4cm) revealed DVM amplitudes of 6.7-8.7m, 6.1-10.6m, and 7.3-13.1m for summer, pre-spawn and spawn, and post-spawn seasons respectively, in year 1 and year 2 (Figure 2.3). Significant effects were found for the season x diel period x total length interaction (*F*=12.44, *P*=<0.01; Table 2.1). Post-hoc testing revealed no significant relationship between burbot size and burbot depth distribution during the day in all seasons (Figure 2.4, all *P*>0.05). However, during the night-time, a significant effect of body size was found (see Figure 2.4), with larger burbot occupying significantly shallower depths than smaller burbot in the pre-spawn 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 post-spawn night period (z-= 2.09, *P*=0.15).

Rate of Vertical Movement (Model 2)

The ROVM model was constructed using 7,893 ROVM per diel period per fish response variable observations, calculated from 481,337 post filter depth detections. Mean ROVM ± SE was observed to be 4.27± 0.34m/hr during the day was and 6.58±0.44m/hr at night. In the reduced model significant effects were observed for the season x diel period x year interaction (Table 2.2). 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 (Figure 2.5; Tukey test, all *P* <0.05), except in year 1 during the pre-spawn and spawning period. Summer daytime vertical activity rates were found to be significantly lower in both years, when compared with all other seasons (Tukey test, all P<0.5).

Temperature Experience (Model 3)

The thermal experience model was produced using 7,567 mean temperature experience (per diel period per fish) response variable observations, calculated from 448,945 post filter raw detections. Observed seasonal temperature experience means ± SE (for day and night respectively) were as follows; summer 8.32 ± 0.29°C and 10.00 ± 0.30°C; pre-spawn and spawn 5.44 ± 0.20°C and 5.86 ± 0.23°C; and post-spawn 1.80 ± 0.08°C and 1.78 ± 0.09°C. In the reduced model significant effects of the season x diel period x year interaction were found (see Table 2.3). In the summer period, burbot consistently experienced warmer water at night than during the day in year 1 (Tukey test, estimate= + 1.2°C, *Z* = 22.17, *P*<0.01) and in year 2 (Tukey test, estimate = + 0.9°C, *Z* = 15.46, *P*<0.01). No consistent pattern of thermal experience was detected in the pre-spawn and spawn period or the post-spawn period across the two years. In the pre-spawn and spawn period, burbot used significantly warmer water at night in year 1 (Tukey test, estimate +0.21°C, *Z*= 3.6, *P* < 0.01), and no difference in diel thermal experience was seen in year 2. In the post-spawn period burbot were found to be experiencing significantly cooler water at night in year 1 (Tukey test, estimate -0.29°C, *Z* = -12.75, *P*=<0.01) although there were no significant differences in year 2 (Tukey test, estimate = -0.06°C, *Z*= -2.51, *P*=0.07, see Figure 2.6).

Probability of Migration (Model 4)

Our model was constructed using 2,888 binary observations, where individuals were detected during both diel periods in a 24hr cycle starting at sunrise. Burbot were observed to migrate on 2,121 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 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 2.4). Post-hoc multiple comparison showed the probability of migration differed significantly only between the post-spawn period and summer, with the probability of migration in the summer being 7% higher than that during the post-spawn period (Tukey test, z=2.63,P=0.02).

Discussion

Data from this study provide support for the hypothesis that adult burbot depth distribution and activity differs 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 bioenergetic 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 a size structured depth distribution in the summer and the pre-spawn and spawning periods 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; Paragamian 2010), which may in part represent a predation avoidance mechanism for a slow-swimming, nocturnal benthic animal, and likely amplifies any bioenergetics gains. However, the evidence of migration in larger individuals suggests predation avoidance alone does not fully explain DVM behaviours. 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 night-time activity is an increase in foraging activity consistent with the feeding opportunity optimisation 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 concluded that a multi-factor 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 dataset 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; Fischer 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°C and 0.9°C in year 1 and 2 respectively), Sims *et al*. (2003) demonstrated bioenergetics gains of up to 4% with a similar gradient (0.4°C and 0.9°C). Indeed, this pattern of thermal experience, when coupled with our evidence of elevated night-time activity and daytime sedentary behaviour, seem 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 post-spawn season where no thermal advantage was detected in both years, also indicate 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 post-spawn 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 night-time size structured depth distribution during the pre-spawn & spawn period and summer, suggest predation avoidance may play a part in modulating depth distributions during these periods. Accordingly, an optimisation of the μ/f ratio for smaller burbot may be achieved through a more risk-averse strategy of deeper depth distribution during nightly migrations during the summer and pre-spawn and spawn periods. 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/cannibalism risk to be 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 74.0cm and a a median length 54.4cm, our trapping method may be downward size selective because in this system we have captured burbot of up to 101.0cm, with 4 fish over 100cm (Harrison,P.M and Gutowsky,L.F.G. *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 103.0cm and an average of 72.2cm (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 x predator length (cm) – 0.487 ,then a burbot of 1010mm would be capable of preying on burbot up to 530mm. Out of our 47 tagged burbot, 18 were less than 530mm. Burbot have a relatively large mouth to total length ratio (Scott and Crossman 1973) and consequently we expect Damsard's Arctic char (*Salvelinus alpinus*) predator based model to 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 Damsard's equation is based on fusiform prey (Arctic charr) 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 thresholds, also play a part in modulating anti-predation 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 literature (Schram *et al.* 2006), we believe that intra-specific 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 88.1cm, (Gutowsky *et al.* 2011; Nitychoruk *et al.* 2013) aggressive predators that perform a clear pattern of DVM in this system (Gutowsky *et al.* 2011; Gutowsky *et al.* 2013; Nitychoruk *et al.* 2013). Again, using Damsgard's (1995) equation, the largest bull trout is capable of consuming burbot up to 46.6cm long. Four of our 47 tagged burbot were less than 46.6cm and 28 of our 47 tagged fish were within 10cm of this size. Furthermore, in a concurrent bull trout study in this system (Gutowsky *et al.* 2013), we witnessed a cannibalism attempt on a 56.0cm angled bull trout (Gutowsky L.F.G and Harrison, P.M *personal observation*). As stated above we expect Damsgard's equation to underestimate length for burbot as prey, and as a consequence, inter-specific 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; Pääkkönen *et al.* 2000).We suspect the failure to detect nocturnal behaviour in the pre-spawn and spawn period in year 1 is be an artefact 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 optimisation 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; Fischer 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 35m 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 (Harrison P, *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 optimisation 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 optimisation 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, optimisation 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 optimisation strategies, we suggest that the DVM of adult burbot is most likely a dynamic multi-factor strategy. Indeed, our data suggest that DVM behaviour may be a strategy whereby 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 six 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 multi-factor 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) suggest that the DVM is a within-individual ‘partial DVM’ or ‘partial migration’ consistent with those described by (Mehner and Kasprzak 2011; Chapman *et al.* 2012a; Chapman *et al.* 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 minimise 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 may be important for the minimisation 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.

Table 2.1 Higher order linear mixed effect 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 f test)	Fixed Effect Levels	Estimate	SE	df	*t*	*P*
Season x Diel period x Year ndf=2, ddf= 7828, f=49.85, P=<0.0001	Pre-Spawn and Spawn x Night x Year 2	-0.369	0.038	7829	-9.765	<0.01
	Summer x Night x Year 2	-0.141	0.031	7829	-4.523	<0.01
Season x Diel period x Total Length ndf=1, ddf= 7828, f=12.44, P=<0.0001	Pre-Spawn and Spawn x Night x Total Length	-0.016	0.003	7829	-4.942	<0.01
	Summer x Night x Total Length	-0.008	0.003	7829	-2.854	<0.01

Standard deviations of random effects (fish ID) variance: intercept = 0.14, residual= 0.62

Auto-regressive correlation estimate at parameter 1 = 0.81, moving average correlation estimate at parameter 1 = -0.64

Table 2.2 Model 2.Higher order reduced linear mixed effects model estimates of inverse hyperbolic sine transformed burbot rate of vertical movement (m/hr), 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 x Diel period x Year ndf=2, ddf=7489, f=23.16, P=<0.0001	Pre-Spawn and Spawn x Night x Year 2	0.83	0.12	7489	6.79	<0.01
	Summer x Night x Year 2	0.40	0.10	7489	3.93	<0.01

Standard deviations of random effects (fish ID) variance: intercept = 0.32, residual= 0.95

Auto-regressive correlation estimate at parameter 1 = 0.86, moving average correlation estimate at parameter 1 = -0.83

Table 2.3 Model 3.Higher order reduced linear mixed model estimates of burbot thermal experience occupancy (°C), showing parameter significance based on marginal conditional F tests, 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 x Diel period x Year	Pre-Spawn and Spawn x Night x Year 2	-0.26	0.1	7510	-2.61	<0.01
ndf=2,ddf=7510,f=26.99, P=<0.0001	Summer x Night x Year 2	-0.61	0.08	7510	-7.15	<0.01

Standard deviations of random effects (fish ID) variance: intercept = 0.92, residual= 2.52

Seasonal variance structure parameter estimates; summer = 1.00, pre-spawn and spawn= 0.68, post-spawn= 0.23

Moving average correlation estimate at parameters;1 = 0.78, 2= 0.94, 3 =0.38

Table 2.4 Model 4.Reduced binomial generalized linear model estimates of DVM probability, showing *Z* value and associated *P* value based on chi-squared test.

Parameter	Fixed effects levels	Estimate (logit)	SE	*Z*	*P*
	Post-Spawn (Intercept)	0.66	0.19	3.45	<0.01
Season	Pre-Spawn and Spawn	0.32	0.16	2.01	0.04
	Summer	0.35	0.13	2.63	<0.01

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

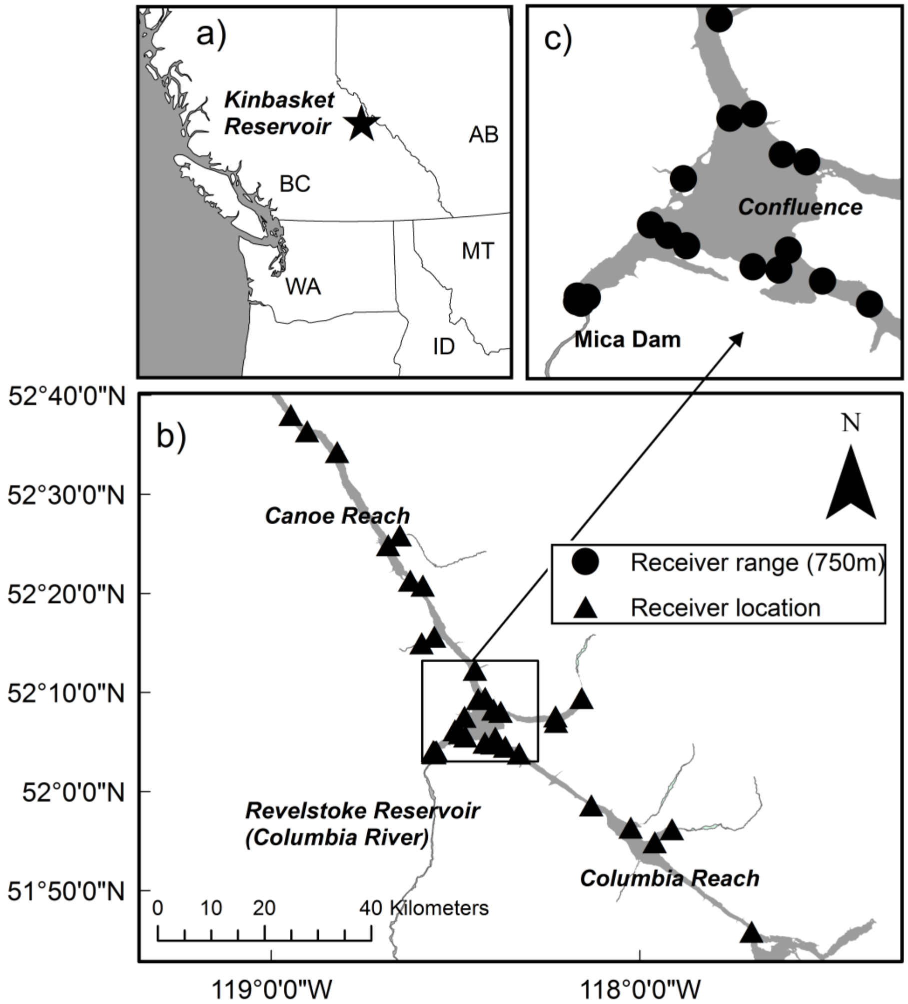

Figure 2.1 Insert a) Kinbasket Reservoir location. Insert b) Map of the study site Kinbasket Reservoir, BC showing receiver range (750m closed circles) for receivers where burbot detections occurred

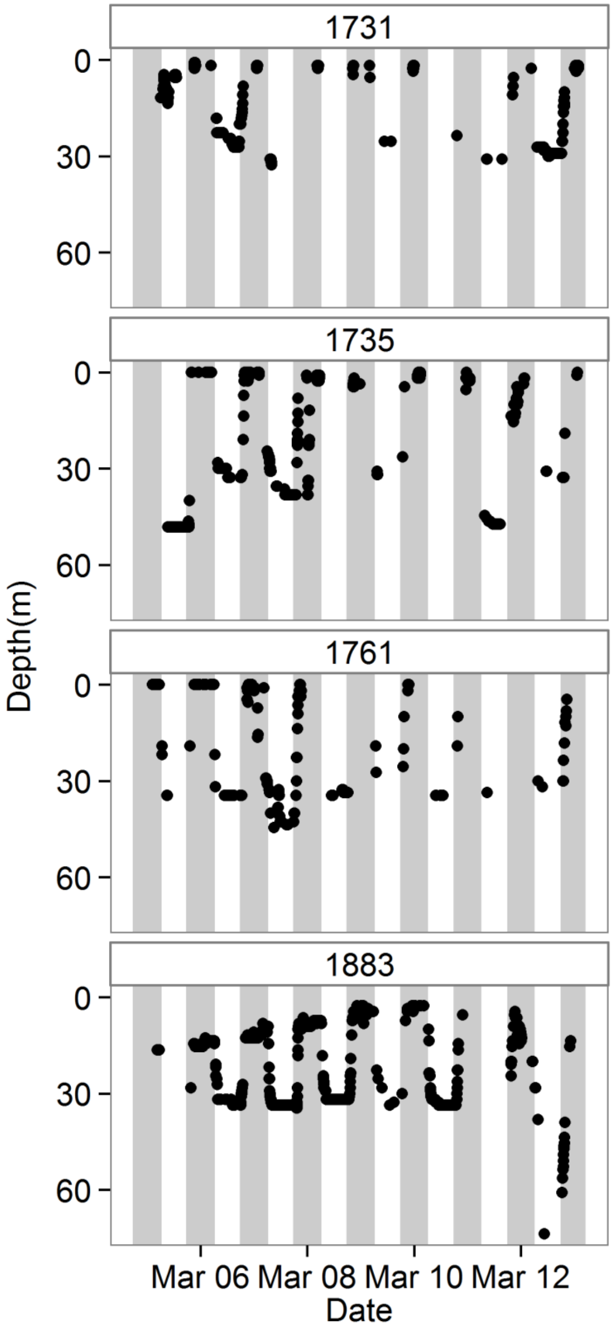

Figure 2.2 An example of raw depth detection data from 4 burbot in a week in March of 2011, with night-time periods in grey and daytime periods in white

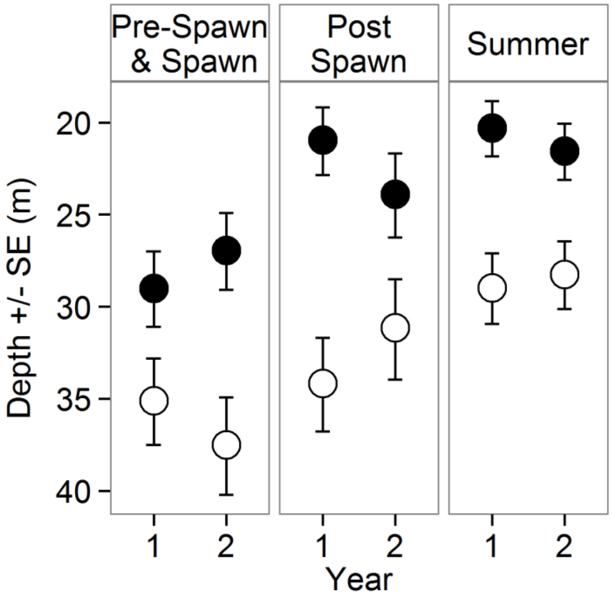

Figure 2.3 Model 1.Back transformed reduced linear mixed model burbot depth (m) estimates for median total length (54.4 cm). Open circles represent daytime depth occupation and closed circles represent night-time depth occupation. Error bars represent standard errors. Significant differences between diel periods were found for all season and year combinations (Tukey test, all $P < 0.05$).

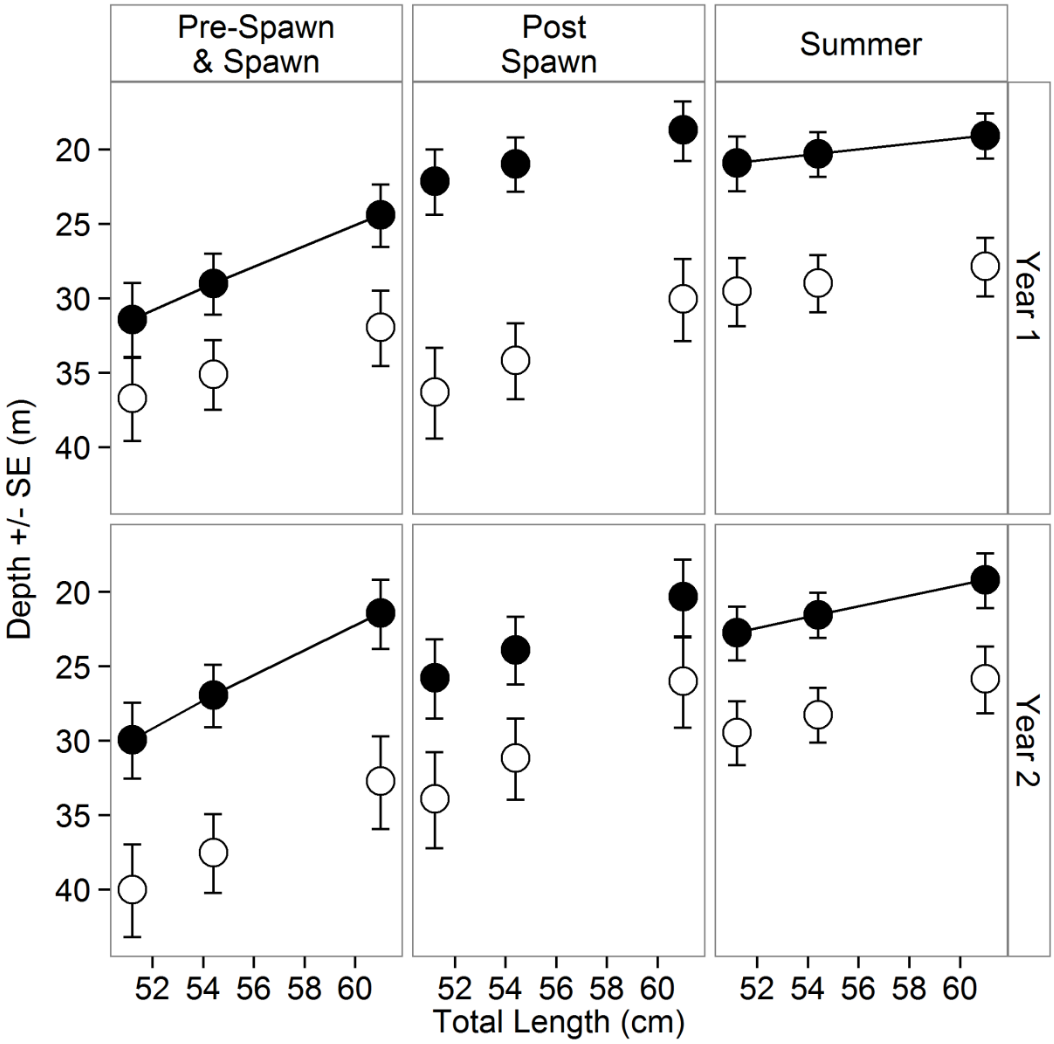

Figure 2.4 Model 1.Reduced back transformed linear mixed burbot depth (m) estimates at 0.25, 0.5 and 0.75 quantile total length among seasons and years. Error bars represent standard errors. Solid lines represent slopes identified as significant (all *P*=<0.05).

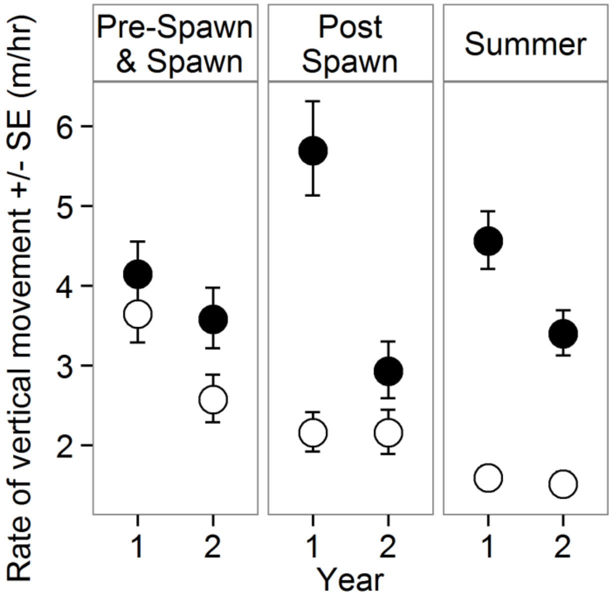

Figure 2.5 Model 2.Back transformed reduced linear mixed effect model estimates of burbot rate of vertical movement (m/hr). Open circles represent day and closed circles represent night. Error bars represent standard errors of predictions. Significant differences between day and night were found in all season and year combinations (Tukey test, all $P < 0.05$) except during the pre-spawn and spawn season in year 1

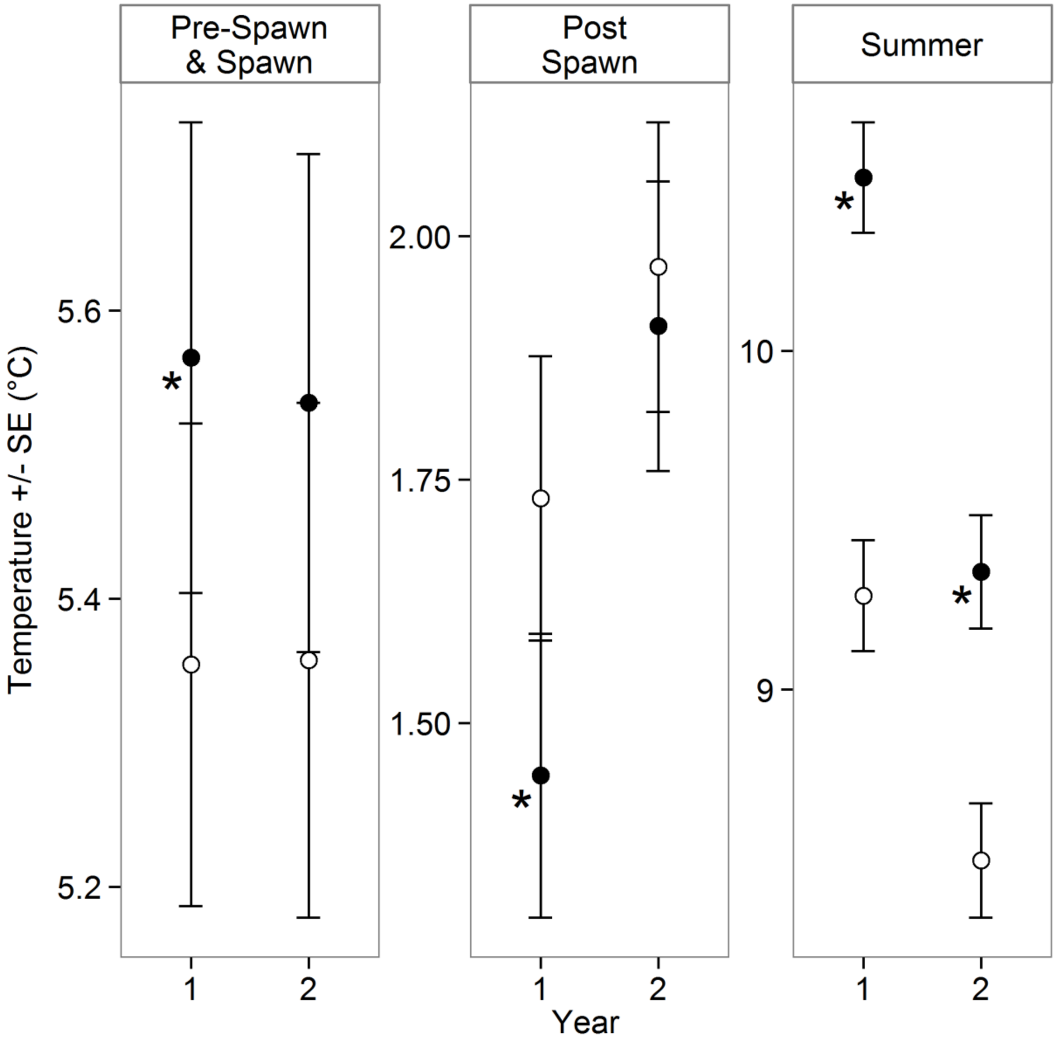

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Figure 2.6 Model 3.Reduced linear mixed model estimates of burbot thermal experience (°C). Open circles represent daytime close circles represent night-time. Error bars represent standard errors. * indicate significant differences between night and day within season and year (Tukey test, all *P* = <0.05)

3 Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*)

Overview

Although personality has been documented in numerous animals and characters, research into personality-dependent spatial ecology has focused on dispersal. Indeed, few authors have investigated the role of other important spatial traits such as home range, movement distance, vertical activity, and site-fidelity and it is not clear whether these behaviours are correlated with dispersal. In this study, we investigated individual differences in home range, dispersal from release, vertical activity, movement distance, and site-fidelity of 44 wild burbot *Lota lota* over 2 years, using an acoustic telemetry array and a Bayesian mixed modeling framework. We tested whether the spatial behaviours met the following criteria for personality-dependent behaviour: repeatability, cross-contextual consistency, and an absence of pseudo-repeatability associated with spatial context choice. We then tested for between-individual correlations among spatial behaviours, indicative of a behavioural syndrome. Our results documented repeatable, cross-contextually consistent, personality-dependent home range, movement, dispersal from release, and site-fidelity. In contrast behavioural differences in vertical activity were inconsistent across sampling years and may have been a product of habitat heterogeneity. Our data indicate a spatial behavioural syndrome occurred independently from dispersal from release, with behavioural types ranging from ‘resident’ individuals with small home ranges, high site-fidelity and minimal movement to ‘mobile’ individuals with large home ranges, high movement rates and little site-fidelity. Our findings suggest

animal personality can play a key role in shaping the space use of individuals and this diversity in spatial behaviours may be too complex to be captured by often used simple linear measures of dispersal.

Introduction

A significant proportion of the variance in many animal behaviours can be explained by consistent between-individual differences, known as animal personality (Gosling and John 1999; Bell 2007; Stamps and Groothuis 2010). However, although movement and space use have important consequences for animal populations including gene flow, spatial distribution, community structure and function, range expansion, colonization, and re-colonization (Bowler and Benton 2005; Ronce 2007; Cote *et al.* 2010), few authors have investigated individual differences in spatial use behaviours, and the exceptions have focussed almost entirely on dispersal (Cote *et al.* 2010).

Behavioural syndromes, defined as correlated suites of behavioural traits, have been documented for a wide range of taxa (Conrad *et al.* 2011) and behaviours (Sih *et al.* 2012). Although behavioural syndromes have often been identified by phenotypic correlations between behavioural traits, it is now recognized that only the between-individual correlations represent a true diagnostic of behavioural syndromes (Dingemanse *et al.* 2012; Dingemanse and Dochtermann 2013; Brommer 2013a). Dispersal behavioural syndromes, which link dispersal behaviour with behavioural traits such as aggression, have been described by a few researchers (see (Clobert *et al.* 2009; Cote *et al.* 2010) for reviews). However, it is unclear whether behavioural traits correlated with dispersal remain consistent throughout the life-time of individuals or are more temporary (Cote *et al.* 2010), and many studies have relied on phenotypic correlation diagnostics. Further, in fishes, direct, long-term evidence of dispersal syndromes are rare and the relationship between dispersal and other spatial behaviours such as home range, site-fidelity, and movement is untested.

Personality-dependent dispersal has been described in western bluebirds *Sialia mexicana* (Duckworth and Badyaev 2007; Duckworth 2008), great tits *Parus major* (Korsten *et al.* 2013), mosquitofish *Gambusia affinis* (Cote *et al.* 2011), and Trinidad killifish *Rivulus hartii* (Fraser 2001). Nonetheless in both fish and other animal populations, evidence of temporally consistent, cross-contextual patterns of personality-dependent dispersal is rare (Miriam *et al.* 2013). Furthermore, only a few authors have investigated the role of personality in other important spatial ecology metrics including: home range (Minderman *et al.* 2010), movement (Fraser *et al.* 2001; Chapman *et al.* 2011; Brodersen *et al.* 2012) and site-fidelity (Brodersen *et al.* 2012). Indeed, individual differences in movement behaviours are a typical feature of spatial ecology datasets, particularly in fishes (Conrad *et al.* 2011; Taylor and Cooke 2012), which often feature ‘resident’ and ‘mobile’ contingent strategies (Skalski and Gilliam 2000; Fraser *et al.* 2001; Morrisey and Ferguson 2011; Radinger and Wolter 2013). Research on this heterogeneity has tended to focus on internal factors, such as body size and ontogeny, and external environmental cues, such as habitat-suitability, temperature, and light (Lucas and Baras 2001). However, few researchers have explicitly quantified the repeatability and contextual consistency of these spatial behavioural differences, particularly in fishes (see (Taylor and Cooke 2014) for an exception).

Although dispersal can be defined as “movement from natal site to breeding site” (Cote *et al.* 2010), others argue for a more broad definition i.e. “the movement between habitat patches” (Bowler and Benton 2005). In this paper we choose the latter definition.

For clarity, we identify the former as “natal dispersal” and the latter as “dispersal from release” to avoid the confusion which can occur as a result of the comparison between dispersal measured at differing scales and contexts (Bowler and Benton 2005). Indeed, we argue that for r strategist animals, natal origin and breeding site criteria are hard to identify and thus rarely met. Accordingly our “dispersal from release” definition allows for direct comparison with dispersal metrics used for fishes (e.g. (Fraser *et al.* 2001; Cote *et al.* 2011; Radinger and Wolter 2013). Moreover, the dispersal from release metric may serve as a useful behavioural measure for managers investigating re-introduction programs or invasion events.

Animal personality research has traditionally been carried out under laboratory conditions, where environmental contexts can be easily controlled (Réale *et al.* 2007b). However, the documentation of personality in a wild context can provide an important validation for animal personality based on captive contexts (Dingemanse *et al.* 2010). Moreover, lab based studies of the spatial behaviour of large bodied animals are not practical. A key challenge associated with documenting personality in the wild has been the statistical disentangling of between-individual, residual, and context driven variances (Brommer 2013a). Accordingly, many field based investigations of animal personality have been criticised for a failure to consider the role of unmeasured context driven differences, which can be amplified in animals free to chose their spatial context (Dingemanse *et al.* 2010). However, several mixed modelling method papers borrowing techniques developed for genetics have recently been published, which provide practical solutions for the partitioning of the contextual, between individual, and residual variances (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013; Brommer 2013b). These papers provide methods for quantification of two key additional criteria for detecting personality in field data: 1) *cross-environmental correlation* i.e. a consistency in the ranking of individuals between categorical contexts defined as imparting plasticity (Brommer 2013b), 2) and *an absence of pseudo-repeatability*, i.e. personality should not be a function of differing experience along an environmental gradient (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013). Accordingly, these methods present an excellent opportunity for more field based animal personality research.

Burbot, *Lota lota* provide an interesting model to test hypotheses regarding potential individual differences in spatial ecology, as a heterogeneity in spatial behaviours within burbot populations has been anecdotally noted (Paragamian and Wakkinen 2008; Dunnigan and Sinclair 2008), but the repeatability and consistency of these differences has not been tested. In this study, we monitor the spatial behaviour of 44 wild, free-swimming burbot in Kinbasket Reservoir, British Columbia, over two years using acoustic telemetry. We test whether burbot home range, horizontal movement, vertical activity, site-fidelity and dispersal from release meet the following personality dependent behaviour criteria: repeatability, cross-contextual correlation, and absence of pseudo-repeatability as a result of spatial context choice. Specifically we test for repeatability in spatial behaviours, after accounting for possible sources of contextual variance defined by backwards model selection; capture location, detection span, season, year, and body length. Next, we test for between-individual cross-contextual correlations across levels of variables previously defined as significant sources of contextual variance. We then investigate potential spatial context choice driven pseudo-repeatability by testing for between-individual correlations between our spatial behaviour metrics and a reservoir distance variable. Finally, we investigate potential spatial behavioural syndromes by testing for between-individual correlations among spatial behaviours.

Materials and Methods

Study Species

Burbot, a large, benthic piscivore (Cott *et al.* 2011), are the only freshwater member of the gadoid family. Burbot have a northern circumpolar distribution (Stapanian *et al.* 2010) and are winter active, spawning in the late winter/early spring, with minimal summer movement (McPhail 2000). Long pre-spawning migrations have been reported by a number of authors (Breeser *et al.* 1988; Paragamian 2000; Paragamian 2000), although burbot in general are considered fairly sedentary (Bergersen *et al.* 1993; Carl 1995). Burbot are also known to be night active (Müller 1973) and perform diel vertical migrations in lake habitats (Harrison *et al.* 2013).

Study System

Kinbasket Reservoir, in southeastern British Columbia, Canada (52°08 N, 118°27 W; Fig. 1), was formed by the construction of the Mica Dam in the upper reaches of the Columbia River in 1976. The reservoir is large (43200 hectares), deep (up to 190m), glacial and snowmelt fed system (Bray 2011). Further detail on the reservoir can be found in (Nitychoruk *et al.* 2013; Martins *et al.* 2013).

Telemetry Array

Forty two acoustic telemetry receivers (VR2W, VEMCO, Halifax, Nova Scotia, Canada) were deployed throughout the reservoir (see Figure 3.1), in the spring of 2010 at minimum reservoir elevation and were downloaded and redeployed in the spring of 2011, and downloaded and retrieved in the spring of 2012. All 42 receivers were retrieved and redeployed in 2011, only 37 receivers were recovered in 2012. Array design allowed for a representative sample of habitat throughout the reservoir and accounted for ~8% of the reservoir surface area. Further details of mooring methods and array configuration can be found in (Gutowsky *et al.* 2013).

Burbot Capture and Tagging

Trapping and decompression procedures followed the recommendations of (Neufeld and Spence 2004). Burbot were anaesthetised in a clove oil bath and total length measured to the nearest cm and weight to the nearest gram. Only fish meeting the <2% tag weight in water to body weight in air ratios were selected for surgery (Brown *et al.* 1999). Seventy-five burbot (50 in 2010 and 25 in 2011) were implanted with temperature and depth sensing acoustic telemetry transmitters (VEMCO V13TP , 45 mm × 13 mm, 6g in water, signal transmission rate 60–180 s, average 120 s, expected battery life 1028 days, VEMCO, Halifax, Nova Scotia, Canada) following the surgical procedure described in (Wagner *et al.* 2009). Details of capture and release locations are provided in Figure 3.1. Sex determination was not possible due to post spawning capture timing. Following full recovery, all burbot were released from the surgery boat, as close as possible to capture location (<500m), and the geographic coordinates were recorded. Further details on capture and tagging procedures are given in (Harrison *et al.* 2013).

Pre-analysis Filtration

Depth time series plots were used to identify and remove from the dataset all fish that appeared to have died or shed their tag post surgery (n= 17, 22%). Code collisions and false detections which can occur as a result of overlapping detections at a single receiver were eliminated by the use of a minimum of 2 detections per 24hr period filter (Heupel *et al.* 2006). Detection span was calculated as the time between first and last detections in a given month and a minimum span of 20 (not necessarily consecutive) days was applied. 14 (18.6%) burbot did not have a sufficient detection span in any month and were subsequently removed from the dataset. The filtration span of 20 days was designed as a compromise between ensuring sufficient data in a given month were available to realistically estimate spatial behaviour and ensuring we were not artificially excluding individuals not frequently within receiver range. Detections within 2 weeks of the surgical procedure were not included in the analysis to remove potential short-term bias in behaviours (Rogers and White 2007).

Spatial Behavioural Metric Calculations

Daily (24hr) center of activity (COA) locations were calculated following methods described by (Simpfendorfer *et al.* 2002). Home range (HR) estimation requires two spatially distinct detections, so for individuals detected at only one receiver in a given month that met the 20 day span filtration criteria, HR was estimated. HR was estimated as the area of a circle (20.42 ha) with a radius of 255m, with the radius equalling the standard deviation (255m) of a fish normally distributed within receiver range (i.e. 0-750m). We consider our 20 day filtration criteria ensured fish assigned the estimated HR value, were likely exhibiting minimal movement. Further, where overlapping receiver ranges allowed greater COA precision, our detection of 20 monthly home range values smaller than the estimate, indicate our value is unlikely to be a large underestimate. The estimated HR value was assigned to 27 fish in a total of 37 months (12.25% of the total number of monthly measures) with 9 individuals accounting for 65% of the estimated HR values. We considered the estimation option to be favourable to the alternative i.e. discarding the data points, as removal would likely inhibit abilities to detect infrequently moving behavioural types. Monthly HRs were then computed based on daily COA locations using the biased random bridge (BRB) method outlined in (Benhamou 2011). The method involved casting our COA data into a trajectory format, applying an uncertainty of locational standard deviation of accuracy measure (255m), and an estimation of a diffusion parameter *D* (calculated using maximum likelihood methods for each fish). We then used the *BRB* function to estimate utilization distributions (UDs) for each fish (Benhamou 2011). HR sizes were estimated at 95% UD and recorded in hectares. All HR analyses were calculated using the *adehabitatHR* package for R. HRs were exported to arcGIS and clipped to a shape file of the reservoir before areas were recalculated.

Horizontal movement metrics were calculated based on our COA dataset and calculated as the sum of all movements in a given month.

Vertical activity was calculated by the sum of absolute changes in depth in a given month, divided by the detection span (hrs) within a given month and recorded in metres per hour.

Monthly site-fidelity was calculated as the Euclidian distance (m) between the current COA and the most recent COA, divided by the time in months elapsed between the two locations.

Monthly dispersal from release site was calculated as the Euclidian distance between the release site coordinates and the monthly COA.

Statistical Analysis

All models were fitted using the Bayesian modelling package *MCMCglmm* for R (Hadfield 2010). Bayesian models necessitate the use of priors, but when prior knowledge of relationships is minimal, flat uninformative proper priors are deemed the most appropriate (Hadfield 2010). Consequently all models below were fitted using flat uninformative inverse Gamma priors (Hadfield 2010), using the univariate or multivariate forms appropriately. Each model was also alternatively fitted with the inverse Wishart prior using univariate or multivariate forms appropriately. Insensitivity to prior type was then confirmed for all models by comparison of the posterior distributions.

Autocorrelation of the fixed effects and variance MCMC chains for all models were assessed using *autocorr* function from the coda package, following the methods described in (Hadfield 2010), to ensure autocorrelation between chains was <0.1. Conservatively long iteration chains were applied to all models consisting of 1300000 iterations, a thinning length of 1000 and a burnin of 300000. Convergence was visually confirmed using the *plot* function for *MCMCglmm*.

Contextual Variance Estimation

Bayesian univariate mixed effects models were fitted with response variables of monthly home range, horizontal movement, vertical activity, site-fidelity, dispersal from release site. Individual fish were used as the random effects. Each model was first fitted with the following fixed effects: season, comprised of winter (Nov-April) and summer (May-October); sampling year, year 1(May 2010- April 2011) and year 2 (May 2011-April 2012); mean centered (Zuur *et al.* 2009) burbot total length (cm), and capture location (a factor variable consisting of 5 locations, see Figure 3.1). For the home range and movement models, detection span (in days, mean centered), was also included in the models. All pair-wise interactions were considered. Backwards selection was performed using non-zero overlapping confidence intervals and P values (<0.05) to determine fixed effects significance. Variables remaining after backwards selection were deemed sources of contextual variance, and used as confounding factors in the repeatability estimation below, and then checked for cross-contextual consistency.

Repeatability Estimation

Repeatability estimates (*r*) and associated 95% confidence intervals for each response variable were calculated based on the posterior distribution from our most parsimonious univariate Bayesian mixed models from above (Dingemanse and Dochtermann 2013). For models where significant fixed effects were identified, adjusted repeatability (*adj.r*) values which included fixed effect structure in the model were calculated. *r* values with confidence intervals not overlapping zero were deemed repeatable (Nakagawa and Schielzeth 2010). Following the recommendations of (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013), individuals with only one sampling point (n=5) were not removed from the dataset.

Cross-contextual Correlation Analysis

Variables previously identified as confounding factors were then assessed for cross-contextual correlations using the univariate Bayesian character state approach described by (Brommer 2013b). The method allows for the computation of between-individual correlations statistics, which represent the consistency in behavioural rankings between levels of categorical fixed effects. The variables found to be significantly influencing movement data were both categorical binary variables (Season and Year), with 2 levels or contexts each (winter and summer, and year 1 vs year 2). We chose the character state approach over the Bayesian random regression approach for its ability to work with the smaller sample sizes (Brommer 2013b). Separate models were fitted for each relevant trait, with fixed effects comprising the appropriate context (character state) variable (*E*), with a random effect comprised of the interaction between *E* and individual fish (ID). Covariance terms for the random effects were determined by the *MCMCglmm* function *us,* which allows for cross character state covariance estimation (Hadfield 2010;Brommer 2013).

Only individuals sampled multiple times in both contexts were included in the analysis (Dingemanse and Dochtermann 2013). Between-individual correlations among environments and associated confidence intervals were calculated using covariance estimates from the posterior distribution following the standard definitions of correlations with the coding provided in Brommer (2013b).

Spatial Pseudo-Repeatability Analysis

Reservoir distance was computed as the Euclidian distance in metres from the centroid of the confluence region to the monthly COA location (Figure 3.1). Kinbasket reservoir consists of a large deep (up to 180m) confluence region formed by a dam to the south. The confluence is fed by two main arms, the Canoe arm and the Columbia arm. As such the reservoir generally becomes increasingly shallower and narrower with increasing distance from the confluence region (see Figure 3.1). The reservoir distance metric, therefore, was designed to capture some of the change in habitat between the lacustrine confluence region and upper reaches of the reservoir. Given that the location of burbot within the reservoir is a behavioural choice, spatial context was not included as a fixed effect in our confounding effect models. Instead the influence of spatial context choice on each of our traits identified as repeatable was assessed using the spatial context variable as a Poisson distributed trait *y*, in the bivariate mixed modeling approach detailed below. In this case, the detection of significant between-individual correlation between a behavioural trait and the confluence distance, would indicate that behaviours vary predictably along the spatial gradient and thus would indicate possible spatial context driven pseudo-repeatability.

Between-individual Correlations Among Traits

Individual level correlations among traits were assessed using Bayesian bivariate mixed models (Dingemanse and Dochtermann 2013). Only fish with repeated measures and simultaneous assays for both traits were included in the models (Dingemanse and Dochtermann 2013). As our primary interest was in the random effects structure, all fixed effects and pairwise interactions terms used in our univariate analysis were included in the bivariate models, regardless of significance. Between-individual, residual, and phenotypic correlations, within trait repeatability values, and all relevant confidence intervals were calculated from the posterior modes of the models (Dingemanse and Dochtermann 2013). For models with Gaussian distributions for both response variables, the correlation significance was confirmed by comparing DIC values from the unconstrained model against DIC values from models where between-individual covariance or residual covariance were constrained to zero. Significance was assigned with a DIC reduction of >2. A pairwise bivariate framework was chosen over a single multivariate model, because of its ability to compare against zero constrained covariance component models, which would not be possible within a single multivariate model (Dingemanse and Dochtermann 2013) . Given the reduced power associated with our sample sizes (n=39) to detect weak correlations, the use of the Bayesian equivalent of a log likelihood ratio test (Dingemanse and Dochtermann 2013) was deemed important as it provided us further confirmation of the significance of correlation in addition to the use of non-zero overlapping confidence interval tests. As DIC is not an appropriate test for Poisson based models (Hadfield 2010), only confidence intervals were used to assess significance in models containing Poisson distributed responses.

Results

930 282 burbot detections were recorded over 2 years. Monthly spatial measures were recorded on 302 occasions for 44 burbot, with a mean of 6.86 (range 1 to 22) not necessarily consecutive replicates per individual. Burbot ranged in length from 44.8cm to 74.1cm. Individual burbot home range averages varied from 20.42 hectares per month to 1471.88 hectares with a median of 145.07 hectares. Home range was significantly repeatable (*r* =0.33, Table 3.1). TL, sampling year, capture location, season, detection span and all possible two way interactions had no significant influence on home range (All *P*<0.05 Table 3.1). The random effect only model was the most

parsimonious model, and, therefore, no cross-contextual correlation analysis was performed. Between-individual level correlation between home range and the reservoir distance metric was not observed, indicating individuals located farther from the confluence did not have larger home ranges, and suggesting that the confluence distance variable was not imparting pseudo-repeatability (Table 3.3, Figure 3.2).

Individual movement distance averages ranged from 0 (km/month) to 162.08 (km/month), with a median of 15.57 (km/month). Movement was significantly repeatable (*adj.r* = 0.32, Table 3.1). TL had no influence on movement and no significant difference in movement was found between sampling years (All P>0.05). No significant interaction effects were observed (All P>0.05). Capture location and detection span also had no influence on movement (Table 3.1). Behavioural plasticity was observed between seasons, with increased winter movement (back transformed model estimates (x+SE,x-SE): winter 43.99(44.04, 43,95) km/month and summer 25.13(41.02,15.40) km/month). Cross context correlation analysis, however, revealed consistent behavioural rankings between seasons (*R* =0.98, Table 3.2), with individuals moving the farthest during the winter also moving the furthest during summer. Between-individual correlations between movement and the reservoir distance were not observed, indicating that individuals that were located farthest from the confluence did not necessarily exhibit the most movement and suggesting an absence of spatial context driven pseudo-repeatability (Table 3.3).

Individual vertical activity averages ranged from 1.0 to 14.3 m/hr, with a median 5.01 m/hr. Vertical activity was deemed significantly repeatable (*adj.r* = 0.42, Table 3.1). Behavioural contextual plasticity was observed between seasons and between sampling years with significantly increased activity in winter and in sampling year 1 (Back transformed model estimates (x-SE, x+SE): year 1 summer 4.7(4.3,5.1) m/hr, year 1 winter 5.6(5.2,6.0) m/hr, year 2 summer 3.5(3.1,3.9), and year 2 winter 4.3(3.8,4.7)).

Total length and capture location had no influence on burbot vertical activity and no interaction effects were observed (all P>0.05). Cross-contextual correlations were observed at the between season level (Table 3.2), however, cross-contextual correlation between years was not observed, indicating the ranking of behaviours was not consistent between sampling years. Individual level correlation between vertical activity and reservoir distance indicative of context driven pseudo-repeatability was observed, with individuals situated farther from the confluence exhibiting decreased vertical activity (Table 3.3).

Individual dispersal from release averages ranged from 143m to 26,179m with a median of 2938 m. Dispersal distance was significantly repeatable (*adj.r* =0.55, Table 3.1). TL and capture location had no influence on dispersal distances (Table 3.1). Contextual plasticity was observed in the season and sampling year interaction. Back transformed model estimates in m(x+SE,x-SE) were as follows: year 1 summer 1977(1540,2489), year 1 winter 3804(3110,4594),year 2 summer 3050(2428,3769), and year 2 winter 3266(2597,4041). Cross-contextual analysis was not performed due to the small number of individuals repeatedly measured in all season x year levels (n=8). Dispersal distance was found to be correlated at the between-individual level with our spatial context variable (Table 3.3).

Individual mean site-fidelity distances ranged from 51.2 to 9648.2 (m/month), with a median of 1632.7(m/month). Burbot displayed significant repeatable individual differences in site-fidelity (*r* =0.22, Table 3.1), with a random effects only model found to be the best predictor of site-fidelity (all P>0.05, Table 3.1), and therefore cross context analysis was not performed. Site-fidelity was not correlated with reservoir distance at the between-individual level (Table 3.3).

Strong between-individual correlations (all *R*>0.5, see Table 3.4 and Figure 3.2) were found among all combinations of home range, horizontal movement and decreasing site-fidelity. No significant between-individual correlations were observed between vertical activity or dispersal and any other trait (Table 3.4, Figure 3.2). Strong residual correlations (R≥0.4) were observed between all combinations of home range, dispersal from release, site fidelity reduction and movement, with weaker positive correlations (R≤ 0.25) observed among all other combinations of traits (see Table 3.4, and Figure 3.2).

Discussion

Our results provide empirical documentation of repeatable, cross contextually consistent, personality-dependent home range, horizontal movement, dispersal and site-fidelity in a free-swimming wild fish. Although repeatability was detected in burbot vertical activity, inconsistency across sampling years, and a correlation with reservoir distance, suggest contextual differences are likely responsible for the heterogeneity observed. Our trait correlation analysis suggests the existence of a spatial behavioural syndrome where behavioural types range from ‘resident’, with small home ranges, minimal movement and high site-fidelity, to ‘mobile’, with large home ranges, high rates of movement, and continuously shifting home range locations. The data also suggest that the spatial behavioural syndrome observed occurs independently from dispersal from release site at the between-individual level.

Although the detection of personality dependent spatial behaviours are relatively rare, our detection of personality-dependent home range, movement, dispersal and site-fidelity complement personality-dependent spatial ecology noted in other studies and for other taxa, including: home range in feral cats *Felis catus* (Barratt 1997), and starlings *Sturnus vulgaris* (Minderman *et al.* 2010)*,* migratory movements and site-fidelity in roach *Rutilus rutilus* (Chapman *et al.* 2011; Brodersen *et al.* 2012), and dispersal in invasive mosquitofish *Gambusia affinis* (Cote *et al.* 2010; Cote *et al.* 2011). Furthermore, our repeatability values are similar to the average values (R=~0.37) reported for most behaviours in a meta-analysis by (Bell *et al.* 2009). Our detection of seasonal plasticity in behaviour, with increased winter movement and dispersal, corresponds with the winter active life history patterns of burbot described in the literature (McPhail and Paragamian 2000; Paragamian and Wakkinen 2008; Harrison *et al.* 2013). Our detection of cross-contextual correlations between seasons for movement distance, suggest that although burbot tended to move more in the winter, individuals that moved the most during the winter also moved the most during the summer period, a pattern consistent with personality-dependent behaviour. For dispersal, small sample sizes of individuals found in all combinations of season and year (n=8) prevented cross context analysis. Our finding that home range, movement, and site-fidelity are not correlated at the between-individual level with the spatial context variable suggests that measured spatial contextual differences are not responsible for the individual differences in observed behaviour and lend support to our personality-dependent behaviour hypothesis. We suspect that correlations between dispersal distance and reservoir distance are likely an artefact of the proximity of our release sites to the confluence region (Figure 3.1), which in turn resulted in those individuals that dispersed the furthest also being located furthest from the confluence.

For vertical activity, while adjusted *r* values suggest personality dependent behaviour, cross-contextual correlation analysis between sampling years suggest inconsistent ranking between years, and indicate we should reject a personality-dependent hypothesis (Dingemanse and Dochtermann 2013; Brommer 2013b). Furthermore, between-individual correlations between vertical activity and reservoir distance suggest context driven behavioural differences and provide further evidence to reject our personality dependent vertical activity hypothesis. We suspect reservoir bathymetry, which is deepest in the confluence (~190m max) and shallower in the more riverine upper reaches (~30m in the Bush Arm see Figure 3.1), may have constrained vertical activity. Although our linear reservoir distance variable could not account for all possible finer scale non-linear habitat heterogeneity, we consider the scale of our analysis was appropriate, given the large size of observed home ranges. Indeed our detection of context driven behavioural differences in vertical activity validates our method of assessing the influence of spatial location on personality measures in the wild. Only a few authors have considered the influence of spatial or habitat context in animal-personality field studies to date (Martin and Réale 2008) and we hope our study will encourage future researchers to explicitly consider and test for the presence of spatial contextual plasticity.

Our documentation of an absence of body-size effect for all spatial behaviours tested, contrasts with the observations of increasing space use with increasing fish size (e.g. home range (Minns 1995) and increasing dispersal distance (Radinger and Wolter 2013)). However, body size relationships were not reported for burbot in (Dunnigan and Sinclair 2008; Paragamian and Wakkinen 2008), and we consider our results are likely a consequence of the mature size of our tagged fish, in comparison with size ranges of fish in Radinger and Wolter (2013) and Minns (1995), which likely span ontogeny. The lack of a capture location effect in any of our models supports our argument that spatial context was not responsible for the heterogeneity in behaviour observed. Likewise our lack of detection span effects suggests that our filtering process resulted in an adequate within-month sampling period to capture burbot spatial behaviours. We cannot exclude the possibility that a proportion of the variance in spatial behaviour could be explained by sex differences, which we were unable to determine due to the post-spawning capture timing. Indeed, sex biased dispersal has been noted in other fishes, e.g., brook charr *Salvelinus fluviatilus* (Hutchings and Gerber 2002). Nonetheless, although the spatial ecology of burbot has rarely been investigated, neither (Dunnigan and Sinclair 2008; Paragamian and Wakkinen 2008) reported sex differences in the home range or spatial ecology of burbot located in locations similar to our study site. Further, no sex-related differences in burbot swimming speed or endurance were reported by either (Jones *et al.* 1974; Vokoun and Watrous 2009). Nonetheless we suggest that ruling out this potential source of pseudo-repeatability would potentially be a valuable exercise for future research. However, burbot's sensitivity to barotrauma represent a tagging challenge and although a pre-spawning (fall) capture might allow for easier sex determination, increased water temperature and increased gonad development would likely increase surgery stress/mortality and reduce catch rates.

We found no evidence for a dispersal syndrome, with the lack of correlation between dispersal from release and other behavioural traits at the between-individual level, indicating that individuals that dispersed further from the release site did not have consistently larger home ranges, higher vertical activity and movement rates, or reduced site-fidelity on a long-term basis. Although our data are not directly comparable to other authors who found dispersal correlated with other behavioural traits (Fraser *et al.* 2001; Edelsparre *et al.* 2013), our data suggest that simple linear dispersal from release measures, which are quite frequently used to interpret the spatial ecology of fishes, may be too simple to capture much of the within population diversity in spatial behaviours. Our detection of significant phenotypic correlations (see Table 3.4) between dispersal and movement, dispersal and home range, and dispersal and site fidelity reduction, might historically have been interpreted as evidence of behavioural syndrome. However our modelling framework allowed us to detect that phenotypic correlation was driven largely by residual correlations. In a simulation study using a study design similar to our research (*n*= 25-50, and with 6 replicates per individual, and a repeatability value of 0.5), (Dingemanse and Dochtermann 2013) show that the power to detect between individual differences was high (>0.8) where correlations were strong(*R*>=0.5) and much lower (power=<0.6) with weaker correlations (*R*<=0.5). Accordingly, we acknowledge our sample size (*n*=39), may have reduced our power to detect more subtle between individual correlations. However, our high number of replicates per individual (7), and good repeatability values (0.55 for dispersal and an average of 0.36 for all traits), likely allowed us to maintain good power to detect strong correlations, and provide support for the hypothesis that dispersal from release was not strongly correlated with other behavioural traits. Indeed, parallels can be drawn between the lack of a correlation between home range and dispersal observed in our study and other studies that suggest dispersal is not always correlated with exploratory behaviour (e.g. great tit (Quinn *et al.* 2011)). Nonetheless, the differing scales and definitions used to describe and measure dispersal throughout the literature complicate comparisons between studies (Bowler and Benton 2005).

Our findings that movement, home range and site-fidelity are all correlated at the between-individual level, suggest a spatial behavioural syndrome with a diversity of behavioural types, ranging from philopatric, “resident” individuals with high site-fidelity, minimal movement and small home ranges, to “mobile” individuals that occupy large home ranges and continuously shift the location of these home ranges. Heterogeneity in fish movement has been documented elsewhere (Crook 2004; Alldredge *et al.* 2011;

Radinger and Wolter 2013; Radinger and Wolter 2013). Our results, however, are among the first to document a spatially and temporally consistent spatial behavioural syndrome. Although the documentation of this ‘mobile’ behavioural type that continuously shift home range location is somewhat at odds with the traditional concept of restricted movement and fixed home range location (Gerking 1959), shifting home ranges have been recorded in lowland river fish (Crook 2004). Furthermore, our data supports the work of others who question the validity of the restricted movement paradigm (Gowan *et al.* 1994; Rodríguez 2002).

Although individual level correlations remain the most important diagnostic of behavioural syndromes (Dingemanse and Dochtermann 2013), our detection of positive residual correlation for most combinations of traits is also of interest (Table 3.4 and Figure 3.3). Residual correlations may indicate a missing covariate and are sometimes known as “within individual correlations”, which in part represent the simultaneous short-term correlations within an individual (Dingemanse and Dochtermann 2013). Indeed the positive residual correlations we observed seem intuitive for our closely related spatial behavioural traits and perhaps occur as a result of a physiological or hormonal covariate. Nonetheless it is important to note that residual correlation can also be a function of correlated measurement errors (Brommer 2013a), and in our case could perhaps be a function of the array design and coverage, differing receiver detection ranges (Mathies *et al.* 2014), and may in part be suggestive of an unmeasured spatial covariate or unmodeled temporal autocorrelation.

Our detection of a mobile behavioural type, independent from dispersal from release may have important consequences for population dynamics and species’ management programs. Our data show mobile behavioural types utilize much larger habitat areas than the average member of the population. These larger home ranges hold consequences for the design and size of conservation areas and reintroduction programs, the carrying capacity of occupied habitats, gene flow, and the selection of behavioural types suitable for captive programs. Although dispersive traits have been shown to be important for range expansion, colonization, re-colonization and invasion (Rehage and Sih 2004; Duckworth and Badyaev 2007), we suspect that the mobile trait observed here may also have an important role in range expansion. Indeed, in freshwater systems which are becoming increasingly fragmented, range expansion opportunities are likely restricted by connectivity bottle-necks (Ricketts 2001) and range expansion opportunity does not necessarily follow a linear pattern of increasing opportunity with distance from natal origin (Van Dyck and Baguette 2005). Therefore, a mobile exploratory behavioural type, which traverses large areas throughout its lifetime, may have an increased likelihood of encountering and passing important connectivity bottlenecks.

The recognition that behavioural type diversity may be important for the resilience of a species to environmental change is gaining momentum (Réale *et al.* 2007b; Sih *et al.* 2012; Wolf and Weissing 2012), and it seems likely that the maintenance of the kind of spatial behavioural type diversity we observed will be important for the conservation of fish and other animal populations. Nonetheless, further work is required to understand the proximate and ultimate causes and the evolutionary and ecological consequences of these behavioural types, and to better account for spatial behavioural diversity in conservation and management policy. At a species-specific scale the diversity in spatial behavioural types observed may help explain the apparent contradiction between the generally sedentary behaviour reported for burbot (Bergersen *et al.* 1993; Carl 1995), and their extremely wide northern circumpolar distribution (Stapanian *et al.* 2010) and has implications for the selection of individuals for planned burbot reintroduction programs (Worthington *et al.* 2010b).

Conclusion

Our study is among the first to document spatially and temporally consistent personality-dependent space use among wild animals, in a wild setting. Our results show personality can play a significant role in determining how animals utilize space, and that personality dependent spatial behaviour may be more complex than the often used linear measures of dispersal would imply. Study findings suggest heterogeneity in fish movement is a product of a diversity of spatial behavioural types ranging from ‘resident’ individuals, who exhibit high site-fidelity, minimal movement and small home ranges, to highly exploratory individuals, who continuously shift home range location, show high rates of movement and exploit much larger home range areas. This within population spatial behavioural type diversity will likely have important implications for spatial conservation and management policy based on mean measures of space use. Identification and preservation of the type of diversity we observed may prove important for maintaining the resilience of fish and animal populations to environmental change.

Table 3.1 . Repeatability of burbot spatial behavioural traits..

Trait	*r*	lower	upper	Significant contexts (P<0.05)	Non-confounding effects (P>0.05)
Home Range	**0.33**	0.20	0.48	None	Season, year, capture location, detection span, total length & all two way interactions
Movement	**0.32***	0.21	0.50	Season	Year, capture location, detection span, total length & all two way interactions
Vertical Activity	**0.42***	0.28	0.58	Season + Year	Capture location, total length & all two way interactions
Dispersal	**0.55***	0.46	0.63	Season x Year	Capture location, total length, and all other two way interactions
Site-fidelity	**0.21**	0.12	0.37	None	Season, year, capture location, total length & all two way interactions

Significant repeatability (*r*) values shown in bold, with associated 95% confidence intervals. The "*" indicates adjusted repeatability value in the presence of significant fixed effects. All traits were cube root transformed and fitted with a Gaussian distribution. For all models, 302 replicates were used in total, from 44 individual fish with mean no of replicates per individual of 6.86 and ranging from a minimum of 1 to a maximum to a maximum of 22

Table 3.2 . Between-individual cross context correlation (R_{12}), and within context repeatability (r_1 and r_2) of burbot spatial behavioural traits previously identified as contextually plastic.

Trait	Context	r_1 [$CI_{lower,}CI_{upper}$]	r_2[$CI_{lower,}CI_{upper}$]	R_{12}[$CI_{lower,}CI_{upper}$]	ΔDIC_{ind0}	*n*	rep
Movement	$Summer_1$ $Winter_2$	**0.13** [0.05,0.40]	**0.28** [0.17,0.53]	**0.98** [0.51,0.99]	**-5.02**	24	244
Vertical Activity	$Summer_1$ $Winter_2$	**0.56** [0.42,0.74]	**0.53** [0.41,0.74]	**0.43** [0.04,0.75]	**-2.58**	24	244
Vertical Activity	Year 1_1 Year 2 $_2$	**0.69** [0.47,0.90]	**0.69** [0.45,0.90]	0.26[-0.51,0.78]	-0.01	8	117

r values in bold represent statistical significance $P<0.05$ based on DIC. ΔDIC_{ind0} represent the change in deviance information criterion (DIC) between the unconstrained model and a model with the individual covariance was set to zero. DIC reduction >2 was considered to be significant. *n* is the number of individuals found in both contexts and *rep* is the total number of paired observations. All traits were cube root transformed and fitted with a Gaussian distribution

Table 3.3. Between-individual (R_{ind}), residual (R_{error}) and phenotypic correlations (R_p) between monthly burbot spatial behavioural traits and our spatial location variable (Poisson distributed distance from the monthly center of activity to the centroid of the confluence region rounded to the metre).

Trait_x	$R_{ind}[CI_{lower,}CI_{upper}]$	$R_{error}[CI_{lower,}CI_{upper}]$	$R_p[CI_{lower,}CI_{upper}]$	*n*	*rep*
Home range	-0.08[-0.67,0.51]	**0.27**[0.14,0.37]	0.01[-0.19,0.23]	39	297
Movement	-0.38[-0.28,0.80]	**0.28**[0.14,0.38]	0.17[-0.02,0.29]	39	297
Vertical Activity	**-0.99**[-0.99,-0.85]	0.05[-0.04,0.19]	**-0.77**[-0.85,-0.50]	39	297
Site-fidelity	0.18[-0.29,0.50]	**0.36**[0.26,0.46]	**0.14**[0.06,0.22]	39	297
Dispersal	**0.75** [0.44, 0.89]	**0.71** [0.64, 0.76]	**0.36**[0.26, 0.44]	39	297

Correlations featuring CIs not overlapping were deemed significant (Bold, $P<0.05$). All spatial traits were cube root transformed and fitted with a Gaussian distribution.

Table 3.4 Between-individual (R_{ind}),residual (R_{error}) and phenotypic correlations (R_p) among monthly burbot spatial behavioural traits.

$Trait_x$	$Trait_y$	$R_{ind}[CI_{lower,}CI_{upper}]$	$R_{error}[CI_{lower,}CI_{upper}]$	$R_p[CI_{lower,}CI_{upper}]$	ΔDIC_{ind0}	ΔDIC_{error0}
Home range	Movement	**0.98**[0.95,0.99]	**0.85**[0.82,0.89]	**0.47**[0.44,0.51]	**-10.77**	**-331.84**
Home range	Vertical Activity	0.25[-0.55,0.86]	**0.14**[0.04,0.27]	0.12[-0.13,0.30]	0.32	**-4.74**
Home range	Site-fidelity	**0.97**[0.80,0.99]	**0.51**[0.42,0.61]	**0.36**[0.29,0.41]	**-11.77**	**-65.91**
Home range	Dispersal	0.86[-0.09,0.97]	**0.51**[0.41,0.60]	**0.30**[0.05,0.45]	1.12	**-69.10**
Movement	Vertical Activity	0.70[-0.17,0.89]	**0.24**[0.11,0.35]	0.20[-0.02,0.41]	-0.73	**-12.49**
Movement	Site-fidelity	**0.89**[0.76,0.99]	**0.41**[0.33,0.54]	**0.37**[0.31,0.43]	**-22.32**	**-46.47**
Movement	Dispersal	0.53[-0.12,0.85]	**0.51**[0.41,0.61]	**0.26**[0.16,0.35]	-0.07	**-71.45**
Vertical Activity	Site-fidelity	0.53[-0.37,0.84]	**0.22**[0.05,0.30]	0.19[-0.10,0.35]	-0.13	**-6.17**
Vertical Activity	Dispersal	-0.39[-0.83, 0.62]	**0.10** [0.01,0.25]	-0.17[-0.40,0.31]	0.30	**-2.55**
Site-fidelity	Dispersal	0.26[-0.18, 0.78]	**0.54** [0.46,0.62]	**0.18**[0.09,0.32]	-0.01	**-86.16**

ΔDIC_{ind0} represents the change in deviance information criterion (DIC) between the unconstrained model and a model with the individual covariance was set to zero. ΔDIC_{error0} represents the change in DIC between the unconstrained model and a model with the residual covariance restrained to zero. ΔDIC >-2 was considered as significant support for the unconstrained model. Correlations deemed significant based on DIC (*P*<0.05) are in bold All traits were cube root transformed and fitted with Gaussian distributions

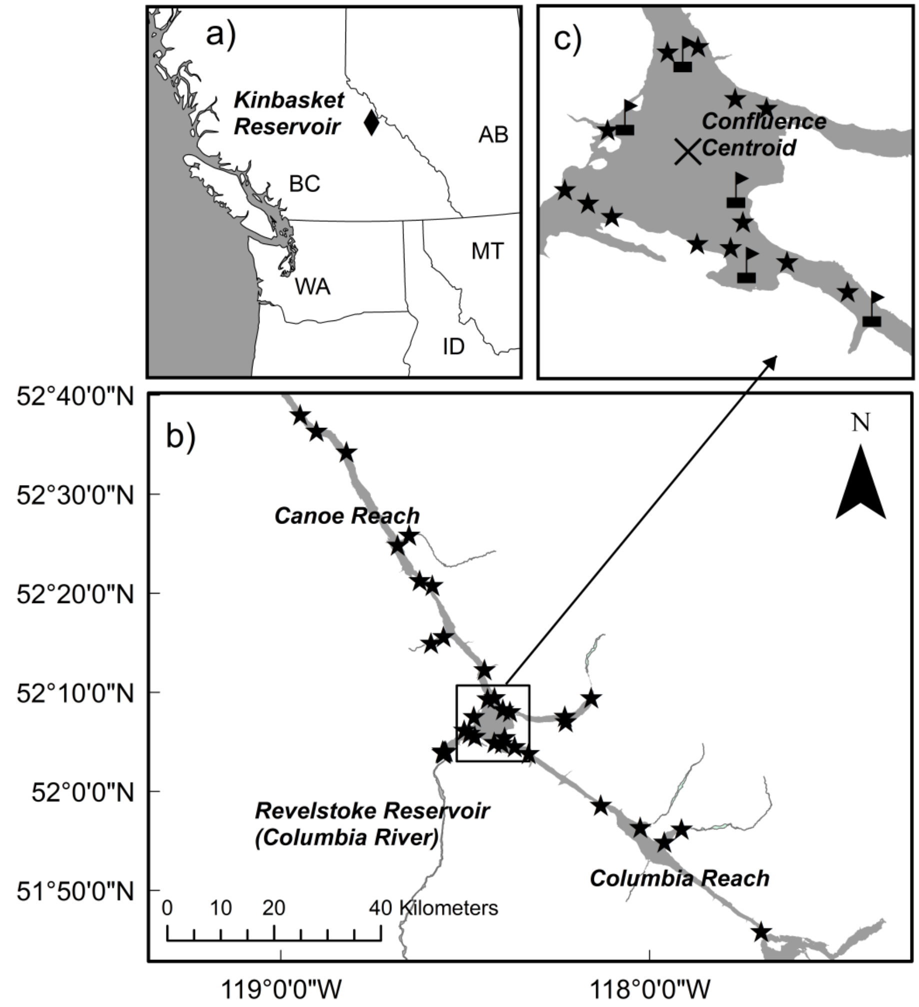

Figure 3.1 a) Diamond indicates Kinbasket reservoir location ; b) Map of the study system, Kinbasket reservoir, British Columbia, Canada, with filled stars representing receiver locations; c) confluence region with an x indicating the centroid of the confluence region, filled stars representing receiver locations and marker buoys representing capture locations

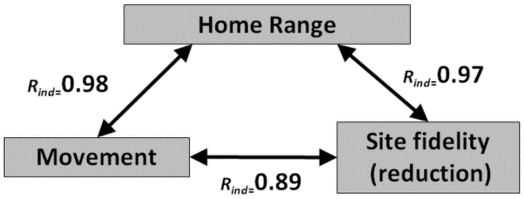

Figure 3.2 Between individual correlations indicative of a spatial behavioural syndrome in wild *Lota lota* in Kinbasket Reservoir, Canada. Arrows used to indicate significant between individual correlations among traits, with associated correlation statistic provided alongside

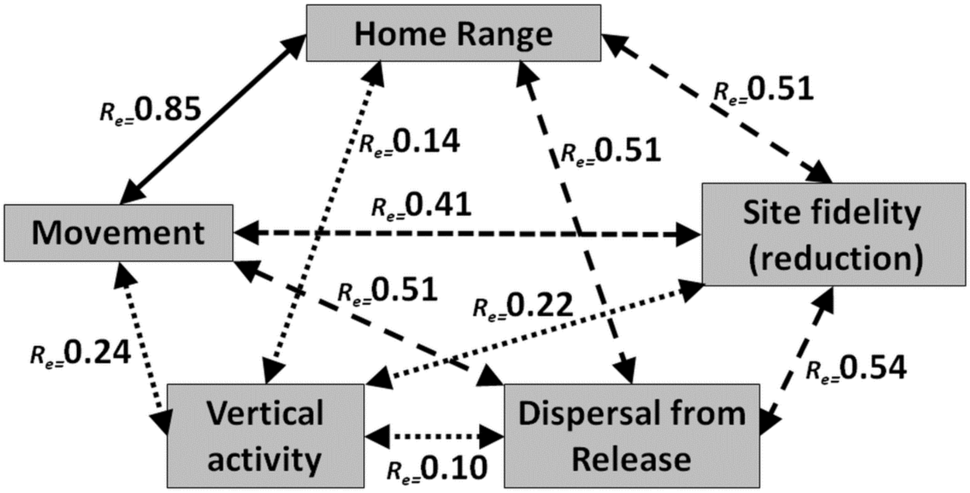

Figure 3.3 Residual correlations between spatial behavioural traits of wild *Lota lota* in Kinbasket Reservoir, Canada. Arrows indicate significant residual correlations between traits, with associated correlation statistic alongside. Line weights indicate the strength of the relationship

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

Overview

Temperature is the dominant environmental variable regulating the physiology of fishes, and therefore behavioural thermoregulation can provide fitness benefits. Behavioural thermoregulation research has focused on summer periods and bioenergetics theory suggests thermal habitat selection may help explain the adaptive value of diel migrations. However, few researchers have examined how thermal habitat selection might change seasonally or explicitly quantified the role of thermal habitat selection on a diel basis. We used animal-borne telemetry with temperature sensors, environmental temperature loggers, and mixed-effects models to test the following hypotheses; behavioural thermoregulation occurs throughout the year, and temperature selection varies on a diel and seasonal basis, in a winter-specialist diel-migrating fish. Burbot demonstrated nightly behavioural thermoregulation throughout the year, with a seasonal shift between selection for very cold temperatures (<2°C) optimal for reproduction during the spawning period and selection for warmer temperatures (12-14°C) optimal for hunting and feeding during non-reproductive periods. During daylight hours, while burbot avoided habitats warmer than optimal for reproduction and feeding during the spawning and non-reproductive periods respectively, active selection was limited to selection for 4-6°C habitat during the pre-spawn period. Our finding suggest that while behavioural thermoregulation explained the night-time migration, behavioural thermoregulation only partially explained day-time behaviour, and thus supports the role of behavioural thermoregulation within a multi-factor diel migration explanation. Together our results show that thermal habitat selection by fishes may be: a more seasonally plastic behaviour than previously recognized, an important tactic to optimise physiological processes throughout the year; and a good predictor of night time habitat occupancy in a diel migrating species.

Introduction

As obligate ectotherms, fish body temperature (T_b) reflects environmental temperature (T_e), with the result that T_e is the dominant environmental variable controlling the physiology and behaviour of fish (Fry 1971; Angilletta *et al.* 2002). In T_e heterogeneous environments, temperature is competed for and exploited to maximise fitness and may be considered a niche resource (Magnuson *et al.* 1979; Attrill and Power 2004). Resource selection, the disproportionate use of a resource in relation to availability (Manly *et al.* 2002), and its opposite measure, resource avoidance, are important behaviours that allow animals to optimise fitness needs (Boyce and McDonald 1999), and detection of resource selection patterns has often advanced our understanding of the relationship between animals and their habitats (Boyce *et al.* 2002). Thermal resource selection, where animals select and avoid thermal habitats to optimise fitness, is often referred to as behavioural thermoregulation (Huey and Stevenson 1979; Hertz *et al.* 1993).

In ectotherms, thermal optimum, the temperature at which a process is maximal, is dependent on physiological and behavioural states (Angilletta *et al.* 2002). Thus thermal optima vary between differing processes such as consumption, respiration, ova maturation, and reproduction (Hasnain *et al.* 2013). Bioenergetics theory suggests that animals can optimize fitness with temporal shifts in thermal habitat selection in response to changes in physiological state, such as the diel pattern of “hunt-warm rest-cool” (Sims *et al.* 2006). However, while the thermal optima of fishes shift seasonally in relation to reproductive and energetic state (Hasnain *et al.* 2013), few researchers have studied the role of behavioural thermoregulation outside of the summer period. In temperate aquatic systems, thermal heterogeneity is reduced in cooler periods compared to the summer. Nonetheless, where thermal habitat heterogeneity exists, exploitation of heterogeneity seems likely, given the known importance of T_e to ectotherm physiology.

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

As a diel bank migrating (Harrison *et al.* 2013), coldwater stenothermic (Pääkkönen and Marjomäki 2000), winter-specialist species (Shuter *et al.* 2012), burbot, *Lota lota,* are a useful model species for testing hypotheses regarding seasonal and diel patterns of thermal resource selection. In this study, we combined animal-borne thermal biotelemetry and T_e logging to investigate thermal resource use, selection and avoidance in 18 burbot, tracked for 1 year, in a large hydropower reservoir in British Columbia, Canada. We used zero-inflated mixed-effects resource selection index models to test the following hypotheses: H1 - behavioural thermoregulation occurs throughout the year, H2 - temperatures selected differ on a diel and seasonal basis.

Materials and Methods

Study Site

Data were collected in Kinbasket Reservoir, a large (43 200 ha), deep (up to 190m) glacial fed reservoir in the Kootenay/Rocky Mountain region of South Eastern British Columbia, Canada. The reservoir is operated for storage and hydroelectric generation and was formed by the construction of the Mica Dam in 1976. The reservoir is fed by two major tributaries, the Canoe River and the Columbia River, which form the main two arms of the reservoir. During the study period reservoir levels reached maximum elevation (754m) on 4th November 2011 and the reservoir was drawn down to a minimum level (722m) on 21st of April 2011. Further details about the study site are described in (Gutowsky *et al.* 2011; Gutowsky *et al.* 2013; Harrison *et al.* 2013; Martins *et al.* 2013; Nitychoruk *et al.* 2013; Harrison *et al.* 2014; Martins *et al.* 2014).

Study Organism

Burbot are a benthic top predator (Cott *et al.* 2011; Cott *et al.* 2013) found in both lake and river systems throughout their northern circumpolar distribution (Stapanian *et al.* 2010). The species is most active during winter (Paragamian and Wakkinen 2008) and are considered nocturnal (Müller 1973; Harrison *et al.* 2013). Typically, burbot spawn in late winter to early spring, with spawning in the study region (Kootenay) thought to occur between February and April (McPhail and Paragamian 2000). Burbot are known to undergo diel bank migrations between the profundal and littoral zone (Cott *et al.* 2015) and diel migration behaviour has been established in the study system (Harrison *et al.* 2013), using a dataset of which this paper is a subset.

Thermal habitat availability

Temperature logger chains featuring tidbit v2 thermistor temperature loggers (Onset Hobo Data Loggers UTBI 001, accuracy ± 0.2°C, Bourne, MA) were deployed at 4 sites (Figure 4.1) within the reservoir (see Table 4.1 for logger chain details), at low pool in April 2011. The Columbia and Canoe sites were chosen because of their location on the two main tributary arms of the reservoir (Figure 4.1). Encampment was chosen because of the high number of burbot detections recorded at the station (Harrison *et al.* 2013), and the Forebay site was chosen as the most downstream site relevant for the study. In addition to the logger chains, a series of shore based logger arrays were deployed at each site between the low pool and high pool marks to ensure coverage of the upper water column during periods of high reservoir fill (see Figure 4.1 for locations and Table 4.1 for details). Reservoir elevation data provided by BC hydro ensured that only data from submerged loggers were included in the thermal habitat dataset. Mean temperatures at depth for each diel period, on each day during the study period, were computed for each logger. Cubic spline interpolation (Livingstone

2003; Jankowski *et al.* 2006) at 5 metre intervals was used to generate nightly and daily site-specific thermal profiles. Because of the varying reservoir levels, the number of loggers used to create a thermal profile varied (see Table 4.1 for details). Site-specific thermal profiles were estimated only on days when a minimum of 3 loggers were submerged. The number of days meeting the criterion at each location is given in Table 4.1. The reservoir operational regime ensured that periods of high thermal heterogeneity, i.e. late summer, coincided with the maximum numbers of submerged loggers. The maximum depth use recorded by burbot at each site during the study period, with a daily correction for reservoir fill elevation, was used to define the lower limit of thermal habitat availability.

Capture and Tagging Procedure

A total of 75 burbot (50 in April/May 2010, and 25 in April/May 2011) were surgically implanted with temperature sensing acoustic telemetry tags (V13TP, 45 mm × 13 mm, 6 g in water, signal transmission rate 60–180 s, accuracy ± 0.5°C average 120 s, expected battery life 1028 days, VEMCO Halifax, Nova Scotia, Canada). Full details of the capture and tagging procedure can found in (Harrison *et al.* 2013; Martins *et al.* 2013; Harrison *et al.* 2014). Briefly, burbot were captured using baited cod traps and decompressed to reduce risk of barotraumas, following the procedures outlined by Neufeld and Spence (2004). Burbot were then anaesthetised in a clove oil bath, an incision was made just offset to the mid-ventral line, the transmitter was inserted into the inter-peritoneal cavity and the incision was closed using three un-interrupted sutures. Re-circulating lake water was applied to the gills throughout the surgery and the entire procedure was performed in <5 minutes. Recovered burbot were released as close as possible to capture site.

Telemetry array

Single omni-directional hydro-acoustic receivers (VR2W, VEMCO Halifax, Nova Scotia, Canada) were positioned at the Columbia and Encampment logger stations (see 4.1). The Canoe site featured an array of 2 VR2W receivers both within detection range (~750m) of the temperature logger array. The Forebay site featured 6 VR2Ws within detection range of the thermal habitat loggers. Furthermore, 2 weeks of data from a thermal logger chain installed at the outer Forebay site (see Figure 4.1) indicated isothermal conditions between this site and the inner Forebay and therefore the 3 VR2Ws placed at the outer Forebay were included in the Forebay group. VR2Ws were deployed as described in (Gutowsky *et al.* 2013) in the spring of 2011 and data were downloaded in the spring of 2012.

Thermal Resource Selection

Resource selection was determined for the individual (*i*) at site (*j*) scale on a diel basis. Diel period was defined by sunset and sunrise times at 52°8'N, 118°28'W. To ensure an adequate sampling period to estimate proportionate use, selection indices were only calculated when individuals were detected 10 or more times within a diel period. Thermal habitat was categorised into 2°C bins. The resource selection index for a given thermal habitat bin W_{ij} was determined as:

$$Wij = \frac{o_{ij}}{Prop_{ij}}$$

Where o_{ij} is equal to the proportion of detections in a given thermal habitat for fish *i* at location *j* and $Prop_{ij}$ represents the proportion of available habitat. W_{ij} index values <1 indicate avoidance, with W_{ij} equal to 1 suggesting neutral selection and W_{ij} >1 suggesting active selection (Manly *et al.* 2002). W_{ij} is often standardised (constrained between 0 and 1) to ease the interpretation of preference, i.e. the likelihood of selection under equal availability. However, standardisation relies on a fixed number of habitat categories (Manly *et al.* 2002), because selection is interpreted as positive when B_{ij} >= 1/*n*, where *n* is equal to the number of habitat categories. As the number of thermal habitats within and among seasons were variable in our dataset, *n* could not be reliably estimated and we avoided standardisation.

Statistical Framework

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

We used a generalized linear mixed model (GLMM) framework (Zuur *et al.* 2009) fitted with a delta normal error distribution (Aitchison 1955), to account for the high levels of zero inflation (75.9%) which occurred as a result of the frequency of unoccupied thermal habitat. The delta approach is a two stage mixing process, suitable for zero-inflated data with a Gaussian non-zero response, that has been extensively applied to zero-inflated continuous fisheries data (Pennington 1983; Helser *et al.* 2004; Anlauf-Dunn *et al.* 2014). The approach is similar to the Zero Altered Poisson (ZAPs) and hurdle models often used for count data (Zuur *et al.* 2012), however, the method allows for a continuous distribution of the non-zero data. Delta model selection estimates (DW_{ij}) were derived using equation 1:

$$DW_{ij} = p_{ij} * NZW_{ij}$$

where p_{ij} is the probability of habitat occupancy, NZW_{ij} is the estimate of W_{ij} for the subset of non zero data, i.e. occupied habitats. For all models separate intercepts were used for each combination of individual fish x thermal habitat category. This random effect structure was chosen over a crossed or nested structure (Pinheiro and Bates 2000; Zuur *et al.* 2009), for the ability to account for the correlation between successive visits to the same habitat, which would not be possible with a crossed or nested structure. Further, separate intercepts for each combination of individual and thermal habitat category make sense from a biological perspective, given that you would likely expect selection for differing habitats to be independent traits in a given fish. Correlation was modelled using a continuous autoregressive correlation structure (AR1), where the lag of 1 was used for consecutive diel periods (Pinheiro and Bates

2000; Zuur *et al.* 2009). Correlation structures were validated using ACF plotting for the habitat occupancy model sets and a combination of ACF plotting and AIC comparison for the *NZWij* model. For both model sets, beyond optimal models used the following categorical fixed effects structure: Thermal habitat (*T*, 2°C temperature bins starting at 0-1.99°C through to18 to 20°C), Season (*S*, Pre-spawn [Nov to Jan], Spawn and Post-Spawn [Feb-Apr] and Summer [May to Oct]), Diel period (*D*, Night and Day), Location (L, Forebay, Encampment, Canoe and Columbia) and all possible 2 and 3-way interactions.

Probability of Occupancy model

Probability of occupation p_{ij} *,or* the probability of being detected at least once in a given thermal habitat, was modelled using a penalised quasi-likelihood generalized linear mixed effects logistic model, fitted using the *glmmPQL* function from the package *MASS* for r (http://cran.r-project.org/web/packages/mass/index.html). Backwards selection was performed using the *wald.test* function from the *aod* package for R (http://cran.r-project.org/web/packages/aod/index.html) which is deemed an appropriate method for quasi-likelihood approximation (Breslow 1990). Beyond optimal models took the form:

$$logit(p_{ij}) = \alpha + \beta_1 \times T_{ij} + \beta_2 \times S_{ij} + \beta_3 \times D_{ij} + \beta_4 \times L_{ij} + \beta_5 \times Int_{ij} + IndTi$$

Where $IndT_i$ is the random intercept represented by individual fish *i* in a given thermal habitat and is assumed to be $\sim N(0, \sigma^2_{IndT})$, p_{ij} represents the probability of a single detection for fish *i* at location *j*, and , Int_{ij} is used to represent all possible 2 and 3 way interactions.

Thermal habitat selection for occupied habitats model

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

$$NZW_{ij} = \alpha + \beta_1 \times T_{ij} + \beta_2 \times S_{ij} + \beta_3 \times D_{ij} + \beta_4 \times L_{ij} + \beta_5 \times Int_{ij} + IndT_i$$

Delta Thermal Habitat Selection Model

Model estimates were derived using equation 1. Conditional confidence intervals (P=0.05) for DW_{ij} estimates were derived using the parametric bootstrap approach (Efron and Tibshirani 1994; Davison and Hinkley 1997), based on the assumption of a near asymptotic distribution of estimates. 100,000 probable parameter estimates were drawn using the *rmvnorm* function from the *mtvnorm* package for R (http://cran.r project.org/web/packages/mtvnorm/index.html) and the variance-covariance matrices from the *nlme* model outputs for the best *NZWij* and probability of occupancy models. The product of the parameter estimates from each model were used to compute100,000 fitted values from which the CIs were estimated. The resulting confidence intervals from the delta model were then used to test hypotheses regarding thermal habitat selection, where overlap with the *Wij* value of 1 indicated neutral selection, and non-overlapping intervals above or below 1 indicated positive selection or avoidance respectively.

Results

18 of the 75 tagged burbot were recorded at receivers within the vicinity of temperature logger chains, resulting in a total of 34,246 detections. Environmental thermal habitat availability profiles were calculated for 1913 diel period based profiles across our four stations (see Table 4.1 for more detail). The combination of these environmental habitat availability and thermal habitat use estimates resulted in a total of 4153 resource selection index observations. A summary of diel depth distribution data in relation to thermal habitat availability over the course of the year can be seen in Figure 4.2.

Thermal habitat availability

Seasonal and diel differences in overall thermal habitat availability proportions were observed, with >80% of available thermal habitat during the pre-spawn period falling between 2 and 6°C for both day and night periods and the range of thermal habitat used in the day and night, respectively, falling between 0 to 12°C and 0 to 10°C. During the spawn and post spawn period, 2-4°C water accounted for up to 68.5% and 67.7% thermal habitat available during the day and night respectively, with 0-2°C thermal habitat accounting for 31.6% and 31.0%, respectively of day and night thermal habitat availability. In the summer period, 66.40% of the used thermal habitat fell between 2 and 6°C. A summary of proportionate thermal habitat availability by season is shown in Figure 4.3.

Thermal Habitat Occupancy

The best model featured a significant three-way interaction among diel period, season and thermal habitat category (Wald $X^2 = 238.7$, df = 26, $P(>X^2) = 0.01$). Location and all interactions involving location were not found to influence burbot thermal habitat use (Wald tests, all $P(>X^2)$ >=0.05) and were subsequently removed from the final model. Model estimates and confidence intervals are plotted in Figure 4.4. Temporal correlation for the residuals were observed (Phi = 0.54) and accounted for, with differences between individuals within habitat categories accounting for 49% of the variance in the dataset. Significant differences between diel periods within thermal habitat categories (diagnosed by non-overlapping 95% confidence intervals) were observed in the spawn and post-spawn periods, with increased probability of use of the 0-2°C thermal habitat category at night, and increased probability of use of the 2-4°C habitat during the day. During the pre-spawn period 0-2°C habitat was available during day and night (4.74 and 4.21% respectively), but never used. 10-12°C habitat was available (0.26%) during the day but never used. During the summer 16-18°C degree habitat was available during the day and night (3.20 and 2.93% respectively), but never used. Similarly, 18-20°C habitat was also available during the day (1.00%) but never occupied.

Thermal habitat selection for occupied habitats

1001 non-zero observations were used to populate the model. A significant season x diel period x thermal habitat interaction effect was observed (Marginal *F* test, denominator df=906, F=10.88, *P*<.0001). Location and all interactions involving location were not found to significantly influence non-zero W*ij* (Marginal *F* test, all *P*>=0.05). In the final model, temporal correlations between consecutive diel periods were observed for individual within thermal habitat (Phi=0.82) and accounted for, and the intercept accounted for 10.1% of variation in the model. Model estimates and confidence intervals are shown in Figure 4.5.

Delta Thermal Habitat Selection Model

During the pre-spawn period burbot showed significant selection for 4-6°C habitat during the day and 8-10°C during the night (bootstrapped CIs >1, P=0.05), burbot avoided 0-2°C during both diel periods, and avoided 10-12°C habitat which was only available during the day (bootstrap CIs <1, *P*=0.05), and showed neutral selection for all other habitats (CIs = 1, P=0.05).

During the spawn & post-spawn period burbot showed significant selection for 0-2°C habitat at night (bootstrapped CI >1, P=0.05), neutral selection for 0-2°C habitat during the day (bootstrapped CI =1, P=0.05) and avoided habitats >2°C during both day and night (bootstrapped CI <1, P=0.05).

During the summer nights, burbot showed positive selection for 12-14°C, neutral selection for habitats between 4-12°C and 14-16°C and avoided habitats <4°C and > 16°C. During summer daytime burbot showed neutral selection for 4-14°C and avoided thermal habitat > 14°C and < 2°C. See Figure 4.6 for full model estimates.

Discussion

Data from this study provide empirical evidence confirming our hypotheses of year round behavioural thermoregulation (H1) and seasonal and diel patterns of thermal selection and avoidance (H2) in burbot.

During the summer and pre-spawn periods, our results suggest night-time migration is associated with a pattern of behavioural thermoregulation towards optima for hunting, feeding and digesting in this night-active, nocturnal predator (Müller 1973; Kavaliers 1980; Harrison *et al.* 2013). Summer night-time selected temperatures (12 to 14°C) were similar to thermal optima for consumption $Topt_c$ reported for burbot (13.6-14.0°C, Rudstam *et al.* 1995; Pääkkönen and Marjomäki 2000; Pääkkönen *et al.*

2003). The selected temperatures were also similar to optimal temperatures for gastric evacuation (12.6°C, Pääkkönen and Marjomaki 1997) which would minimise stomach fullness to enable maximum nightly food intake (Jeschke *et al.* 2002). In addition, the selected temperatures were close to the species' final temperature preferendum (*FTP*), (14.2°C (Hofmann and Fischer 2002)), that is the lab defined temperature to which fish will consistently select over a range of thermal experience values (Jobling 1981; Hasnain *et al.* 2013). Use of temperatures similar to *FTP* during nightly diel migrations has been noted in wild *coregonids* (Busch and Mehner 2009; Mehner *et al.* 2010), however, our results confirm active selection for *FTP*. While the relationship between *FTP* and specific physiological thermal optima have not been quantitatively established for burbot, FTP is often closely linked to an optimisation of physiological and bioenergetic processes (Beitinger and Fitzpatrick 1979; Reynolds and Casterlin 1979; Jobling 1981; Hasnain *et al.* 2013) and closely matches temperatures that minimise the costs of swimming (Ohlberger *et al.* 2008). The selection for the warmest available habitat (8-10°C) seen during the pre-spawn suggest a similar attempt to optimise thermal conditions for hunting, feeding and digesting.

The nightly selection for very cold water (<2°C) during the spawn and post-spawn may optimise thermal conditions for pre-spawning maturation and the spawning event. Lacustrine burbot spawn at night in the littoral zone (McCrimmon 1959), and while spawning takes place in the water column (Fabricius 1954), eggs quickly sink and mature within the substrate (McPhail and Paragamian 2000). Burbot spawning has been observed at between 0 and 4°C ((McPhail and Paragamian 2000) and references therein), Zarski *et al.* (2010) noted spawning maturation was fastest when temperatures rapidly declined to 1°C and Wismer and Christie (1987) suggested an optimum spawning temperature of 1.2°C. Burbot eggs have among the coldest optimum incubation temperatures of all freshwater temperate species (Teletchea *et al.* 2009), thus nightly selection of <2°C may benefit eggs post spawn even though such temperatures are below those described as optimal for egg survival (3.8°C(Vught *et al.* 2008), 3°C (Taylor and McPhail 2000)). Nonetheless, selection of these <2°C temperatures would ensure an avoidance of thermal habitat likely to cause mortality as 100% burbot ova mortality has been recorded at >8.1°C (Vught *et al.* 2008), >5°C (Zarski *et al.* 2010) and >6°C (Taylor and McPhail 2000)). In winter when temperatures fall below 4°C, available <2°C habitat tends to be located closer to the surface (Figure 4.2) and it is possible that the selection of these very cold temperatures could be function of selection for a non-thermal habitat variable associated with shallow depth. However, given the importance of temperature in the reproductive processes of ectotherms (Huey 1991; Pankhurst 1997; Guderley and Pörtner 2010), temperature is likely the most critical determinant of habitat selection.

Our observations of a general daytime pattern of avoidance of thermal habitat >14°C and <4°C during the summer and >2°C habitat during the spawn and post-spawn imply an avoidance of suboptimal thermal habitat for consumption and reproduction respectively. With the exception of the selection observed for 4-6°C habitat during the pre-spawn, significant active selection was not observed, indicating that selection for thermal habitat may not be as important during the day as at night. While speculation as to the non-thermal advantage of this daytime behaviour is beyond the scope of this paper, previous research has suggested that during inactive non-feeding periods, predation risk to fitness gain ratios may be optimised by the occupation of low risk habitats (Harrison *et al.* 2013).

Together our results suggest that while selection for physiological optima provides an effective explanation for the night time migration, thermal habitat selection only partly explains daytime behaviour. Accordingly the data provide support for the contribution of behavioural thermoregulation in a multi-factor hypothesis for diel migration, similar to hypotheses proposed by Harrison et al (2013) and Mehner et al (2012). The results, however, do not support a stand-alone bioenergetics diel migration hypothesis as proposed by Sims *et al.* (2006), under which one would expect to find a consistent pattern of selection for cooler habitat during the day. While heterogeneity in diel patterns of thermal experience have previously been used to test hypotheses regarding physiological advantage (Brett 1971; Sims *et al.* 2006; Andrews *et al.* 2009), our results are among the first to utilise detailed thermal habitat availability datasets to provide empirical evidence of a diel pattern of selection and avoidance during diel migrations.

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

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

Although heterogeneity in thermal habitat was reduced in winter compared to summer conditions, behavioural thermoregulation still occurred during the winter period. While lake-based research is scarce, thermal habitat selection is an important tactic used to survive winter in riverine salmonids (Cunjak 1996), such as avoidance of freezing temperatures (Cunjak *et al.* 1998), and the selection of warmer groundwater input (Cunjak and Power 1986). Our research indicates winter thermoregulation may also be important in lake environments. Further, the fitness gains from behavioural thermoregulation in winter are likely amplified in a winter feeding species (Hölker *et al.* 2004; Shuter *et al.* 2012). Accordingly, thermal heterogeneity in winter may be more important in structuring lake fish distribution than previously considered, and more research is needed to understand how shorter winters might impact freshwater fish, particularly winter specialists. Indeed, winter specialist species are already considered particularly vulnerable to winter temperature increases (Pörtner 2006; Pörtner and Peck 2010; Shuter *et al.* 2012). The selection for very cold thermal habitat (<2°C) by burbot during the late winter further highlight this vulnerability.

Burbot are often found in regulated systems in North America (Stapanian *et al.* 2008; Stapanian *et al.* 2010), and our results have several implications for the management of these systems. Temperature increases in winter due to water discharge from reservoirs have shown to be detrimental to downstream riverine burbot (Hardy and Paragamian 2013). Our results suggest that in reservoir chain systems, such as those common in the Columbia River basin (Waples *et al.* 2008), lacustrine burbot may also be susceptible to discharge related winter warming. As a poor swimmer, burbot may be vulnerable to entrainment (Martins *et al.* 2013). Given the detection of strong selection for <2°C water during the spawning period, and for 12 to 14°C water in summer, the hypothesis that entrainment vulnerability may be increased in littoral located turbine intakes that draw water at these temperatures, during these periods, warrants further investigation. Furthermore, egg stranding has been documented in several fish species in regulated systems (Nagrodski *et al.* 2012), and our findings suggest that where benthic <2°C thermal habitat is restricted to very shallow depths, the potential for reservoir drawdown to strand burbot eggs, requires investigation, particularly as reservoir drawdown often coincides with the late winter spawning period.

In conclusion, our findings are among the first to explicitly quantify the role of thermal habitat selection in diel migration behaviour. Results show that behavioural thermoregulation towards optimal temperatures for reproduction, hunting and feeding, consistently explain night-time behaviour throughout the year. In contrast we did not detect a consistent pattern of selection for cooler habitat during the daytime period, which would be expected from a bioenergetics based “hunt-warm rest-cool” diel migration strategy (Sims *et al.* 2006). Instead, our findings provide support for the role of behavioural thermoregulation within a multifactor DM hypothesis. Behavioural thermoregulation has long been acknowledged as an important tactic for maximising fitness during summer periods (Huey and Stevenson 1979). However, our work suggests this tactic may also be important during winter periods, and that temperatures selected for can shift seasonally in response to reproductive state. Furthermore, this requirement for cold thermal habitat during the reproductive period highlights a potential vulnerability to increased winter temperatures. Given the importance of temperature for ectotherms, a thorough understanding of the relationship between fish and thermal habitat, particularly in winter, is essential for a complete understanding of fish ecology. Our findings demonstrate that consideration of thermal ecology at the diel and seasonal scale has the potential to significantly advance knowledge in this area.

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Table 4.1 Summary of environmental temperature logger data and fish detections by site. See Figure 4.1 for site locations

Site	Max no. active loggers	Mean no. active loggers	No of days >=min logger no threshold	Max depth recorded by fish at site (m)	Fish detections received (n)
Canoe	4	3.38	152	87.3	77 (2)
Columbia	4	3.41	137	100.1	41 (2)
Encampment	10	7.4	305	128.3	19 162 (9)
Forebay	37	24.2	366	188.3	10 104 (12)

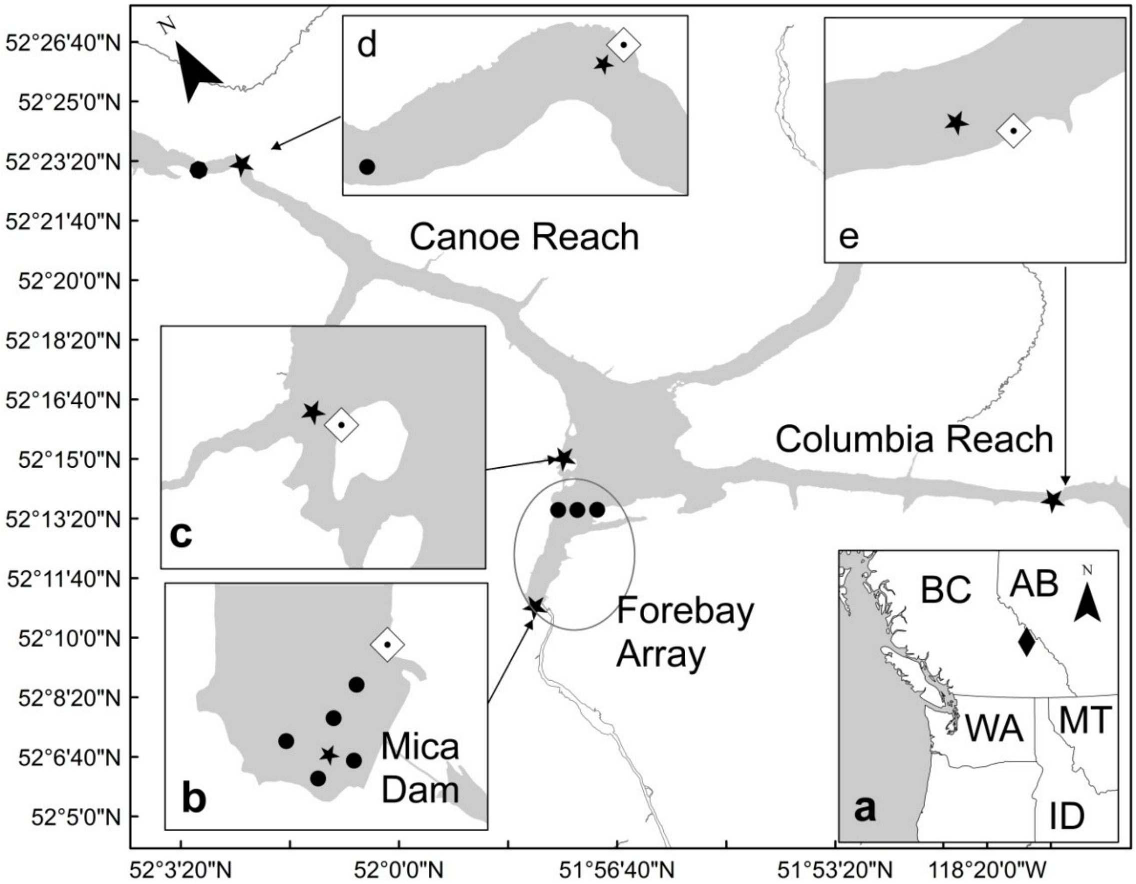

Figure 4.1 Map of Kinbasket Reservoir telemetry and temperature logging array. Filled stars indicate VR2W receivers complete with thermistor chains. Filled circles indicate VR2W only stations. Squares indicate shore-based thermistor arrays. Inset A shows the location of the reservoir (filled diamond) in relation to western North America. Inset B shows details of the Forebay Site near the dam face. Inset C features the Encampment Site, Inset D shows the Canoe Site and Inset E details the Columbia Site.

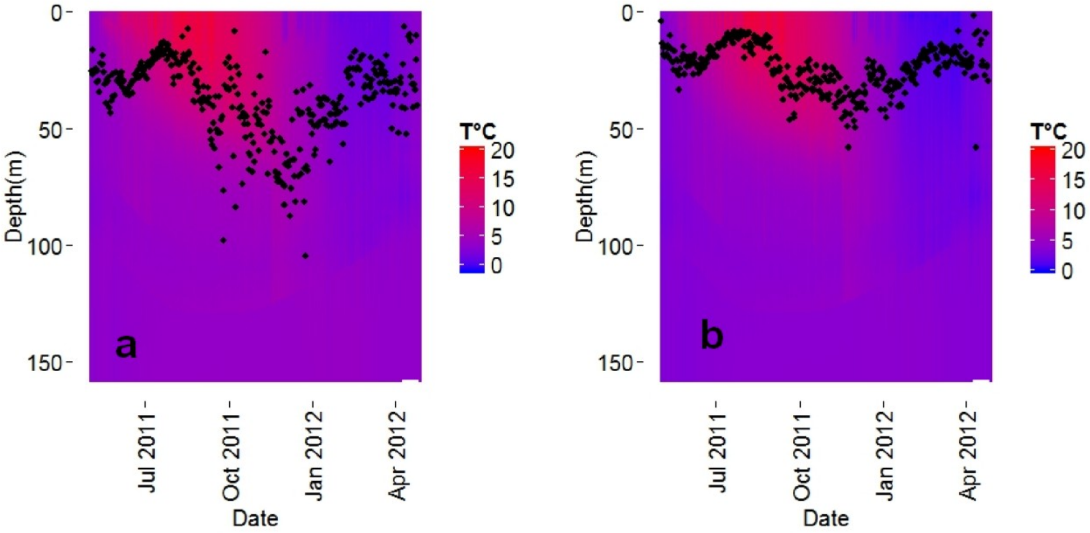

Figure 4.2 Diel thermal depth profile of burbot in Kinbasket Reservoir. Filled circles represent the daily population mean depth (n=18). Background colours indicate the mean temperature at depth across all sites. Panel A represents day and panel B night.

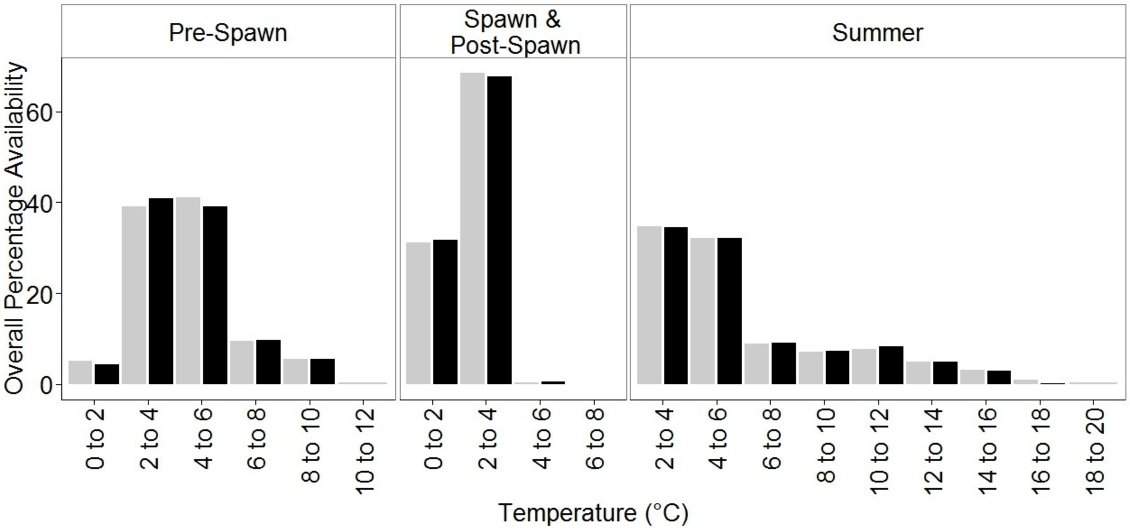

Figure 4.3 Percentage availability of thermal habitat in Kinbasket Reservoir, with day and night represented by grey and black bars, respectively**.**

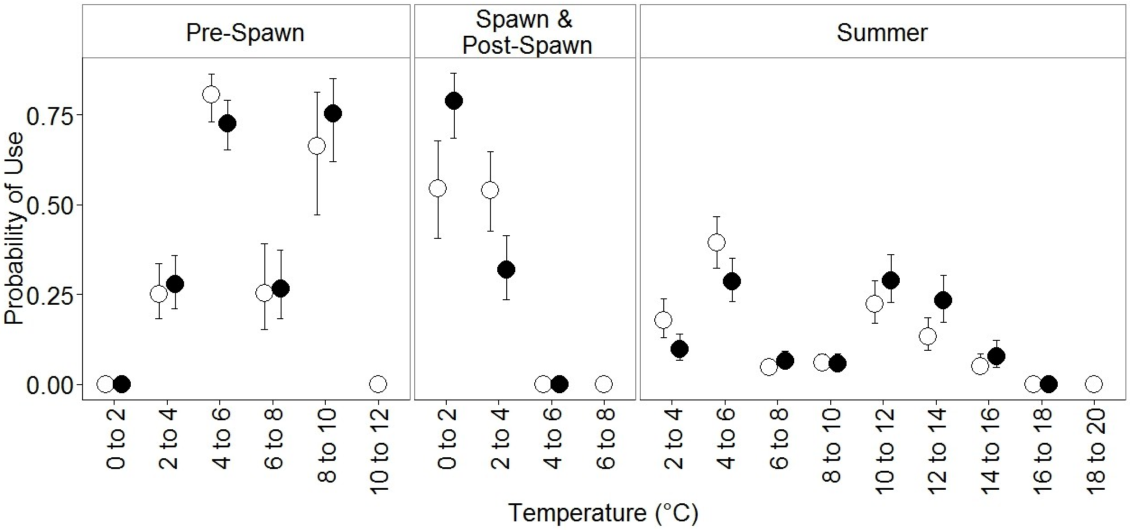

Figure 4.4 Model estimates for probability of detection within thermal habitat categories for burbot in Kinbasket Reservoir, Canada. Open and closed circles represent daytime and night-time respectively. Error bars represent conditional 95% confidence intervals.

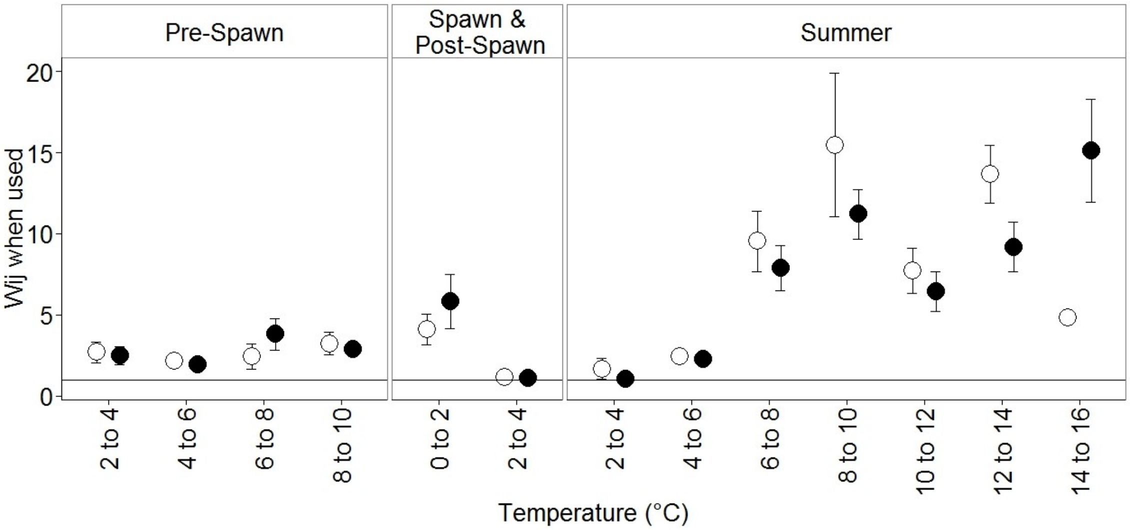

Figure 4.5 Model estimates of burbot Manly's selection index values for thermal habitat categories based on the subset of non-zero data, i.e. occupied habitats. Horizontal line is at the value of 1 *Wij*, and error bars represent conditional 95% confidence intervals**.**

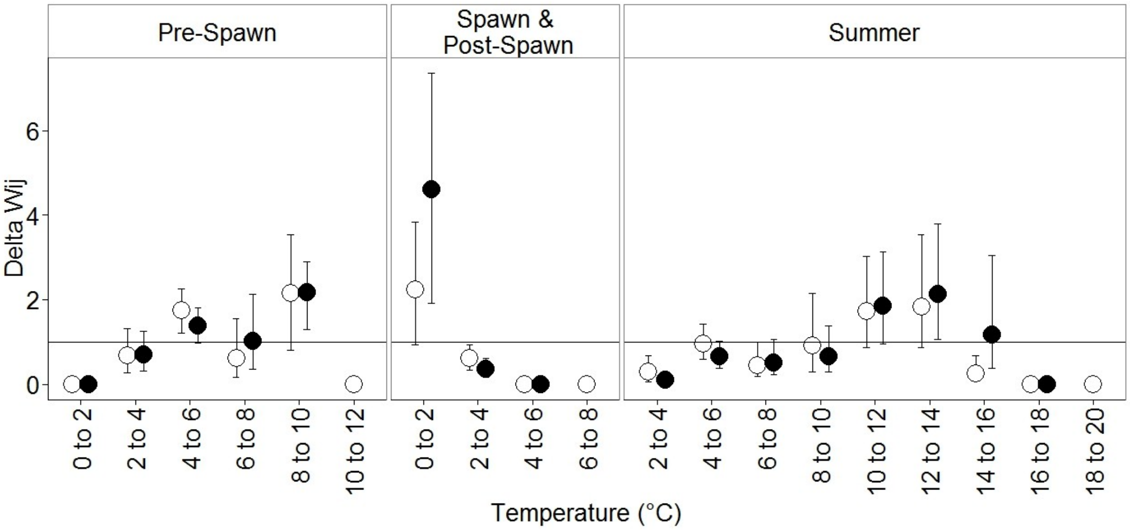

Figure 4.6 Delta-normal model estimates for Manly’s selection index values (W_{ij}) by thermal habitat. Horizontal line is at the value of 1 W_{ij}, and error bars represent conditional bootstrapped 95% confidence intervals.

5 Burbot *Lota lota* and large hydropower in North America: Benefits, threats, and research needs for mitigation

Overview

Demand for hydropower in North America is growing rapidly, and interactions between burbot and large hydropower infrastructure are increasingly common. Populations towards the southern extent of the North American burbot range are threatened and hydropower has been implicated in the decline. Here we use a traits-based approach to review the likely threats and benefits of hydropower to riverine and reservoir burbot. Next we synthesise this knowledge to assess overall impacts and identify key research needs for hydropower mitigation. We found riverine burbot downstream of hydropower systems most vulnerable to large hydropower impacts, due to winter discharge regime spawning disruption. Thus, a more precise definition of environmental flow and temperature requirements for riverine burbot is necessary to design discharge regimes that balance hydropower generation and burbot conservation objectives. For reservoir burbot, we found that trophic depression and reservoir winter drawdown can have impacts on burbot prey availability and littoral habitat stability, respectively. Nonetheless burbot often successfully exploit this lacustrine-like environment. We found that while turbine entrainment vulnerability and passage mortality risk differ between life-stages, the overall risk to burbot populations from entrainment is likely low, due to low adult vulnerability to exposure, and high juvenile resilience to removals. Thus we identify quantification of the potential for reservoirs to act as source populations for downstream impacted zones, and investigations into methods of improving reservoir recruitment such as fertilization and

spawning habitat improvements, as key knowledge gaps. Finally, our findings highlight the Pacific watershed focus of existing burbot hydropower research and emphasise the need for status assessments and ecological research above and below hydropower in North American Arctic and Atlantic watersheds, where large hydropower and burbot interactions are common, yet rarely studied.

Introduction

Hydroelectric facilities change natural lentic and lotic ecosystems to reservoir and regulated rivers (Stanford *et al.* 1996; Rosenberg *et al.* 1997; Rosenberg *et al.* 2000). These changes can have both positive effects, but most commonly carry negative consequences for fish populations (Murchie *et al.* 2008). Approximately 1000 large hydropower generation dams (>10m head height) are in operation in North America, with 596 in Canada (Environment Canada 2010) and 420 in the US (Global Reservoir and Dam Database 2015, see Figure 5.1). Together these facilities account for around 60% (Smokorowski *et al.* 2011)) and 6.6% (US Energy Information Administration 2014) of electricity production in Canada and the US, respectively, and demand is growing rapidly.

Hydropower reservoirs disrupt the natural flow regime (Poff *et al.* 1997; Lytle and Poff 2004; Poff and Zimmerman 2010), by regulating discharge, often with consequences for fish populations (see [Bunn and Arthington 2002] for a review). Large reservoirs typically feature hypolimnetic withdrawals, which lower downstream water temperatures during the summer (Webb and Walling 1993) and increase temperatures in the winter (Quinn *et al.* 1997). Given the importance of temperature for fish physiology (Huey and Stevenson 1979; Huey 1991), these thermal habitat changes often have fitness consequences (Olden and Naiman 2010). While many species occur in both lacustrine and fluvial environments, trophic structure and ecological processes differ between lake and river environments, and the change to a reservoir habitat often has consequences for the native fish community (Baxter 1977; Fernando and Holčík 1991). Hydropower reservoirs also often disrupt habitat connectivity (Lucas and Baras 2001), which is considered vital for fish life history (Nilsson *et al.* 2005; Arthington *et al.* 2010), and hydropower operational activities can result in fish entrainment through turbines (Coutant and Whitney 2000) and habitat loss associated with reservoir drawdown and dewatering (Nagrodski *et al.* 2012).

Hydropower development is concentrated towards the southern extent of the North American burbot range (~40°N, see Figure 5.1) and burbot-hydropower interactions are increasingly common (Stapanian *et al.* 2010). Burbot populations towards the southern extent of the North American range are threatened (Stapanian *et al.* 2010) and hydropower development has been implicated in the decline of these populations (Hardy and Paragamian 2013). As burbot occupy riverine (Evenson 1993; Evenson 1997) and lacustrine (McPhail and Paragamian 2000) habitats, the impacts of hydropower development can be broadly categorised in impacts on riverine populations downstream of hydropower and those on reservoir populations.

Historically, little was known about burbot biology and the species was ignored by scientists and managers (Stapanian *et al.* 2010). However, the value of burbot is increasingly being recognized. A web of science search (3rd March 2015) for the terms “burbot” and “lota lota” identified; 456 burbot specific manuscripts since1994, compared to compared to just 117 in the previous part of the 20th century, and five burbot-specific symposia since the year 2000 (Paragamian and Willis 2000; Paragamian and Bennett 2008; Paragamian and Stapanian 2011; Stapanian and Madenjian 2013). Nonetheless, few broad burbot-specific synthesis papers exist, with the exception of two population status reports (Stapanian *et al.* 2008; Stapanian *et al.* 2010). Furthermore, our search identified 372 burbot specific papers published since McPhail and Paragamian’s (2000) comprehensive review of burbot biology and life history.

Given the high potential for burbot-hydropower interactions in North America, a review of the effects of hydropower on burbot populations, will be important for the future conservation of the species. In this paper, we use a traits-based assessment approach (Rubach *et al.* 2011; Ĉada and Schweizer 2012) to review the threats and benefits of hydropower to burbot populations. We assess the effects of flow alterations, thermal habitat changes and disruption of downstream connectivity for riverine burbot below hydropower structures, and we investigate the consequences of turbine entrainment, reservoir drawdown, trophic depression and upstream connectivity disruption for reservoir burbot. Next we synthesise the knowledge to assess and compare relative impacts to populations, and identify potential conservation issues, before concluding with an outline of key research needed to; conserve riverine burbot below hydropower facilities, better understand and manage burbot in reservoirs, and improve the design of future hydropower development for burbot conservation.

Threats to River Populations

Flow Alterations

Falling winter discharges are an important trigger for pre-spawning migrations in fluvial burbot populations, with spawning occuring during low flow periods in late winter (Breeser *et al.* 1988; Paragamian *et al.* 2005; Paragamian and Wakkinen 2008; Paragamian 2010). In the Kootenai River Idaho, pre-spawning migrations were significantly reduced when hydropower-regulated discharges exceeded 300m/sec and in years with high winter discharges, burbot delayed migration and spawning failed to occur (Paragamian *et al.* 2005). Successful spawning was only observed when drought conditions reduced winter discharge to an average of 174m/sec (Paragamian *et al.* 2005; Hardy and Paragamian 2013). Hydropeaking or ramping, where turbines are turned on or off in relation to diel and even hourly fluctuations in demand for electricity, results in highly variable flows downstream of turbines, and has been shown to often have a significantly negative effect on downstream biota (Bunn & Arthington, 2002). As a poor swimmer (Jones *et al.* 1974) burbot may also be vulnerable to such unpredictable changes in flow velocity.

Thermal Habitat Change

As a winter spawning (Cott *et al.* 2013), cold water stenothermic, winter specialist species (Shuter *et al.* 2012), burbot are potentially sensitive to increases in temperature associated with winter hydropower discharge regimes. Burbot spawn at 0-4°C (see[McPhail and Paragamian 2000] and references therein), and spawning cannot be induced at temperatures above 6°C (Zarski *et al.* 2010). Burbot egg incubation has been observed at temperatures ranging from 0-6°C ([McPhail and Paragamian 2000] and refs therein), with optimum hatch rates reported at 3.8°C(Vught *et al.* 2008) and 3°C (Taylor and McPhail 2000). 100% egg mortality has been recorded at >8.1°C (Vught *et al.* 2008), >5°C (Zarski *et al.* 2010) and >6°C (Taylor and McPhail 2000). In addition to acting as an physiological requirement for successful spawning and egg incubation, winter temperatures below 6°C, have also been shown to act as an important trigger for burbot spawning migrations (Paragamian and Wakkinen 2008; Hardy and Paragamian 2013). Furthermore, the slow rate of cooling associated with reservoir thermal mass may have an impact on burbot reproductive success, as evidence from Zarski *et al.* (2010) showed that a fast rate of cooling from 6°C to 1 °C significantly improved spawning success under hatchery conditions. For more northern riverine burbot populations, cooling induced by summertime hypolimnetic withdrawal has the potential to impact population fitness if temperatures fall below optimum thresholds (see table 1 & 2). Researchers are increasingly recognizing the importance of maintaining the pattern of natural temperature variation for ensuring ecosystem integrity (see Caissie (2006) for a review). Ramping and peaking can also cause disruptions to the natural thermal regime (Olden and Naiman 2010), and have the potential to result in increased variability in the availability of optimal thermal habitat for burbot.

Barriers to Upstream Habitat Connectivity

Large hydropower infrastructure without fishways, represent a barrier to upstream movements of all life-stages of burbot. Successful passage of burbot has been recorded in low head (<10m) fishways, including vertical slot and Denil fishways in Northern Canada (Schwalme *et al.* 1985), a vertical slot fishway in the Czech republic (Slavík and Bartoš 2002), and through nature-like fishways in a Swedish project (Calles and Greenberg 2007). We could find no published evidence of burbot fishway use on high head dams (>10m). This may reflect the absence of fishway construction on high head hydropower dams in Canada and in the US, which were not traditionally installed at the time of operation (Katopodis and Williams 2012; Hatry *et al.* 2013). Nonetheless, Vokoun and Watrous (2009) suggest that flow velocities found in most large fishways would present a serious challenge to burbot ascent. Indeed, burbot are poor swimmers (McPhail and Paragamian 2000; Peake 2008). For example, Jones *et al.* (1974) found large burbot incapable of sustaining velocities >25cm/sec for extended periods of time, with a mean critical swim speed of 39cm/sec and Vokoun and Watrous (2009) observed switching to sprint swimming at very low velocities. In the absence of site specific data, we suggest that any hydropower development, regardless of fishway status, with a head height of >10m, is likely to represent a complete barrier to upstream burbot migration.

Threats to Reservoir Populations

Turbine Entrainment

Fish entrainment, the “involuntary downstream movement of fish through water release structures such as turbines” (Ĉada *et al.* 1997; Coutant and Whitney 2000), can result in immediate or delayed mortality, due to physical contact with passage structures or through pressure changes, and increased susceptibility to predation post entrainment. While the entrainment of downstream migrating diadromous juveniles has received considerable attention in the literature (Coutant and Whitney 2000; Scruton *et al.* 2002), less research has been carried out on the entrainment of resident fishes such as burbot (Martins *et al.* 2014). Adult burbot entrainment has occasionally been noted in the literature (Skaar *et al.* 1996; Spence and Neufeld 2002; Dunnigan and Sinclair 2008; Spinelli 2010), however burbot-specific entrainment vulnerability and passage mortality studies are rare (see Martins *et al.* [2013] for an exception). In the absence of such studies we follow the traits based assessment procedure outlined by Ĉada and Schweizer (2012) and discuss burbot traits in relation to entrainment passage exposure, i.e. the likelihood of becoming entrained, and to turbine passage mortality.

In adult burbot, fall/winter movement patterns are common and include pre-spawning adfluvial migrations (Paragamian and Wakkinen 2008) and within reservoir movements (Harrison et al. 2014). As a winter-active species (McPhail and Paragamian 2000; Harrison *et al.* 2013), burbot are often quiescent during the summer (Hölker *et al.* 2004). Consequently, turbine passage exposure risk is likely highest during the fall-winter period, which may explain the general pattern of fall-winter adult entrainment described by Dunnigan and Sinclair (2008) and Martins *et al.* (2013). Nonetheless, the timing of entrainment vulnerability is site specific, with Spinelli (2010) reporting elevated entrainment during the summer and fall in Hauser Reservoir, Montana and Spence and Neufeld (2002) observing entrainment in early spring (March) in the Duncan Reservoir, BC.

Life-history strategy and associated movements can result in within system heterogeneity in entrainment risk. Life-history diversity within burbot populations include; littoral, deepwater and tributary spawning (Paragamian and Wakkinen 2008; Jude *et al.* 2013), and entrainment risk may differ between strategies. Burbot display large within-population individual differences in spatial behaviour (Harrison et al., 2014) and different behavioural types may have differing vulnerabilities to entrainment risk, with the more mobile exploratory behavioural types being more at risk of chance encounters with turbine entrances.

As a benthic species (Cott et al. 2015), hypolimnetic located turbine entrances may increase entrainment exposure for burbot. Burbot are night active (Müller 1973; Kavaliers 1980; McPhail and Paragamian 2000; Fischer 2004; Harrison *et al.* 2013) and exhibit diel migrations (DMs) between deep and shallow benthic habitat (Bergersen *et al.* 1993; Carl 1995; Harrison *et al.* 2013). Accordingly, risk of exposure may increase in shallower intake locations at night. Burbot depth use varied from <1m to 180m in a Columbia river reservoir (Harrison *et al.* 2013), and up to 366m in Lake Superior (Boyer *et al.* 1989) and as a consequence no turbine entrance depth could be considered entirely risk free.

As poor swimmers (McPhail and Paragamian 2000; Peake 2008), burbot may be vulnerable to high flows around turbine intakes. Nevertheless, turbine entrance velocities may not be high enough to significantly challenge burbot. Data suggest that even for hydropower systems with very large capacity, such as the Mica Dam in British Columbia, flow velocities in the forebay reach a maximum of ~0.2m/sec within 20 metres of the turbine intake (Langford *et al.* 2012).

The low vulnerability suggested by our traits based approach is mostly supported by the limited available literature on entrainment rates. For example, Martins et al., (2013), calculated an annual entrainment removal rate of 0.7% (n =75, 2 years) through Mica Dam, British Columbia, and data calculated from the observations of Dunnigan and Sinclair (2008) suggest annual removal rates at 1.6% (n=40, 18months) through Libby Dam. While the entrainment of 2 burbot through Duncan Dam observed by Spence and Neufeld (2002), suggest a high annual removal rate (32%), low sample sizes (n= 15) and short study duration (5 months) indicate confidence in the validity of this removal rate is low. Further while 6,555 burbot were estimated to be entrained over 2 years in the Hauser Dam in a hydroacoustic entrainment study (Spinelli 2010), upstream population size was not quantified and removal rates could not be estimated.

Early life history (ELH) burbot display a number of traits that may render them susceptible to turbine passage exposure. ELH burbot undergo three distinct life stages; passive drifting in the early post hatch larval stage (Jude *et al.* 2013), a juvenile pelagic phase with active swimming and diel vertical migration behaviour (Probst and Eckmann 2009; Donner and Eckmann 2011) and a settlement phase featuring profundal habitat use (Fischer 1999; Miler and Fischer 2004). For the larval passive drifting and juvenile pelagic phases, poor swimming performance (Wang and Appenzeller 1998) and pelagic habitat use, are traits which suggest entrainment passage vulnerability (Coutant and Whitney 2000). Further, juvenile pelagic phase DVM may influence entrainment vulnerability, depending on the relative depth of intake locations and the diel cycle of turbine operations. For settlement phase burbot, profundal habitat use and increased swimming performance (Fischer 1999; Miler and Fischer 2004) result in reduced entrainment passage vulnerability. While turbine-specific research is absent, a similar ontogenic shift in entrainment vulnerability of ELH burbot has been observed in cooling water intakes in the Great Lakes (Mansfield *et al.* 1983), where the authors noted high numbers of larval and juvenile pelagic burbot becoming entrained, but lower numbers of settlement stage burbot.

While examples of adult burbot surviving turbine passage have been reported through the Libby dam Montana, USA (Dunnigan and Sinclair 2008) and Duncan dam, British Columbia, Canada (Spence and Neufeld 2002), samples sizes of entrained fish have been too small to realistically estimate mortality rates. In general it is known that adult passage mortality is species specific (Hogan *et al.* 2014), ranging from 40-100% for adult European eels *Anguilla anguilla* (Montén 1985), through 21% for adult American shad, *Alosa sapidissima* (Bell and Kynard 1985), down to 9% for Lake Sturgeon *Acipenser fulvescens* (McDougall *et al.* 2014). Swim bladder morphology is a key predictor of turbine mortality (Brown *et al.* 2014), as decompression is often the largest stressor in turbine passage (Trumbo *et al.* 2014). As a physoclistous species (Bruesewitz *et al.* 1993), burbot are likely to have higher mortality than physostomous species (Brown *et al.* 2009; Brown *et al.* 2014). Further the deepwater habitat use likely increases burbot susceptibility to barotraumas induced by turbine passage, due to an increased acclimation pressure (Stephenson *et al.* 2010; Brown *et al.* 2014). Adult burbot turbine passage mortality vulnerability is further evidenced by their high susceptibility to capture barotraumas, which occur when burbot are captured from even modest depths (<10m) (Bruesewitz *et al.* 1993; Neufeld and Spence 2004)).

For adult burbot, which can reach lengths of >100cm (McPhail and Paragamian 2000), large body size may increase the likelihood of turbine passage mortality, as larger fish are more susceptible to turbine strikes (Deng *et al.* 2005; Deng *et al.* 2007).

Integument type is also a useful trait in predicting turbine passage survival (Ĉada and Schweizer 2012), as passage through turbines can yield abrasive contacts with hard structures and shear stresses (Neitzel *et al.* 2004). Fishes such as burbot, which have a very thick mucus layer (Ashton *et al.* 2013) and small, hard to remove scales (McPhail and Paragamian 2000), tend to be less susceptible to damage and delayed mortality from abrasions and shear stresses (Ĉada and Schweizer 2012). Nonetheless while the thick integument of burbot may offer some protection, given their large size and high susceptibility to barotrauma, adult burbot turbine passage mortality is likely high.

Given the known size dependency of entrainment passage mortality (Ĉada 1990; Turnpenny *et al.* 1992; Ĉada *et al.* 1997; Deng *et al.* 2005; Deng *et al.* 2007), juvenile settlement stage burbot may have a higher passage survival than adult burbot. Juvenile resident fish entrainment mortality has not been well studied and the most comprehensive research into juvenile turbine passage mortality has been on out-migrating salmonid species, where turbine passage mortality was found to be 7-13% through high head dams in a 25 year study (Bickford and Skalski 2000). While entrainment passage mortality likely differs between resident and migrant fish species, Bickford and Skalski's (2000) research provides the best available estimate of juvenile entrainment mortality. Notwithstanding species-specific effects, given the small size of juvenile pelagic phase burbot (25-40mm [Fischer 1999]) in comparison to out-migrating salmonid smolts, lowered mortality rates would be expected.

It has been hypothesised that larval entrainment mortality may be higher than for juveniles (Coutant and Whitney 2000) because less robust swim bladders render larval fish more susceptible to barotraumas (Brown *et al.* 2014). While mortality through high head turbines is often higher than through low head structures (Ĉada and Schweizer 2012), estimates of larval mortality are limited to low head turbines. Ĉada (1990) reported ichthyoplankton mortality as low as ~5% through low head turbines. Accordingly, we suspect that although larval burbot turbine passage mortality through high head dams is likely higher than the 5% estimate for low head structures provided by Ĉada (1990), all available evidence suggest turbine passage mortality of ichthyoplankton such as larval burbot remains low (Coutant and Whitney 2000).

Reservoir Drawdown

Many large hydropower impoundments in North America operate a winter drawdown regime, refilling the reservoir with the spring/summer runoff (Wantzen *et al.* 2008). For a winter spawner such as burbot (Cott *et al.* 2013), this regime has the potential to adversely affect spawning success. Lacustrine burbot spawn in quite shallow water (<2m) and winter drawdown may lead to a reduced spawning habitat availability and possible egg stranding and freezing (Stapanian *et al.* 2010). Bergersen *et al.* (1993) reported that a 13m drawdown on Bull Lake, Wyoming led to a virtual elimination of burbot spawning habitat. Further, winter drawdown and dewatering have the potential to restrict access to reservoir tributaries for adfluvial spawners (Gaboury and Patalas 1984), and appear to restrict spawning movements of burbot in Duncan Dam, British Columbia (Spence and Neufeld 2002). Drawdowns also negatively impact the littoral benthic invertebrate community (Furey *et al.* 2006), which form the main prey items for juvenile settlement stage burbot. Further the occupation of the littoral zone in lakes by settlement stage burbot (Taylor and McPhail 2000) suggests a vulnerability to stranding, which is common in juveniles of many species (Nagrodski et al. 2012).

Trophic Depression

As a top predator (Cott *et al.* 2011), burbot are susceptible to the shifts in the structure and function of the trophic community which occur as function of reservoir creation (see [Baxter 1977; Rosenberg *et al.* 2000] for a review of the general effects of reservoirs on fish). Reservoir trophic depression is a common issue in upland reservoirs (Grimard and Jones 1982) particularly in the Pacific watershed (Stockner and Shortreed 1985; Stockner and Macisaac 1996; Stockner *et al.* 2000), and Arctic watersheds (for example, Williston Reservoir on the Peace River [Stockner *et al.* 2005]). In these systems, reservoir creation is initially followed by a short-lived trophic upsurge as nutrients leach from flooded lands (Matzinger *et al.* 2007), followed by long-term trophic depression as available nutrients are used, and nutrient load from inputs is locked away by hypolimnetic sediment deposition (Grimard and Jones 1982; Stockner *et al.* 2000). The elimination of littoral habitat and littoral community associated with winter drawdown is thought to contribute to trophic depression via a reduction in carbon input (Stockner and Macisaac 1996). Trophic depression often causes crashes in the pelagic fish community i.e. kokanee and juvenile sockeye salmon *Onchorynchus nerka* (Stockner and Macisaac 1996; Bradford *et al.* 2000; Perrin *et al.* 2006), and pelagic fish are thought to compromise a high proportion of the diet of lacustrine burbot (Wagner 1972; Schram *et al.* 2006). Importantly, reservoir trophic depression may also act as a limiting factor for survival of ELH stage burbot (Hardy *et al.* 2008). Starvation is a key factor controlling larval survival and sufficient nutrient availability is necessary for the production of burbot larvae first foods (Ghan and Sprules 1993). Similarly, nutrient availability is important for the production of the larger zooplankton which account for the majority of ELH stage diet (Wang and Appenzeller 1998).

Downstream Connectivity

Given turbine entrainment mortality for the physoclistous, large bodied, adult burbot is likely high (see entrainment section for more detail), large hydropower may act as an impermeable barrier to downstream connectivity for adult burbot. On the other hand, large hydropower likely acts a more permeable barrier for downstream movements of ELH burbot, as turbine entrainment mortality of larval and juvenile members of most species is fairly low (Ĉada *et al.* 1997; Coutant and Whitney 2000; Ĉada and Schweizer 2012; Brown *et al.* 2014),

Benefits to Riverine Populations

Hypolimnetic withdrawals that lower summer water temperatures have the potential to affect burbot populations. In situations where pre-dam water temperatures often exceed preferred temperatures (12-14°C, see table 1 and 2), hypolimnetic cooling effects may be advantageous for burbot populations. Horton and Strainer (2008) hypothesized increases in burbot abundance in the Missouri River were associated with dam-derived thermal habitat cooling. Similarly, colonisation of the Green River Drainage of the Upper Colorado River, where burbot are not native, has been attributed to dam cooling downstream effects from hypolimnetic withdrawals (Gardunio *et al.* 2011).

Benefits to Reservoir Populations

Reservoir construction impacts the upstream thermal regime, most notably in the impounded zone, where the thermal regime shifts from a riverine regime, typically characterised by strong diel and seasonal fluctuations, to a much more stable lacustrine type regime, often featuring summer thermal stratification (Webb and Walling 1993; Olden and Naiman 2010). In general, during the summer, stratified impoundments result in a hyperlimnion that provides much cooler thermal habitat than would be found in the original river system. In contrast summer epilimnion temperatures may be higher than summer river temperatures. Burbot are adapted to survive in both riverine and lacustrine systems (McPhail and Paragamian 2000), and the shift to a lacustrine like thermal regime may not come at a significant fitness cost. Both juvenile and adult burbot have been hypothesised to gain a bio-energetic advantage by exploiting warm water within the epilimnion to hunt at night and by occupying the cold hyperlimnion during the day to optimise digestion (Donner and Eckmann 2011; Harrison *et al.* 2013 respectively, see table 1 for burbot thermal optima). Further, burbot perform a seasonal and diel pattern of thermal habitat use, that appears to optimise physiological function in Kinbasket Reservoir, British Columbia (Chapter 3). The cold hypolimnetic layer of a reservoir may also provide an important summer daytime thermal refuge for burbot in systems where global warming is increasing thermal stress.

While pelagic fish communities may not exist in reservoirs immediately post fill, the vacant pelagic zooplanktivorous niche is usually quickly filled as a result of a hydropower flooding of natural lakes, stocking, and pre-existing riverine species which can exploit a pelagic niche (Baxter 1977; Fernando and Holčík 1991). As a top piscivore, pelagic fishes form the majority of lacustrine adult burbot diet (Wagner 1972; Schram *et al.* 2006) and burbot appear to be able to exploit a similar niche in impoundments (Black *et al.* 2003).

Synthesis of Overall Impacts to Riverine Burbot Populations

Our synthesis suggest that the hypolimnetic withdrawal winter discharge regimes, and the associated winter warming and elevated winter flow, provide the most significant threat to riverine burbot downstream of hydropower facilities. Regulated discharge has been suspected as factor in the decline of burbot populations downstream of hydropower infrastructure (McPhail and Paragamian 2000; Stapanian *et al.* 2010) and high winter discharges and increased temperatures have been strongly linked to the collapse of the Kootenai River burbot population below the Libby Dam in Idaho (Hardy and Paragamian 2013). As burbot are poor swimmers (Jones *et al.* 1974), large hydropower infrastructure with or without fishways, likely represents an impermeable upstream barrier to riverine burbot. The importance of longitudinal connectivity for fish life history is well known (Lucas and Baras 2001) and the negative effects as a result of hydropower disruption of connectivity have been documented in many fish species (Northcote 1998; Calles and Greenberg 2009). Longitudinal connectivity disruption may have consequences for riverine burbot, which have been observed to sometimes migrate long distances (Evenson 1993; Evenson 1997). Nonetheless, genetically distinct stocks of burbot have been detected above and below natural barriers (Powell *et al.* 2008) and Underwood *et al.* (INPRESS) suggest that although localized burbot movements between lakes and rivers on the same tributary are fairly common, even modest natural barriers can result in distinct meta-populations within the same watershed.

In terms of benefits, our synthesis suggest that summer cooling effects from hypolimnetic withdrawal discharge have the potential to provide a summertime thermal refuge to riverine burbot populations at the southern end of burbot range, that may be important in light of global warming. Nevertheless, in general riverine burbot populations downstream of hydropower infrastructure are much reduced in comparison to pre-dam conditions (for example the Columbia River (Cope 2008), Missouri River below Garrison Dam (Stapanian 2010)). Our synthesis suggest that while the loss of habitat connectivity associated with dam construction may play a part in this decline, upstream connectivity disruption is likely not a significant threat in comparison to the effect of winter discharge routines, which are the chief hydropower threat to riverine burbot due to the disruption to spawning associated with elevated flows and temperatures during the late winter period.

Synthesis of Overall Impacts to Reservoir Burbot Populations

While turbine entrainment has been hypothesised as a possible factor in the decline of burbot populations in reservoirs (Stapanian *et al.* 2010; Hardy and Paragamian 2013), detailed empirical data on the population-level effects of entrainment are lacking. Adult burbot entrainment has occasionally been reported, however research based on reasonable sample sizes and sufficient sampling periods (for example, Martins *et al.* (2013)), combined with our traits based assessment, suggest adult entrainment removal rates are low.

While burbot population work has not been extensive, existing population models indicate burbot can sustain high removal rates. For example, Ahrens and Korman (2002) suggested that the West arm of the Kootenai Lake historical burbot population sustained a harvest removal of up to 20% per annum. Further, burbot possess a number of the key demographic traits indentified by (Ĉada and Schweizer 2012) as indicative of a species capable of sustaining entrainment removal. Female burbot are highly fecund, often producing over 3 million eggs per year per individual (Roach and Evenson 1993), and these offspring have very high natural mortality (Ghan and Sprules 1993). Further, burbot; reach sexual maturity early and at a small size (Stapanian and Madenjian 2007), are iteroparous and can live up to 20 years (Guinn and Hallberg 1990), ensuring very high lifetime reproductive output. Given that available evidence suggest adult entrainment rates are fairly low and population models (Ahrens and Korman 2002) and burbot life history traits indicate a certain amount of resilience to removals, threat to burbot populations from adult turbine entrainment risk may be fairly low. Nonetheless, given that; entrainment vulnerability is known to be very site specific (Coutant and Whitney 2000) site by site monitoring and assessments are recommended where possible. The very high ELH natural mortality (Ghan and Sprules 1993) and high fecundity of burbot (Roach and Evenson 1993), suggest potential for population levels impacts associated with ELH entrainment are also low. Again, given that research into the entrainment vulnerability of ELH stages of resident species, including burbot, is fairly limited (Ĉada and Schweizer 2012), where possible, we recommend site-specific assessments are necessary to appropriately validate the prediction.

Given the importance of littoral habitat for settlement phase (Taylor and McPhail 2000) and adult lacustrine burbot (Harrison *et al.* 2013; Cott *et al.* 2015), and the evidence which suggests lacustrine burbot spawn in the shallow littoral zone (McPhail and Paragamian 2000), damage to the littoral habitat as a result of winter drawdowns, may be a more important threat to reservoir burbot than turbine entrainment. Similarly, because the main prey items for both ELH and adult burbot have been shown to be vulnerable to oligotrophication (Stockner and Shortreed 1985; Stockner and Macisaac 1996; Stockner *et al.* 2000), reservoir trophic depression is also likely a greater threat to reservoir burbot than entrainment.

In terms of benefits, while comparisons with pre-dam conditions are difficult due to insufficient baseline data, our findings suggest that hydropower reservoirs can provide suitable thermal and trophic niches for burbot, and support burbot populations (for example Kinbasket Reservoir (Harrison *et al.* 2013; Martins *et al.* 2013), Arrow Lakes Reservoir (Arndt and Baxter 2006), Duncan Lake (Spence and Neufeld 2002) in British Columbia and Lake Kookanusa, Montana (Skaar *et al.* 1996)). Nonetheless, opportunities to improve reservoir habitat for burbot exist and efforts should be focused on the mitigation of the negative effects of winter drawdown on littoral habitat and the effects of reservoir trophic depression on burbot prey.

Research needs for mitigation of hydropower impacts

Burbot and hydropower outside of the Pacific Northwest

In general, burbot populations in Arctic and Northern Atlantic watersheds of North America are fairly secure (Stapanian *et al.* 2010). However, our review highlights the lack of data available on the status of burbot in the many large hydropower systems that exist outside of the Pacific watershed. Tellingly, we could find no reference for the status of burbot populations above or below the four largest reservoirs in Canada, that all lie within the range of burbot (Stapanian 2010), in North America (The Daniel-Johnson Dam in Northern Quebec (ranked 5th largest reservoir in the world); The Williston Reservoir, Northern British Columbia (ranked 7th largest reservoir in the world) and the Robert-Bourassa Reservoir and La Grande-3 Nord Reservoir both in Northern Quebec (ranked 11th and 12th in the world respectively). Indeed, the abundance of large hydropower (>10m head height) and mega-dams (>100m head height) within the North American range of burbot, which exist outside of the Pacific watershed, is evident in Figure 5.1. Given our suggestion that hydropower has consequences for both riverine and reservoir dwelling burbot, status assessments of burbot populations below and above hydropower infrastructure in Atlantic and Arctic watersheds should be priority for burbot conservation. Further, investigations into the ecology of burbot residing within these hydropower impacted systems are needed to determine the broader geographic applicability of Pacific watershed based findings.

Environmental flows and thermal requirements of spawning riverine burbot

Given our identification of winter discharge regimes as the chief hydropower threat to riverine burbot, mitigation remains a priority for riverine burbot conservation. Nonetheless, the operational changes required to mitigate hydropower impacts are hard to implement (Hardy and Paragamian 2013), as a winter drawdown is required to prevent flooding from spring snowmelt, and the current drawdown and fill routine common in North America is driven by seasonal demand for power. The reluctance of hydropower authorities to change detrimental regimes has been illustrated by the Kootenai system, where power authorities have been unable to implement regimes requested for burbot conservation (Hardy and Paragamian 2013). Accordingly research to precisely define the timing and environmental flow and temperature requirements of spawning burbot is needed to design discharge regimes that can balance burbot conservation with hydropower objectives.

Potential for impoundments to act as source populations for downstream

Our synthesis suggests hydropower reservoirs can support burbot populations, and burbot population below hydropower systems are often in decline, in part due to reproductive disruption. Larval drift is an important dispersal mechanism for many fishes in both riverine (Lechner *et al.* 2014) and lacustrine systems (Höök *et al.* 2006), including burbot in the Great Lakes (Jude *et al.* 2013) and in burbot in rivers (Fisher 2000). Turbine passage has been identified as a key dispersal mechanism for YOY of species in the river Danube delta (Janáč *et al.* 2013) and data suggest upstream lake and reservoir systems can be sources for downstream recruitment of burbot (Paragamian *et al.* 1999; Hubert *et al.* 2008; Underwood et al INPRESS). Our traits based assessment suggests; burbot produce large numbers of pelagic larvae and juveniles that are vulnerable to entrainment (Ĉada and Schweizer 2012), that ELH entrainment survival is likely high (Ĉada *et al.* 1997; Coutant and Whitney 2000; Ĉada and Schweizer 2012; Brown *et al.* 2014) and upstream populations can probably withstand high ELH removal rates. Accordingly, we suggest the viability of reservoirs to act as source populations for downstream populations, warrants further investigation. While a direct quantification of burbot ELH entrainment rates might help to establish levels of population connectivity, direct methods are logistically difficult in large reservoirs due to the difficulty associated with netting large turbine outflows (Skaar *et al.* 1996). Further, while lab based simulations of turbine entrainment have potential to quantify passage survival (Richmond *et al.* 2014), they cannot assess the ability of survivors to contribute to recruitment. Therefore, genomic sequencing and other genetic methods (see (Hughes *et al.* 2009) for a review) may be the most practical approach to quantify downstream population connectivity. Should downstream population connectivity be quantified and established as viable, then improvements to reservoir burbot productivity (see below) have the potential to at least partially compensate for the negative effects on downstream riverine burbot.

Fertilization for reservoir trophic depression

In ultra-oligotrophic lakes and reservoirs suffering from trophic depression, fertilization experiments have resulted in; primary productivity increases and improved phytoplankton abundance (Stockner and Shortreed 1985), increased zooplankton abundance (Thompson 1999), increases in the pelagic fish production (for example kokanee (Hyatt *et al.* 2004)), and increased growth of a top predator, rainbow trout, *Onchorynchus mykiss* (Johnston *et al.* 1999). While increased burbot growth was noted post fertilization in the Arrow Lakes reservoir in British Columbia (Arndt and Baxter

2006), more research is needed to understand the effects of fertilization for burbot. However given that pelagic fishes form the majority of lacustrine adult burbot diet (Wagner 1972; Schram *et al.* 2006), the prospects for increased burbot growth post fertilization are promising. The nutrient dependence of the phytoplankton, copepods and rotifers which are important ELH burbot prey items (Wang and Appenzeller 1998), also suggests nutrient restoration has potential for improving ELH recruitment in impoundments suffering from trophic depression. As a caveat, while trophic depression is found in reservoirs outside of the Pacific watershed (e.g. Lake Williston on the Peace river (Stockner *et al.* 2005)), fertilization experiments have generally been limited to the Pacific region (Stockner and Macisaac 1996; Stockner *et al.* 2000). Further, fertilization has sometimes resulted in negative effects such as blue-green algae and ungrazable diatom blooms (Hyatt *et al.* 2004).

Life history of burbot in reservoirs

Burbot reservoir life-history is an important knowledge gap (Dunnigan and Sinclair 2008). Burbot display several distinct life history strategies including, deepwater spawning, reef spawning, tributary spawning, and littoral spawning in natural lakes (Jude *et al.* 2013). While lake spawning and tributary spawning burbot may contribute to reservoir burbot stocks (Paragamian and Wakkinen 2008), the existence of each strategy and relative contribution to reservoir recruitment needs to be defined. Differing life history strategies likely have different implications for the management of reservoir drawdown, as shallow lake spawning could increase vulnerability to late winter drawdown egg dewatering (Bergersen *et al.* 1993; Stapanian *et al.* 2010) and tributary spawners may be vulnerable to drawdown imposed tributary access restriction. Accordingly, a greater understanding of the precise spawning habitat requirements of lake spawners is a necessary step in targeting spawning habitat improvement and drawdown mitigation works. Improvements in our understanding of the exact timing and location of reservoir burbot spawning events are required to better design drawdown operational changes to reduce likelihood of egg dewatering. Equally, at a site-specific scale, identification of tributary spawning locations is necessary to target access and habitat improvement works.

Considerations For Future Hydropower Projects

Mitigation of the effects of existing hydropower on fisheries is often difficult to achieve (Fraley *et al.* 1989). However many research opportunities exist to enable the design of future hydropower constructions with fewer impacts on burbot populations. While the upstream passage of burbot past existing hydropower facilities was not identified as the most significant threat to burbot populations in our review, habitat connectivity remains an important feature of sustainable hydropower (Lucas and Baras 2001). Accordingly, more work is needed to investigate the effectiveness of fishways for non-salmonid species (Hatry *et al.* 2013) that will enable the design of fishways to pass poor swimmers such as burbot. In our review, we identify ELH turbine passage survival as likely important for population connectivity. Thus, research to test the burbot specific passage mortality of new turbine designs will be important, particularly for ELH stages. Initial work suggests new turbine designs can pass fish well (>98% survival of <20cm fish) and actually improve power output (Hogan *et al.* 2014), however burbot specific applicability is yet to be quantified.

Conclusions

Our review emphasises the threat to riverine burbot caused by winter discharge regimes, and highlights the decline of riverine burbot populations in comparison to pre-dam conditions. Accordingly, we suggest that better definitions of the precise environmental flow and temperature requirements for successful riverine spawning are needed to design winter regimes suitable for meeting burbot conservation and hydropower objectives. In contrast to riverine burbot, reservoir burbot appear capable of occupying and exploiting reservoir habitat. Nonetheless, reservoir life history is not well understood and the effects of littoral habitat loss associated with winter drawdown need quantification. While entrainment of burbot has previously been hypothesised as a possible factor in burbot declines (Stapanian *et al.* 2010), our review suggests that the risk to burbot populations from adult entrainment is likely low, due to low entrainment vulnerability and an ability to withstand relatively high removal rates. Further, given that our traits based assessment suggest ELH burbot are vulnerable to entrainment, have high passage survival, and populations can likely withstand high ELH removal rates, the ability of entrained ELH burbot to contribute to downstream recruitment needs quantification. Further we suggest that if downstream connectivity can be validated, then research should focus on methods of improving ELH recruitment in reservoirs, such as fertilization and spawning habitat improvements. Finally, an overarching theme that emerged from our synthesis of hydropower related burbot work, is the current Pacific watershed focus. Given the potential for hydropower facilities to result in consequences to burbot populations highlighted in this review, status and ecological assessments of burbot above and below hydropower in Arctic and Atlantic watersheds regions should be prioritised to ensure the conservation of the species.

Table 5.1 Lab derived thermal preferendia of burbot *Lota lota*. T_{pref} refers to final thermal preference. CT*Max* represent critical thermal maximum with acclimation temperature in brackets. $\mathrm{T}Opt_{\mathrm{con}}$, $\mathrm{T}Opt_{\mathrm{gro}}$, and $\mathrm{T}Opt_{\mathrm{resp}}$ represent thermal optima for consumption, growth and respiration respectively with associated maxima in brackets

Reference	T_{pref} (°C)	Total length (cm)	CT*Max* (acc)	$\mathrm{T}Opt_{\mathrm{con}}$ ($\mathrm{T}Max_{\mathrm{con}}$)	$\mathrm{T}Opt_{\mathrm{gro}}$ ($\mathrm{T}Max_{\mathrm{gro}}$)	$\mathrm{T}Opt_{\mathrm{resp}}$ ($\mathrm{T}Max_{\mathrm{resp}}$)	Other
(Hofmann and Fischer 2002)	11.4	10-20					
(Hofmann and Fischer 2002)	14.2	20-30	27.5 (9.8)				
(Hofmann and Fischer 2003)				17.9	16.9		
(Hölker *et al.* 2004)							Food consumption fell >20°C
(Shodjai 1980)							Food consumption fell >20°C
(Rudstam *et al.* 1995)				13.7(21)			
(Pääkkönen and Marjomäki 2000)				13.6 (>23.4)			
(Pääkkönen *et al.* 2003)			27 (12.6)*	14 (28)		23(27)	Optimum Respiration 23°C

Table 5.2 Field derived measures of thermal habitat use and preference

Source	Upper and lower temperature preferendum	Other Metrics	Stock location
(Carl 1995)	10-12 °C	Occasional forays into >20°C waters	Lake Opengo, Ontario
(Scott and Crossman 1973)	15.6-18.3°C	Upper limit of 23	Unknown
(Bruesewitz 1990)	9-13°C	na	Lake Michigan, US
(Hackney 1973)	7-10°C	Avoid temps >23°C	Lake Opengo, Ontario
(Edsall *et al.* 1993)	8-13°C		Lake Michigan, Ontario
Van Dijk,G.Staaks and I.Hardewig Unpublished data (Hölker *et al.* 2004)	11.4-14.2°C		Unknown
Harrison et al.,(2015)	12- 14°C (Summer Night)	<2°C Spawn Night	Kinbasket Reservoir, BC

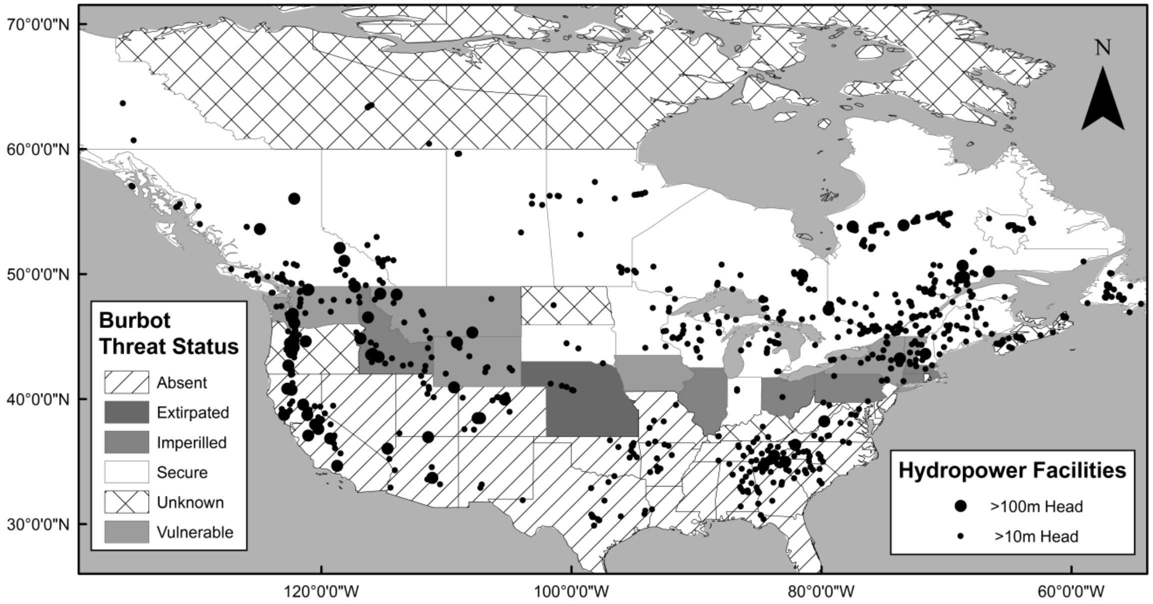

Figure 5.1 Range of burbot Lota lota in relation to large hydropower in North America. Burbot provincial and state scale threat status was derived from Stapanian et al (2010). Hydroelectric facilities data from GRanD Database, available at http://atlas.gwsp.org.

6 General Discussion

This thesis, which investigated the vertical distribution, spatial behaviour and thermal habitat selection of a reservoir resident species, burbot *Lota lota*, has considerably advanced our understanding of burbot ecology and behaviour, and the behaviour and ecology of fishes in general. Further, thesis findings have many important implications for wildlife conservation and management, at both a species-specific and broader ecological scales. The study has provided the first species-specific empirical evidence of several behavioural patterns including: diel migrations, spatial behavioural syndromes, and seasonal and diel shift in thermal habitat selection, in adult burbot. In the review chapter, the synthesis of existing knowledge has advanced understanding of the threats and benefits of hydropower to burbot populations. At broader ecological scales, Chapter 2, makes a significant contribution to the debate surrounding the ultimate causes of diel migrations, while in Chapter 3 important advances in the understanding of the role of animal personality in shaping spatial ecology were achieved, and in Chapter 4 considerable progress towards improved understanding of the temporal dynamics of thermal habitat selection was accomplished.

Contributions to knowledge

While diel migrations (DMs) have been anecdotally noted in adult burbot (Bergersen *et al.* 1993; Carl 1995), Chapter 2 provided the first species-specific empirical confirmation of this behaviour in adult burbot, and the first attempt at a species-specific explanation for the behaviour. Together, the findings in this chapter suggested that DM was best explained by a complex multi-factor trade-off hypothesis. It was hypothesised that the elevated nightly activity and shallow water use observed in burbot, given the known benthic behavioural pattern of the species (Cott *et al.* 2015), implied active feeding in the littoral zone at night. It was argued that the size structured nightly depth distributions observed, combined with knowledge regarding the cannabilistic behaviour of burbot (Gallagher and Dick 2015), indicated that shallower water use at night may increase predation threat for burbot. Further, the detection of elevated temperature experience at night for at least six months a year, combined with a clear diel pattern of activity, was hypothesised to represent a “hunt-warm rest cool” bioenergetics optimisation strategy (Sims *et al.* 2006). The evidence provided to support this multifactor hypothesis, made an important contribution to our understanding of the long term fitness gains associated with the commonly adopted DM behaviour. Further, while multifactor DM explanations are increasingly becoming accepted as the most likely explanation for DM (Busch *et al.* 2011; Mehner 2012), more empirical examples, as provided by this chapter, are needed to confirm the generality of this hypothesis.

The findings presented in Chapter 3, provided the first species-specific empirical account of a spatial behavioural syndrome in adult burbot, and may help to explain how a species which is generally considered sedentary (Bergersen *et al.* 1993; Carl 1995), has become one of the most widely distributed freshwater species in the northern hemisphere (Stapanian *et al.* 2010). At a the broader ecological scale, the finding that individual differences in spatial ecology were not well captured by simple linear metrics of dispersal, have important implications for behavioural ecology, where dispersal metrics are most commonly used to describe spatial behaviours (see for example (Clobert *et al.* 2009)). Further, the identification of consistent individual differences in home-range, site fidelity, and movement, add to the growing number of behaviours in which personality dependence has been documented (see (Bell *et al.* 2009)for a review).

The documentation of a resident to mobile spatial behavioural syndrome axis, provided a novel empirically based explanation for the movement heterogeneity which is common in spatial ecology datasets (Taylor and Cooke 2012; Radinger and Wolter 2013), and has previously only been investigated in relation to internal factors and environmental cues. As a consequence the thesis work has significantly enriched our understanding of animal space use and movement.

Chapter 4 provided the first species-specific account of an interesting pattern of thermal habitat selection that shifted on a diel and seasonal basis, in adult burbot. In particular the evidence that indicated a selection for very cold temperatures during the spawning period at night, made an important contribution to our understanding of the thermal ecology of adult burbot in reservoirs. At a broader scale, the large seasonal shifts in temperatures selected, has not been seen in many species (see (Mortensen *et al.* 2007) for an exception based on Arctic char, *Salvelinus alpinus*). Further the diel patterns of selection and avoidance, suggested a temporal plasticity in thermal habitat selection that has not previously been recognized. The detection of behavioural thermoregulation outside of the summer period, suggested thermoregulation may be a more important tactic in the winter than previously acknowledged, and the thesis results compliment the research suggesting salmonids make use of thermal refugia during winter periods (for example (Cunjak and Power 1986; Cunjak 1996; Cunjak *et al.* 1998)).

In Chapter 5, the synthesis of existing knowledge, provided an enhanced level of clarity regarding the relationship between hydropower and burbot. Turbine entrainment has often been hypothesised as a potential factor in the decline of burbot around hydropower infrastructure (for example (Hardy and Paragamian 2013)). However, the synthesis of all available data on burbot entrainment and on traits influencing entrainment vulnerability, suggested that while entrainment passage exposure vulnerability likely differs between life-stages, as does passage mortality, low probability of adult entrainment, and low population level risk associated with entrainment removals, indicated the overall relative risk of entrainment to populations is likely small. The collation of population connectivity data further suggested that the ability of early life history entrainment to act as a dispersal route requires investigation. Finally, while the negative effects hydropower on burbot have received considerable attention in the literature (see for example (Hardy and Paragamian 2013)), this review emphasised the somewhat neglected point that hydropower can also have benefits for coldwater stenothermic piscivorous species such as burbot. Indeed, the review chapter highlighted the ability of burbot to successfully exploit reservoir thermal habitat and prey on the pelagic fish community that are often found in hydropower reservoirs (Fernando and Holčík 1991).

Species-Specific Implications of Findings

The thesis also provided many findings with important implications for conservation and management of burbot. Given that the depth distribution of fishes in relation to turbine intake depth likely influences entrainment vulnerability (Martins *et al.* 2014), the detection of DMs in reservoir resident burbot seen in Chapter 2, has implications for improved characterisation of turbine entrainment risk. The observed diel depth distribution pattern suggests that turbine intakes located at shallower depths, may increase entrainment risk to burbot at night, and deeper intake locations may increase entrainment risk during the day. Further, the distinct diel pattern of activity detected, suggests relative entrainment risk is likely higher during night-time periods, when burbot are most active. The DM observed, when coupled with information suggesting that burbot are strongly benthic throughout the migration (Cott *et al.* 2015), and the evidence of increased activity indicative of feeding at night, emphasise the importance of littoral habitats for reservoir and lake burbot. Accordingly, mitigation of the negative effects of winter drawdowns on littoral habitat may be important for reservoir burbot. Furthermore, the importance of littoral habitats for burbot, should be recognised in relation to anthropogenic activity that has the potential to result in littoral habitat alteration, reduction or loss. The empirical identification of DM, provides important information relevant to researchers seeking to capture burbot for stock assessment and research. Burbot are difficult and time consuming to capture, and often suffer from barotrauma as a result of capture from depth (Neufeld and Spence 2004). Given that the likelihood of barotrauma is reduced by capture at shallow depths (Bruesewitz *et al.* 1993; Neufeld and Spence 2004), our detection of very shallow water use at night during the late winter period, and a general pattern of DM, may help researchers design capture programs that minimise the barotrauma risk.

The influence of differing behavioural types (BTs) on individual vulnerability to anthropogenic disturbances is increasingly being recognised (see (Wolf and Weissing 2012) for a review). The importance of a diversity of behavioural types for population resilience and the evolutionary ecology of species, is also becoming increasingly apparent (Réale *et al.* 2007a; Wolf and Weissing 2012). Evidence suggests that anthropogenic disturbances featuring heterogeneity in risk between behavioural types, can result in lowered behavioural type diversity (Biro and Post 2008; Olsen *et al.* 2012). Thus, the detection of a resident to mobile behavioural syndrome axis in Chapter 3, likely has implications for burbot entrainment vulnerability. Accordingly, the hypothesis that more mobile types with large home ranges and continuously exploratory behaviour patterns may be more vulnerable to turbine passage exposure warrants further investigation. Furthermore, differing behavioural types are thought to be relevant to species reintroduction strategies (Wolf and Weissing 2012). Accordingly, the detection of a resident to mobile behavioural syndrome axis, may be relevant to planned burbot re-introduction programs in the UK (Worthington *et al.* 2010a; Worthington *et al.* 2010b; Worthington *et al.* 2011; Worthington *et al.* 2012) and elsewhere. Accordingly, capture strategies for wild burbot destined for re-introduction programs, should be designed, where possible to include behavioural type diversity.

The distinct seasonal and diel patterns of thermal habitat selection detected in Chapter 4, may also be relevant to understanding entrainment vulnerability. The night-time selection for; 12-14°C habitat during the summer period and for <2°C habitat during the spawning period, that was observed, indicate that intake locations which draw water at these temperatures, during these periods, may increase entrainment vulnerability. The selection for, and apparent requirement for very cold (<2°C) habitat, observed during the spawning period, has important implications for the conservation of burbot in light of climate change vulnerability, and highlights a potential vulnerability to increased temperatures during the winter period. Further, the detection of selection for these very cold temperatures, provides information that may prove useful for researchers attempting to predict how the geographic range of burbot will shift in response to climate change (for an example of a similar predictive model see (Sharma *et al.* 2007)).

Broad Implications of Findings

In addition to the species-specific implications of the thesis, the thesis research has several important implications for general conservation and management of species. The detection of a profundal-littoral migration in a benthic top predator (Chapter 2) has advanced the understanding of within lake fish movements and compliments the suggestion by (Gorman *et al.* 2012a; Gorman *et al.* 2012b) that DM in benthic species

(DBM (Cott *et al.* 2015)), may provide an important trophic linkage between profundal and littoral habitats. Accordingly, conservation of benthic diel migrating species, may be more important for lake ecosystem integrity than previously acknowledged.

The detection of personality dependent spatial ecology (Chapter 3), has several implications for general spatial management and conservation policy. The findings suggests that if similar patterns are evident in other species, then the mean measures of space use, which are often used in the design of spatial conservation policies (for example marine protected areas (Abecasis *et al.* 2014)), may not adequately capture the space needs of animal populations. Dispersal personality traits are thought to be important in the range expansion of species (Rehage and Sih 2004), gene-flow (Wolf and Weissing 2012) and the carrying capacity of habitats (Réale *et al.* 2007a). Similarly, the detection of a spatial behavioural syndrome, that occurs independently from dispersal from release, may also have implications for range expansion, gene-flow and the carrying capacity of habitats. In freshwater systems, range expansion opportunities do not necessarily increase in a linear fashion in relation to distance from natal origin, due to connectivity bottlenecks and habitat fragmentation (Ricketts 2001; Van Dyck and Baguette 2005). Accordingly, the mobile, continuously exploratory behavioural type that was identified, may have an increased likelihood of exposure to and successful passage through connectivity bottlenecks.

The detection of temporal plasticity in thermal habitat selection (Chapter 4), also has implications for the conservation and management of a winter specialist species. The findings which indicated a strong, reproductive requirement for very cold habitat during the winter period, provide additional support to the growing consensus that winter specialist species may be particularly vulnerable to the shorter and warmer winters associated with climate change (Pörtner 2006; Pörtner and Peck 2010; Shuter *et al.*

2012). Furthermore, the diel pattern of thermal habitat selection seen during the summer period indicates that cold water stenothermic species are capable of exploiting thermal habitat conditions found in large hydropower reservoirs in ways which optimise physiological function. Accordingly, the thesis findings highlight the potential for hydropower reservoirs to provide suitable thermal habitat for coldwater species, which may provide important thermal refugia in light of predicted temperature rises and the abundance and expected growth of large hydropower, particularly in North America (see Chapter 5).

Future Directions

The findings from Chapter 2, which suggested than on average, 27% of burbot tagged, did not perform a diel migration on a given night, provide an interesting opportunity for further research. When less that 100% of a population perform a migration, the migration is known as a partial migration (Chapman *et al.* 2012a). While the majority of research into partial migrations has focused on seasonal migrations, recent research has suggested partial migrations are also common at a diel scale (Mehner and Magnan 2014). Nonetheless, the proximate mechanism behind the decision to stay resident during the diel migration, and the long term evolutionary benefits of this behaviour, are not well understood (Miriam *et al.* 2013). Density dependence has been hypothesised as a factor in the decision to stay resident (Mehner and Magnan 2014). However, given that individual differences are known to contribute significantly to the variance in most behaviours (Bell *et al.* 2009), and have been linked to seasonal partial migrations (Chapman *et al.* 2011), it seems likely that the tendency to perform diel migration may also be a personality dependent trait. Individual differences in probability of diel migration and other relevant metrics such as migration amplitude, and migration length, have not to our knowledge been quantitatively investigated, and telemetry data would provide a good framework to investigate hypotheses regarding these behavioural metrics. Indeed, a greater understanding of the factors influencing the decision to migrate or stay resident, has good potential to inform on both the proximate and ultimate causes of DMs (Mehner and Magnan 2014). Furthermore, the use of a multivariate Bayesian mixed effects modelling framework, such as applied in Chapter 3, presents an opportunity to investigate between individual correlations between DM and other traits that might indicate a behavioural syndrome.

Given the detection of a spatial behavioural syndrome in adult burbot in Chapter 3, more research is now needed to test the consistency of these findings in alternative species. Along with individual differences in behaviour, behavioural ecologists are becoming increasingly interested in how behavioural plasticity across environmental gradients differs between individuals, known as behavioural reaction norms (BRN) (Dingemanse *et al.* 2010; Stamps 2015). These between individual differences in behavioural plasticity are thought to have many consequences for ecology and evolution, including population stability and resilience to environmental change, and may be linked to animal personality (Dingemanse and Wolf 2013). However, the generality of BRN occurrence across species and characters has not been well established (Mathot *et al.* 2012). Given that mixed effect model based investigations into individual differences in behavioural plasticity tend be very data hungry (van de Pol 2012), large acoustic telemetry datasets have good potential to contribute to BRN research. The partial diel migration findings in Chapter 2 suggest DM can be a plastic behaviour. Furthermore the daily scale of diel migrations is likely to provide a suitably high number of replicates for BRN modelling. Accordingly, a telemetry based BRN investigation into diel migrations has good potential to improve our understanding of DM behaviour, and advance a general understanding of BRNs.

Given the identification of spatial behavioural syndromes (Chapter 4) as being of potential importance to conservation and management of species, the ability to easily and quickly identify or predict spatial behavioural types, *a priori*, would be useful for conservation managers. Moreover, identification of physiological correlates of personality traits, have the potential to further our understanding of the proximate and ultimate causes of animal personality (Stamps and Groothuis 2010). Personality traits are thought to be physiologically linked to pace-of-life syndrome, or coping style, where proactive and reactive types differ in hormonal response (Réale *et al.* 2010; Careau *et al.* 2010). Indeed, several personality traits have been correlated with physiological post-stressor exposure traits, such as heart rate, breathing rate and cortisol production (Ferrari *et al.* 2013). Accordingly, an investigation into the ability of the above traits to capture spatial personality type, *a priori*, could provide useful information.

Behavioural traits that can be observed at the time of capture, if shown to be correlated with behavioural syndromes, also have the potential to be useful predictors of spatial personality type. Angling can be a useful capture method for certain species (for example bull trout, (Gutowsky *et al.* 2011), and will likely result in a certain amount of stress to the individual fish (Thompson *et al.* 2008). Given that the behavioural response to stress of individuals is related to coping strategy and personality type (Koolhaas *et al.* 1999), correlations between behaviour during angling and personality type, warrant investigation. In a recent study, fishing rod mounted tri-axial accelerometry, has proved a useful tool to estimate measures of fish behaviour during angling, such as fight length and fight intensity (Brownscombe *et al.* 2014). Accordingly, if these angling behavioural metrics can be standardised to account for the variance associated with body size, hooking location and water temperature, potential exists to test the hypothesis that these behaviours are correlated with personality traits.

While personality traits and behavioural syndromes are increasingly being detected and recorded in the scientific literature (Bell *et al.* 2009), the relationship between these personality traits and anthropogenic disturbance vulnerability have not been extensively explored (Réale *et al.* 2007a; Wolf and Weissing 2012). While behavioural syndromes have been linked to vulnerability to commercial (Olsen *et al.* 2012) and recreational fisheries (Wilson *et al.* 2011), more research is required to test hypotheses regarding the potential for differences in vulnerability to other anthropogenic stressors..

Bioenergetics based explanations for diel migrations have received considerable attention in the literature (Brett 1971; Bevelhimer and Adams 1993; Mehner *et al.* 2010). Our detection of a diel pattern of thermal experience in Chapter 2 and our detection of diel pattern of behavioural thermoregulation in Chapter 4, imply that the selection of temperatures that are optimum for feeding and hunting at night, likely have positive fitness consequences for burbot during the summer period. Nonetheless a greater insight into the fitness consequences of diel migrations for burbot, could be achieved through a bioenergetics estimation of fitness gains associated with the migration. While in Chapter 2, we used vertical activity as a proxy for activity, potential exists to obtain a more precise estimation of activity levels and behavioural state, through the use of tri-axial accelerometry (Broell *et al.* 2013). Furthermore, concurrent sampling or telemetry of burbot prey organisms (such as seen in (Stockwell *et al.* 2010)), could help strengthen the hypothesis that occupation of the littoral zone at night provides increased feeding opportunity. A diel based comparison of stomach content and fullness, might also be of value to provide an empirical confirmation of elevated nightly feeding rate (Eggers 1977), however capture during daylight hours is difficult for the nocturnal burbot (Bernard *et al.* 1991). Bioenergetics models exist for burbot (for example (Pääkkönen *et al.* 2003)), and if activity and feeding rate could be estimated, the estimates could be combined with temperature experience data from Chapter 2 to estimate the fitness gains from the migration.

In addition to the knowledge gaps identified as a result of the data chapters (Chapters 2 to 4) discussed above, the synthesis in Chapter 5 also resulted in a number of key recommendations for future research. In this chapter a shift in geographic focus of burbot and hydropower research away from the current Pacific watershed focus was identified as a key research need for North American burbot populations. Further, the need for a more precise knowledge of environmental flow and temperature requirements of riverine burbot was highlighted as important. Recommendations were also made to improve our understanding of the ecology of reservoir dwelling burbot and these included; investigations into the ability of entrained early life history burbot to contribute to downstream recruitment, and life-history studies to determine the role of adfluivial and lake spawning life-forms to reservoir recruitment. The chapter also highlighted the need for investigations to determine the habitat requirements and locations of spawning for both life history types, and experiments to define the utility of methods of improving recruitment in reservoirs, such as lake fertilisation. Finally, empirical investigations into the potential effects of littoral habitat loss associated with winter draw-downs on burbot production, were identified as an important research need.

Conclusions

This thesis has made a considerable contribution to the understanding of burbot behavioural ecology in reservoirs and revealed a number of previously unidentified behavioural phenomena in adult burbot including; diel migrations, personality dependent spatial ecology and behavioural thermoregulation at a diel and seasonal scale. The findings of the study have made species-specific contributions and have furthered our general understanding of important behavioural processes in freshwater biology, including: contributions to our understanding of the ultimate causes of diel migrations, advances in our understanding of the contribution of animal personality in shaping the spatial ecology of fishes, and improvements in our understanding of the role of thermal habitat selection in the winter phenology of fishes. The thesis has provided a detailed account of the relevance of the above findings to conservation, management and policy, at both a species-specific and a wider ecological scale. In addition to the findings and implications associated with the data chapters, the review chapter synthesised the knowledge gained from existing literature, to significantly advance our understanding of the relationship between hydropower and burbot ecology. Finally, this thesis has highlighted many interesting remaining questions regarding the behavioural ecology of burbot, and has identified several key research areas with good potential for furthering our understanding of; the proximate and ultimate causes of diel migrations, the role of animal personality in partial migrations, the physiological and behavioural correlates and consequences of spatial behavioural syndromes, the fitness consequences of thermal habitat selection, and the impacts of hydropower on a fascinating winter-specialist diel-migrating species.

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