

SEASONAL THERMAL HABITAT USE AND BATHYMETRIC DISTRIBUTION OF  
BURBOT IN TANADA AND COPPER LAKES, ALASKA

By

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## Abstract

Burbot *Lota lota* are a cold water, benthic, primarily piscivorous species that inhabits lakes and rivers throughout their Holarctic distribution. Habitat requirements for Burbot are still poorly understood, in part due to the disregard this species has received in fisheries management plans. From June 2009 through September 2011, I investigated the seasonal movements and bathymetric distribution of Burbot in Tanada and Copper lakes, Alaska, using archival tags programmed to record water depth and temperature. One hundred and forty Burbot (70 in each lake) were surgically implanted with archival tags, and 1 year later fish were recaptured to retrieve the archived data (Tanada Lake: 15 fish; Copper Lake: 9 fish). During the ice-out period in spring (mid-May through June), Burbot initiated a migration to the littoral zone (mean depth = 10.72 m; mean internal temperature = 9.4°C). In the summer months (July and August) when lakes were stratified and photoperiod was nearly constant, Burbot occupied the thermocline (mean depth = 7.28 m; mean internal temperature = 12.1°C). During fall months prior to the ice-up period (September and October), occupancy depth shifted to the profundal zone (mean depth = 22.09 m; mean internal temperature = 6.3°C). Under the ice, Burbot remained in the profundal zone and a putative spawning period was observed during February and March when Burbot from both lakes migrated from the profundal zone to  $\leq 5$  m in depth (mean internal temperature = 2.1°C). Throughout the year Burbot displayed a pattern of diel vertical movements with activity levels peaking during crepuscular hours. However, during the summer when photoperiod was nearly constant, Burbot were relatively sedentary, with only 22% of depth records indicating movement (changes in depth  $\geq 1$  m). Results from this study indicate that photoperiod and water temperature were highly correlated with seasonal depth occupancy and activity levels in Burbot.



## Table of Contents

	Page
Title Page .....	i
Abstract .....	iii
Table of Contents .....	v
List of Figures .....	vii
List of Tables .....	ix
List of Appendices .....	ix
Acknowledgements .....	xi
General Introduction .....	1
Chapter 1 .....	9
Introduction .....	9
Study Site .....	12
Methods .....	14
Fish capture .....	14
Archival Tags .....	16
Development of Thermal Profiles .....	16
Data Analyses .....	17
Results .....	19
Recapture Summary .....	19
Thermal Habitat Use and Depth Selection .....	21
Diel Vertical Movements .....	30
Discussion .....	34
Conclusion .....	40
Literature Cited .....	41
Appendices .....	49



## List of Figures

	Page
Figure 1. Copper and Tanada Lakes, located within the upper Copper River drainage in southcentral Alaska. ....	13
Figure 2. Thermal profiles (top panels) and mean daily depths (bottom panels) $\pm$ 95% confidence interval (shaded area) of recaptured Burbot from (a) Tanada and (b) Copper lakes. ....	22
Figure 3. Burbot migrations from the profundal zone to the littoral zone over two 10-day periods from (a) 20-30 June 2010 in Tanada Lake (fish 1821) and (b) 10-20 June 2010 in Copper Lake (fish 1995). ....	27
Figure 4. Mean internal temperature (THU) $\pm$ 95% confidence interval (shaded area) for recaptured Burbot in (a) Tanada Lake and (b) Copper Lake, along with available water temperatures (isoclines). ....	28
Figure 5. Burbot migrations from the littoral zone to the profundal zone over two 10-day periods from (a) 1-10 September 2009 in Tanada Lake (fish 1779) and (b) 20-30 August 2010 in Copper Lake (fish 2063). ....	29
Figure 6. Hourly activity rates throughout the study period of recaptured Burbot in Tanada Lake (dotted line) and Copper Lake (solid line); bold flat line in each panel is the corresponding median length of the photoperiod for the month. ....	32
Figure 7. Mean hourly depth occupancy with 95% confidence interval (error bars) of recaptured Burbot from (a) Tanada Lake and (b) Copper Lake. ....	33



## List of Tables

	Page
Table 1. Archival tag deployment and retrieval summary from recaptured Burbot in Tanada and Copper lakes (2009-2011).....	20
Table 2. Archival tag output summary from recaptured Burbot in Copper and Tanada lakes (2009-2011).....	23
Table 3. Monthly activity rates in recaptured Burbot from Tanada and Copper lakes, Alaska (2009-2011).....	31

## List of Appendices

	Page
Appendix A. Mean depth and internal body temperature of recaptured Burbot from Tanada Lake. ....	49
Appendix B. Mean depth and internal body temperature of recaptured Burbot from Copper Lake. ....	50
Appendix C. IACUC Approval.....	51





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## General Introduction

Burbot *Lota lota* have a Holarctic distribution and reside exclusively in freshwater environments (McPhail and Lindsey 1970; Stapanian et al. 2010). Throughout their geographic distribution, Burbot inhabit the large, cold water rivers and lakes within north temperate regions (McPhail and Paragamian 2000; Hofmann and Fischer 2002). Burbot are a cold water, benthic, primarily piscivorous species that prey on invertebrates and other fishes. Characterized as poor swimmers, Burbot are ambush predators that feed primarily at low light levels (Scott and Crossman 1973; Boyer et al. 1989). Similar to their marine gadid relatives, Burbot have high fecundity and spawn between November and May, typically under the ice in water temperatures from 0 to 4°C (Scott and Crossman 1973).

Throughout their life cycle, lacustrine Burbot are known to utilize several different habitat types (Breeser et al. 1988; Hofmann and Fischer 2002). Classified as photo-sensitive, larval Burbot in the large lakes of the Northern Hemisphere hatch between March and May and almost immediately begin to prey on zooplankton in the pelagic zone, with the type and size of their prey increasing with body size (Clady 1976; Ghan and Sprules 1993; McPhail and Paragamian 2000; Probst and Eckmann 2009). As schooling, pelagic predators for the first two to three months of life, larval Burbot undergo diel vertical movements (DVM) corresponding to crepuscular periods of the day, presumably to follow migrating zooplankton (Fischer 2004; Miler and Fischer 2004). Larval Burbot transition to the juvenile stage during their first summer, with amplitudes of DVMs increasing with body size and increasing pigmentation density (Girsa 1972; McPhail and Paragamian 2000; Probst and Eckmann 2009; Donner and Eckmann 2011).

By the end of their first summer, a second ontogenetic habitat shift occurs as juvenile Burbot transition from the pelagic zone to benthic habitats of the littoral zone (Scott and Crossman 1973; Wang and Appenzeller 1998; Fischer 1999, 2004; Miler and Fischer 2004). Once in the littoral zone, juvenile Burbot become photo-negative and exhibit an increase in negative buoyancy (Donner and Eckmann 2011). The littoral zone offers several advantages for growth and survival of juvenile Burbot. Warmer water temperatures allow juveniles to optimize growth and food intake (Hofmann and Fischer 2003), and rocks and boulders provide cover under which they hide during the day (Boag 1989). During this life stage, Burbot shift to nocturnal foraging, with peak activity rates coinciding with invertebrate emergence from the substrate at dawn and dusk (Fischer 2004).

Upon reaching maturity between ages 3 and 7, Burbot undergo a final habitat shift, moving from the littoral to the profundal zone (Scott and Crossman 1973; Evenson 2000; Pääkkönen 2000; Hofmann and Fischer 2002). As adults, Burbot are voracious predators and can consume up to 30% of their own body mass per feeding event (Pääkkönen and Marjomäki 1997). Although their diet is typically dominated by fish, Burbot display seasonal variations in diet, with the consumption of invertebrates common during summer months (Lawler 1963; Rudstam et al. 1995; Pääkkönen 2000). The optimization of both foraging activity and growth has been strongly correlated with water temperature, and the profundal zone of large lakes often provides that preferred range of temperatures, particularly during summer months following lake stratification (Carl 1992; Edsall et al. 1993).

The observed proclivity of adult Burbot for deeper habitats, particularly during summer months, is that their physiological performance is maximized at cold water temperatures. The pumping capacity of the Burbot heart and food intake have been shown to decline with

increasing water temperature, while both oxygen consumption and gastric evacuation rates increased (Pääkkönen and Marjomäki 1997, 2000; Tiitu and Vornanen 2002; Pääkkönen et al. 2003). The most recent temperature preferendum estimated for adult Burbot was 14.2°C (Hofmann and Fischer 2002), which supported the observations of Pääkkönen and Marjomäki (2000) that maximum relative daily food intake occurred at 14.4°C. Despite their preference for cold water temperatures, there are several instances where Burbot have been observed at temperatures > 20°C (Carl 1995). However, at temperatures of 23.4–25°C, Burbot experienced their maximum oxygen consumption, potentially resulting in harmful effects on their metabolism and aerobic performance (Pääkkönen and Marjomäki 2000; Pääkkönen et al. 2003). For Burbot to tolerate warmer water, they must down regulate their metabolism, resulting in lower food consumption and reduced energy expenditures (Hardewig et al. 2004). Given the physiological responses of Burbot to warm water, particularly in summer, it is not surprising that much of the existing data has shown that this species is commonly found in cooler waters at deeper depths, and that warming water temperature trends have resulted in declines in abundance and range.

Extensive research has been conducted on Burbot residing in North American lakes, with the initial focus related to their decline in the Great lakes region due to Sea Lamprey *Petromyzon marinus* predation. In lakes Michigan, Huron, and Ontario, Burbot abundance declined dramatically from 1930 to 1960, but rebounded in the late 1980s after the implementation of the Sea Lamprey control program (Christie 1973; Wells and McLain 1973; Stapanian et al. 2006). In many Great Lakes studies, Burbot were commonly found at depths  $\geq 23$  m at water temperatures that of 8–13°C (Bailey 1972; Edsall et al. 1993). More recent research has shifted to the management of declining Burbot populations in the northwestern United States and Canada as populations began to decline in response to hydroelectric structures that manipulated

the flow and thermal regimes of lakes and rivers (Paragamian et al. 2000, 2005; Paragamian and Wakkinen 2008). In the Kootenai River, Idaho, and Kootenay River and Kootenay Lake, British Columbia, Canada, Burbot populations declined after the construction of Libby Dam (Paragamian et al. 2000). Both increased winter flow rates ( $\sim 500$  versus  $200 \text{ cm} \cdot \text{s}^{-1}$ ) and increased winter water temperatures ( $4^\circ$  versus  $1^\circ\text{C}$ ) in the Kootenai River resulted in deleterious effects on the spawning success and survival of Burbot (McPhail 1997; Paragamian et al. 2000, 2005). Despite a complete closure of the fishery in 1992, Burbot stocks have yet to rebound, and current rehabilitation efforts have focused on regulating winter flow rates and providing a colder winter thermal habitat regime (Paragamian and Wakkinen 2008). Similar impacts to Burbot populations from dam construction have also been documented in Wyoming; for example, winter water drawdowns in Bull Lake resulted in a reduction in spawning substrate that reduced reproductive success (Hubert et al. 2008). In the Tongue River, Burbot were completely extirpated after construction of Tongue River Reservoir in Montana (Eiserman 1964; Bergersen 1993). In contrast to these studies that have documented habitat limitations, some Alaskan Burbot fisheries have also been reduced with overfishing appearing to be the primary causal mechanism (Parker et al. 1989; Lafferty et al. 1990, 1991, 1992; Bernard et al. 1993).

The Copper River drainage, located in Southcentral Alaska, supports numerous lacustrine Burbot populations that have provided up to 30% of the reported statewide harvest of Burbot (Mills 1986). During the 1970s and 1980s Burbot harvest in the Copper River drainage increased to over 9,000 fish per year (Schwanke and McCormick 2010). In 1985 alone, the annual statewide harvest survey reported a total harvest of 27,230 Burbot, with 22,015 fish coming from southcentral Alaska (Mills 1986). Due to concerns of overharvest, a stock assessment program was initiated by the Alaska Department of Fish and Game (ADF&G) to

monitor population abundance and determine sustainable harvest levels. Baited hoop traps set for 48 hours were the primary method of gear used to capture Burbot (Bernard et al. 1991). Because Burbot are physoclistous, sampling of fish from depths  $> 10$  m have complications due to physiological effects associated with decompression trauma (i.e., barotrauma; Bruesewitz et al. 1993; Neufield and Spence 2004). After recording Burbot mortality that ranged from 67 to 95% due to sampling, the ADF&G limited sampling depths to  $\leq 15$  m (Bernard et al. 1993). Under that criterion, many Alaskan lakes had large sections unavailable to sampling due to their bathymetry. However, observations from this stock assessment program and from other studies examining Burbot movements have found that at certain times of the year Burbot actively occupy the littoral zone and are not strictly confined to profundal habitats (Lafferty et al. 1991; Bernard et al. 1993; Carl 1995; Harrison et al. 2013; Cott et al. 2015).

Spring and fall water temperatures in the littoral zones of lakes provide favorable conditions for Burbot food consumption and growth (Hofmann and Fischer 2003). During those periods, catch rates of Burbot sampled from depths  $\leq 15$  m were approximately two times greater than catch rates during the intervening summer months (Bernard et al. 1993). Considered a night active species during summer months, Burbot utilize shallow, warm littoral habitats during spring and fall, and descend to become sedentary in deeper, cooler profundal waters during the day (Müller 1973; Fischer 2004; Harrison et al. 2013; Cott et al. 2015). As apex predators within the majority of the systems they occupy, this behavior suggests an adaptation to temporal variations in foraging efficiency (Løkkeborg 1998; Løkkeborg et al. 2000). In contrast to the increase in foraging efficiency within the littoral zone, migrations into deeper waters during the day are considered a bioenergetic adaptation. This is termed a “hunt warm, rest cool” strategy and this adaptation has been documented in both Atlantic Cod *Gadus morhua* and Spiny Dogfish



*Squalus acanthias* that were found to use DVMs to increase bioenergetic efficiency by reducing their metabolism in nonfeeding hours (Clark and Green 1991; Sims et al. 2006). This same behavior pattern was recently documented in a Burbot study in Kinbasket Reservoir, British Columbia, Canada, where fish were documented occupying different water temperature gradients between day and night habitat uses (Harrison et al. 2013). The effectiveness of this strategy diminishes in mid-summer as both photoperiod and water temperatures within the littoral zone increase and, resulting in a reduction in activity and a migration to the profundal zone (Bernard et al. 1993; Carl 1995; Cott et al. 2015).

Once Burbot have moved into the profundal zone, they are no longer available to non-lethal sampling and, with the exception of their winter spawning movements, little is known about their habitat use outside of the spring and fall sampling events. Previous studies in lakes and rivers used various types of telemetry tags to investigate Burbot movement patterns. However, sample sizes were often small and the number of relocations per fish was limited by water depth or the number of receiving devices (Bergersen et al. 1993; Carl 1995; Paragamian and Wakkinen 2008). Radio signals can only be consistently detected at depths  $\leq 5$  m (Dunnigan and Sinclair 2008) and acoustic tags rely on fish swimming within close proximity of the tracking device (e.g., a hydrophone). In the Kootenai River, Idaho-British Columbia, 66 Burbot were radio tagged from 1996–2003, but only 11 fish provided data, with observations of 29–182 relocations per fish (Paragamian and Wakkinen 2008). In a more recent investigation of Burbot movements in the Kinbasket Reservoir, British Columbia, Canada, 75 Burbot were radio tagged over 2010–2012; however, despite deploying 42 hydrophones, only 8% of the reservoir had acoustic coverage (Harrison et al. 2013). A similar study conducted in 2013 used acoustic tags to follow four Burbot over a three-month period that were tagged in Alexie Lake in the

Northwest Territories, Canada (Cott et al. 2015). Although both of these studies increased our understanding of Burbot movements and habitat selection, they both relied on statistical modelling. Despite efforts that have been put forth to evaluate Burbot habitat selection and movements, each tag type has unique limitations depending on where and how it is used to collect data.

The development of archival tags has addressed some of these limitations. The advantage of archival tags is that they are able to internally record uninterrupted temperature and depth data for extended periods of time, up to multiple years depending on the tag. Since the data are stored internally, retrieval of the tag and/or fish is necessary. The requirement for tag recovery potentially results in fewer fish that provide data; however, low sample sizes are offset by the high resolution of the data provided by the tag. Archival tags that collected ambient water temperature and depth measurements every minute for 135 to 155 days were used elucidate seasonal migrations in Pacific Halibut *Hippoglossus stenolepis* (n = 8; Seitz et. al. 2003). Diurnal vertical movements from nine Atka Mackerel *Pleurogrammus monopterygius* were evaluated using archival tag data, with results indicating that current stock-assessment methods using bottom trawls may not provide accurate estimates given observed movement patterns (Nichol and Somerton 2002). Although few fish were included in both of these studies, the volume and quality of the data provided new and significant insights on fish behavior.

The objective of my study was to describe the thermal habitat, seasonal occupancy depth, and temporal activity patterns of Burbot within Tanada and Copper lakes, Alaska. To accomplish this objective, Burbot were tagged with archival tags at depths ranging from 1 to

30 m. These detailed observations will provide new and meaningful insights into their life history and temporal habitat use for both fisheries researchers and managers.

## Chapter 1

### Introduction

Burbot *Lota lota* have a Holarctic distribution and reside exclusively in freshwater environments (McPhail and Lindsey 1970; Stapanian et al. 2010). Throughout their geographic distribution, Burbot exist in both riverine and lacustrine forms and inhabit the large, cold water rivers and lakes within north temperate regions (McPhail and Paragamian 2000; Hofmann and Fischer 2002). Burbot are a cold water, benthic, primarily piscivorous species that prey on invertebrates and other fishes. Characterized as poor swimmers, Burbot are ambush predators that feed primarily at low light levels (Scott and Crossman 1973; Boyer et al. 1989). Similar to their marine gadid relatives, Burbot have high fecundity and spawn between November and May, typically under the ice in water temperatures of 0–4°C (Scott and Crossman 1973).

Throughout much of their range adult Burbot are typically associated with the profundal zone of lakes where cold water temperatures, particularly in the summer months, maximize their physiological processes (Scott and Crossman 1973; Carl 1992; Edsall et al. 1993; Pääkkönen and Marjomäki 1997, 2000; Hofmann and Fischer 2002; Pääkkönen et al. 2003). In the more northern latitudes, however, cooler thermal regimes in lakes result in the distribution of Burbot across all depths (Bernard et al. 1993). Spring and fall water temperatures in the littoral zones of lakes provide favorable conditions for Burbot food consumption and growth (Hofmann and Fischer 2003). Considered a night active species during summer months, Burbot utilize diel vertical movements (DVMs) foraging in shallow, warm littoral habitats during spring and fall, and descend to become sedentary in deeper, cooler profundal waters during the day (Müller 1973; Fischer 2004; Harrison et al. 2013; Cott et al. 2015).

The DVM pattern is a common strategy used by aquatic organisms. The typical pattern involved with DVMs is to migrate into warm, food-rich waters during the evening, followed by a movement to the cold hypolimnion during the day (Lampert 1989; Mehner et al. 2007). General hypotheses proposed to explain the adaptive significance of DVMs include bioenergetic efficiency, foraging opportunity, and predator avoidance (Scheuerell and Schindler 2003). The bioenergetic efficiency hypothesis suggests that an individual will select a thermal habitat that maximizes growth by foraging in warm water and then migrating into colder water to reduce metabolic costs (Wurtsbaugh and Neverman 1988; Bevelhimer and Adams 1993). The foraging opportunity hypothesis predicts that predators, to maximize foraging and growth, will closely track their prey, as was observed in Lake Superior when Lake Trout *Salvelinus namaycush* were found to track the DVMs of Ciscoes *Coregonus artedii* (Levy 1990; Jensen et al. 2006). As suggested by the name, the predator avoidance hypothesis states that prey conduct daily vertical movements in response to predators (Clark and Levy 1988; Scheuerell and Schindler 2003). Although the majority of research that has explored the biological advantages of DVMs has focused on pelagic organisms such as zooplankton, pelagic planktivores, and pelagic piscivores (Clark and Levy 1988; Scheuerell and Schindler 2003; Jensen et al. 2006), recent investigations have explored the advantages of a DVM strategy in benthic predators (Sims et al. 2006; Harrison et al. 2013; Cott et al. 2015).

Diel vertical movements in apex predators suggest an adaptation to temporal variations in foraging efficiency (Løkkeborg 1998; Løkkeborg et al. 2000). In contrast to the increase in foraging efficiency within the littoral zone, migrations into deeper waters during the day are considered a bioenergetic adaptation. This is termed a “hunt warm, rest cool” strategy and has been documented in both Atlantic Cod *Gadus morhua* and Spiny Dogfish *Squalus acanthias* that

were found to use DVMs to increase bioenergetic efficiency by reducing their metabolism in nonfeeding hours (Clark and Green 1991; Sims et al. 2006). This same behavior pattern was recently documented in Burbot studies conducted in Kinbasket Reservoir, British Columbia, and Alexie Lake Northwest Territories, Canada, where fish were documented occupying different water temperature gradients between day and night habitat uses (Harrison et al. 2013). The effectiveness of this strategy diminishes in mid-summer as both photoperiod and water temperatures within the littoral zone increase, resulting in a reduction in activity and a migration to the profundal zone (Bernard et al. 1993; Carl 1995; Cott et al. 2015).

Once Burbot have moved into the profundal zone, they are no longer available to non-lethal sampling and, with the exception of their winter spawning movements, little is known about their habitat use outside of the spring and fall sampling events. Previous studies in lakes and rivers used both acoustic and radio tags to investigate Burbot movement patterns and habitat selection. However, sample sizes were often small and the number of relocations per fish was limited by water depth or the number of receiving devices (Bergersen et al. 1993; Carl 1995; Paragamian and Wakkinen 2008). Signals from radio tags can only be consistently detected at depths  $\leq 5$  m (Dunnigan and Sinclair 2008) and acoustic tags rely on fish swimming within close proximity of the tracking device (e.g., a hydrophone). Despite efforts that have been put forth to evaluate Burbot habitat selection and movements, each tag type has unique limitations depending on where and how they are used to collect data; however, the development of archival tags has addressed some of these limitations. An advantage of archival tags is that they are able to internally record uninterrupted temperature and depth data for extended periods of time, up to multiple years depending on the tag. Since the data are stored internally, retrieval of the tag and/or fish is necessary. The requirement for tag retrieval potentially results in fewer fish that

provide data; however, low sample sizes are offset by the high resolution of the data that the tag provides.

The objective of my study was to describe the thermal habitat, seasonal occupancy depth, and temporal activity patterns of Burbot in Tanada and Copper lakes, Alaska. To accomplish this objective, Burbot were tagged with archival tags at depths ranging from 1 to 30 m. These detailed observations will provide new and meaningful insights into their life history and temporal habitat use for both fisheries researchers and managers.

### **Study Site**

Tanada and Copper lakes are located in the Wrangell-St. Elias National Park and Preserve (WRST) within the upper Copper River drainage (Figure 1). Classified as oligotrophic lakes, both lakes are fed by seasonal streams that originate in the nearby mountains and have outlets that drain into the upper Copper River. Tanada Lake is approximately 1,100 ha in surface area and has a maximum depth of 52 m, while Copper Lake is 730 ha in surface area and has a maximum depth of 72 m. Tanada Lake also supports Lake Trout, Arctic Grayling *Thymallus arcticus*, Sockeye Salmon *Oncorhynchus nerka*, Longnose Sucker *Catostomus catostomus*, Round Whitefish *Prosopium cylindraceum*, and Slimy Sculpin *Cottus cognatus*. Copper lake supports the same species assemblage as Tanada Lake, with the addition of the non-anadromous form of Sockeye Salmon (Kokanee).

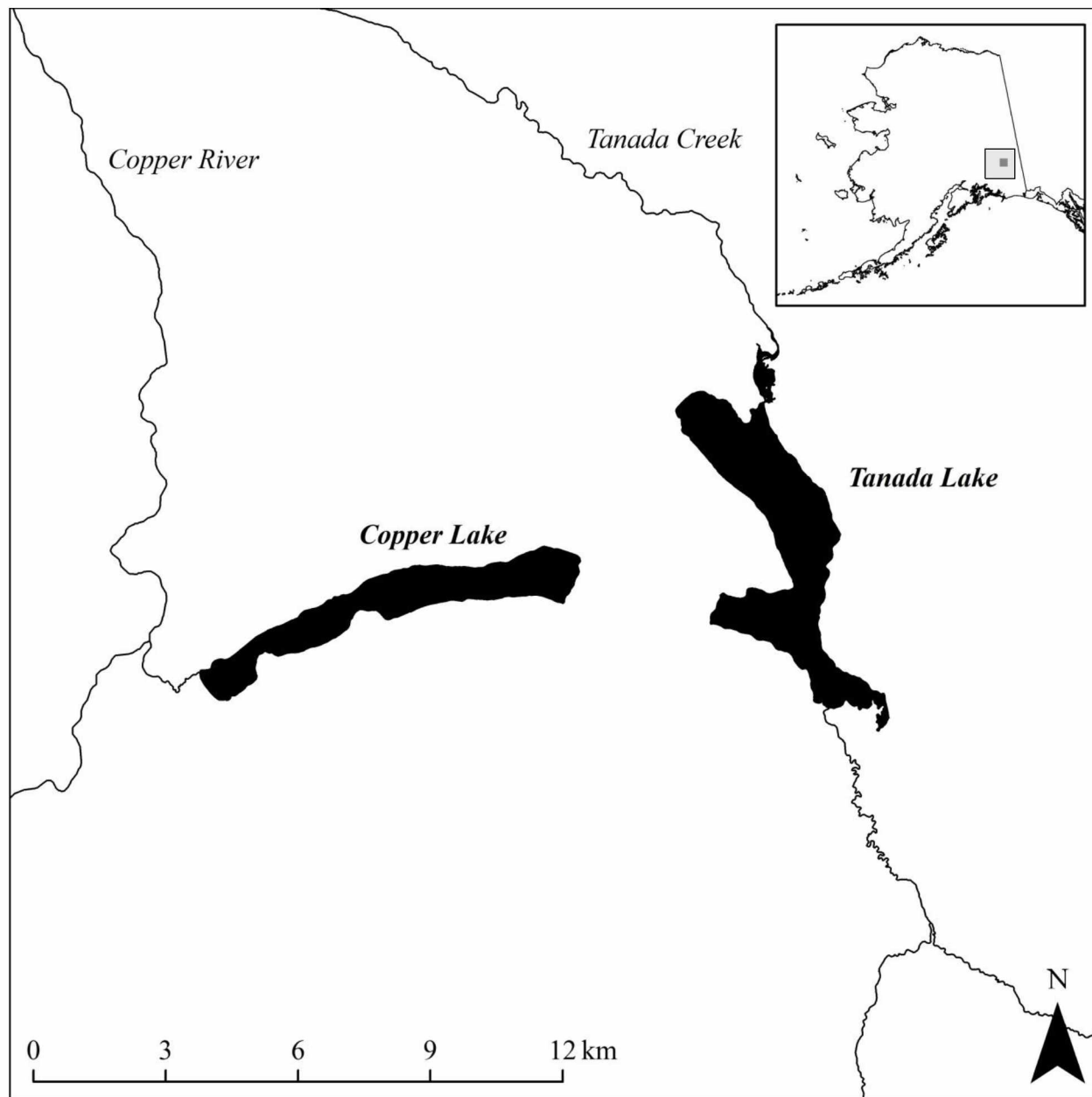


Figure 1. Copper and Tanada Lakes, located within the upper Copper River drainage in southcentral Alaska. The shaded box in the State of Alaska insert contains the Copper River drainage and location of study lakes.



## Methods

### *Fish capture*

Burbot were captured and tagged in Tanada Lake from 30 June 2009 through 14 July 2009 and in Copper Lake from 14 June 2010 through 5 July 2010. In both lakes, Burbot were captured in baited hoop traps with 25-mm mesh netting set on the bottom as described in Bernard et al. (1991). Hoop traps were 3 m long and consisted of seven metal rings that slowly tapered in diameter from 61 cm at the trap entrance to 46 cm at the cod end. Each hoop trap was baited with containers of frozen Pacific Herring *Clupea pallasii*. All hoop traps were identified by a numbered buoy attached to the cod end, and traps soaked for 48 hours (two net nights).

Although hoop traps are typically not set at depths  $> 15$  to avoid barotrauma-induced mortality that can occur for Burbot captured at greater depths (Bernard et al. 1993), the current study aimed to determine seasonal occupancy depths of Burbot, which required the collection of fish from depths up to 30 m. Barotrauma for Burbot from hoop traps set at depths  $> 15$  m was avoided by using a one-step decompression stop (Neufeld and Spence 2004). A barotrauma stop involved retrieving hoop traps to an intermediate depth of 10 m for at least six hours before being retrieved to the surface. Both lakes had depths  $> 30$  m, but hoop traps were not set at deeper depths because multiple decompression stops would have been required to prevent barotrauma.

Archival tags (Model Lat1400, 128k version; Lotek Wireless Fish and Wildlife Monitoring, New Brunswick, Canada) were surgically implanted into 140 Burbot (70 per lake). Tags were cylindrical in shape, 11 mm in diameter, 35 mm in length, and weighed 2 g in water. Each archival tag was programmed to record barometric pressure and internal fish body

temperature every 15 minutes for 469 days, at which point recording stopped and all data collected up to that point remained stored within the tag. The resolution of both internal fish body temperature and barometric pressure were reduced from the maximum of 12 to 10 bits to extend tag longevity. Based on Lotek specifications, pressure accuracy was  $\pm 1\%$  and since 1dBar = 1 m, tags were accurate to 1 cm. Temperature accuracy was no greater than 0.2°C.

The same surgical procedure was used for both lakes. Once fish were selected for tagging, they were moved from a freshwater sampling tub to another tub where they were anesthetized in a clove oil solution at a concentration of 60 mg·L<sup>-1</sup> (Anderson et al. 1997; Peake 1998). Archival tags were surgically implanted in the abdomen through an incision made along the centerline of the abdomen where it was widest and approximately 4 cm anterior to the vent (Breeser et al. 1988; M. Evenson, ADF&G, personal communication). Fish were measured for total length (TL) to the nearest 1 mm and released at the surface in the same location they were captured.

In both lakes, fishing effort focused on the even distribution of tags by location, water depth (m), and Burbot TL (50-mm TL increments; 350–800 mm). In Tanada Lake, 35 tags were implanted in Burbot captured at shallow depths (0–15 m) and 35 tags were implanted in fish captured at deep depths (20–30 m). In Copper Lake, the final distribution of tags resulted in 31 tags deployed in Burbot at shallow depths (0–15 m) and 39 tags deployed in fish at deeper depths (20–30 m). Recapture efforts for Burbot in Tanada Lake took place from 21 June through 9 July 2010 and during 5–21 September 2010, while recapture efforts in Copper Lake occurred during 7–23 September 2011. To maximize tag recoveries, greater sampling effort was allocated to locations of each lake that had previously, supported higher densities of Burbot based on prior sampling event catch rates. All recaptured fish were euthanized, measured for TL (nearest 1

mm), sexed, stomach contents were analyzed, and otoliths were removed for age estimation using the break-and-burn method as described in Christensen (1964).

### *Archival Tags*

Archival tag data from recaptured Burbot were downloaded and reformatted into Excel spreadsheets. Each 15-minute archival tag record contained a date/time stamp, barometric pressure readings (dBar) that were converted to depth (1 dBar = 1 m), and internal body temperature (°C). Barometric pressure drift beyond Lotek specifications ( $> \pm 1\%$ ) was analyzed by comparing the barometric pressure at tag deployment to the barometric pressure at tag retrieval. Given that both measurements were recorded at the surface and should be identical, barometric pressure drift was determined to be negligible in both lakes.

### *Development of Thermal Profiles*

To characterize the available thermal habitat for Burbot transects of 10 Hobo temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) were programmed to record water temperature each hour at specified depths. Three vertical transects were placed within the deepest ( $\geq 50$  m) basins of each lake at the beginning of the Burbot tagging events. Loggers were placed at the surface and depths of 1.5, 3, 5, 10, 15, 20, 25, 30, and 50 m. Transects remained under the ice during winter and were not retrieved until after the last Burbot recapture event was completed in each lake. Water temperature data from the loggers were matched to individual fish according to the corresponding depth, internal body temperature, date, and time.

## *Data Analyses*

Data analyses focused on occupancy depth, thermal habitat use, and activity patterns for Burbot throughout four periods (i.e., ice-out, ice-free, ice-up, and the ice-cover periods). The ice-out period corresponded to mid-May through June, and consisted of the time frame when both water temperature and photoperiod began to increase. July and August were the ice-free period which was defined as the period at which both lakes were thermally stratified. The ice-up period was September and October when surface water began to cool, and the ice-cover period was November through mid-May, during this period both lakes were isothermal. For explanatory purposes, the ice-cover period was further divided to examine behavior during the pre-spawn, spawn, and post-spawn periods. Temporal thermal habitat use (THU), depth distribution, and activity rates for Burbot in each lake were examined using data from both archival tags and temperature loggers. Thermal habitat use was plotted by averaging the hourly mean internal temperature for each Burbot relative to the available water temperatures among all available depths. The analysis of THU focused on July and August when water temperatures were highest, which offered the greatest suite of thermal regimes among depth strata. June and September were excluded from THU analysis because in June the lakes were often still ice-covered (or waters were just beginning to warm) and September is when they began to cool and turnover. Daily changes in internal body temperature were analyzed using a two-tailed Student's t-test, which compared the internal body temperature of fish at noon to the internal body temperature at midnight. During the remainder of the year (October through May), both lakes were isothermal and fish occupied cold water temperatures, regardless of depth. Descriptive statistical analyses (i.e., means, ranges, and medians) were conducted to summarize THU among recaptured fish.

Temporal thermal regimes, photoperiod, lake characteristics (i.e., thermocline formation), dissolved oxygen levels, and life-history traits (i.e., spawning movements) were all assumed to

contribute to the seasonal depth distribution of Burbot (Scott and Crossman 1973; Bernard et al. 1993; McPhail and Paragamian 2000; Harrison et al. 2013; Cott et al. 2015). To relate these determinants to seasonal migration patterns, the mean daily depth for all recaptured Burbot were combined and plotted, this plot was presented along with the annual water temperature profiles created from the temperature loggers. Depth and internal temperature occupancy graphs for each recaptured fish were generated to compare individual fish behavior and evaluate deviations from the overall trends. Historical limnological data from Tanada and Copper lakes that had been collected previously by the National Park Service were used to estimate seasonal changes in dissolved oxygen with depth. The published data, along with depth profiles indicating shallow depth occupancy consistent with spawning behavior, were also used to predict the winter spawning period. Changes in depth by Burbot due to one or more of the aforementioned factors were evaluated based on extent of vertical movements. Brief movements were defined by Burbot moving up or down in the water column on a daily basis and then returning to the same approximate depth, while significant movements were considered a migration and resulted in a prolonged change in occupancy depth (i.e., migration from the littoral to the profundal zone).

Vertical movements (consecutive depths  $\geq 1$  m apart) were used to estimate seasonal movement patterns and daily activity rates of Burbot. Time frames that indicated increased activity were further analyzed to describe environmental cues (i.e., photoperiod, changes in water temperature, time of day) that potentially triggered this increase in activity by Burbot. For each month, the proportion of active fish and occupancy depths were plotted hourly (24 hours) and compared to determine daily peak activity among months. Photoperiod data for these analyses was recorded by the United States Naval Observatory Astronomical Applications Department in Gakona, Alaska, which is located 97 km west of the study area.

## Results

### *Recapture Summary*

Fifteen tagged Burbot were recaptured from Tanada Lake, with nine fish captured during the spring recapture event in 2009 (18 June–03 July) and five fish captured during the fall event (02–23 September; Table 1). One fish was caught by a sport angler in February 2009. Six of the recaptured fish were caught in deep trap nets, and the remaining eight fish were captured in shallow trap nets. The tag recovered by the sport angler was categorized as a deep capture based on the last recorded depth record for that fish. For all recaptured tags, six Burbot were tagged at deep locations and recaptured in shallow traps, three fish were tagged in shallow traps and recaptured at deep locations, and the remaining six fish were tagged and recaptured at their original capture depth. Fourteen of the recaptured fish were mature females and the sex of the one fish captured by the sport angler was unknown. Absolute growth ranged from 9 to 70 mm TL (mean = 50.21 mm), and the estimated ages of Burbot ranged from 7 to 17 years (mean = age 9). Time at large ranged from 237 to 444 days and, on average, the archival tag for each fish contained 36,000 archival records (range = 22,782–42,649).

Eight tagged Burbot were recaptured from Copper Lake during one recapture event in fall 2011 (10–22 September) and one was caught by a sport angler in April 2012 (Table 1). Two recaptured fish that were tagged at deep locations were recaptured in shallow traps, one fish that was tagged from a shallow trap was recaptured at a deep location, and five fish were tagged and

Table 1. Archival tag deployment and retrieval summary from recaptured Burbot in Tanada and Copper lakes (2009-2011).

Tag	Date		Days at Large	Depth (m)		Length (mm)		Growth (mm)	Sex	Age
	Capture	Recapture		Capture	Recapture	Capture	Recapture			
<b>Tanada Lake</b>										
1821	6/30/09	9/14/10	441	2	9	440	510	70	Female	8
1766	6/30/09	6/26/10	361	6	6	815	824	9	Female	17
1828	7/1/09	6/26/10	360	9	13	539	566	27	Female	10
1756	7/1/09	9/19/10	444	9	15	460	500	40	Female	7
1780	7/2/09	6/26/10	359	9	26	531	540	9	Female	9
1755*	7/3/09	2/25/10	237	7	1	631	Unknown	Unknown	Unknown	Unknown
1758	7/3/09	6/23/10	357	21	10	550	575	25	Female	9
1779	7/3/09	6/23/10	355	22	3	475	488	13	Female	6
1803	7/3/09	6/23/10	355	23	10	565	574	9	Female	9
1788	7/3/09	9/14/10	438	6	10	466	535	69	Female	8
1800	7/3/09	9/14/10	438	28	9	546	580	34	Female	Unknown
1817	7/4/09	6/22/10	353	17	13	485	505	20	Female	7
1824	7/4/09	6/23/10	354	6	28	556	567	11	Female	11
1790	7/4/09	9/12/10	435	20	10	580	612	32	Female	7
1794	7/5/09	6/24/10	354	9	26	615	662	47	Female	13
<b>Copper Lake</b>										
1995	6/9/10	9/18/11	466	28	14	460	485	25	Male	Unknown
2224	6/9/10	9/13/11	461	15	15	820	850	20	Female	18
2063	6/11/10	9/12/11	462	27	26	394	415	21	Male	5
2023	6/16/10	9/16/11	456	20	23	375	395	20	Male	6
2014	6/16/10	9/15/11	456	21	30	654	755	101	Female	11
2024	6/18/10	9/13/11	452	23	12	442	480	38	Male	8
2001	6/18/10	9/12/11	451	23	22	435	485	50	Male	7
2096	6/19/10	9/20/11	454	15	19	347	355	8	Female	5
2048	6/21/10	Unknown	Unknown	24	Unknown	400	Unknown	Unknown	Unknown	Unknown

\* Tags 1775 from Tanada Lake and 2048 from Copper Lake were both turned in by sport fishermen without additional biological information.

recaptured at their original capture depth. Three fish were females, five fish were males, and the sex of the fish captured by the sort angler is unknown. Absolute growth ranged from 8 to 101 mm TL (mean = 35 mm), and estimated ages ranged from 5 to 18 years (mean = age 9). The time at large ranged from 451 to 466 days and, on average, each tag contained 44,000 archival records (range = 43,268–44,714).

### *Thermal Habitat Use and Depth Selection*

Temporal vertical migrations and occupancy depths of Burbot in Tanada and Copper lakes corresponded to water temperature (Figure 2). The first major migration that resulted in a change in occupancy depth occurred at the onset of the ice-out period, which was when both water temperature and photoperiod increased. Following the ice-out period when lakes were thermally stratified and photoperiod was near constant, there was little to no change in occupancy depth, with Burbot primarily occupying the littoral zone. Prior to the onset of the ice-up period when water surface temperatures began to cool, Burbot began migrating from the littoral zone back to the profundal zone. Under isothermal conditions during the ice-cover period, Burbot were observed residing at intermediate occupancy depths until ascending back to the littoral zone during the putative spawning period from February through March, after which fish returned to the profundal zone.

In Tanada Lake, all recaptured Burbot showed variations in their movements throughout the year and had internal temperatures that ranged from 0 to 18.5°C (mean = 4.6°C; Table 2). During the ice-out period, the average daily occupancy depth was 8.63 m (SE = 0.10 m; range = 0–51 m), and the mean internal temperature of fish during this period was 9.4°C (SE = 0.10°C).



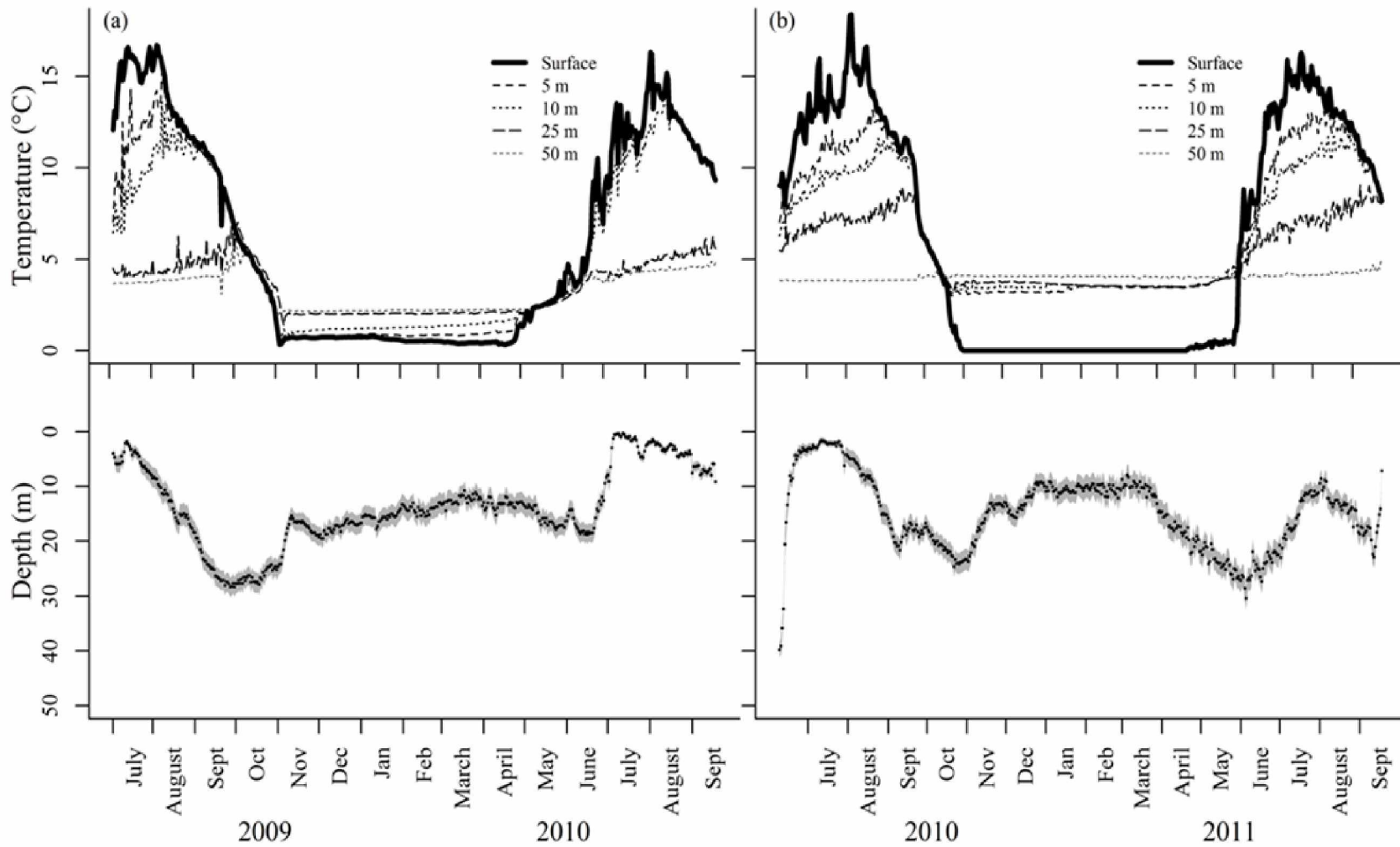


Figure 2. Thermal profiles (top panels) and mean daily depths (bottom panels)  $\pm$  95% confidence interval (shaded area) of recaptured Burbot from (a) Tanada and (b) Copper lakes.

Table 2. Archival tag output summary from recaptured Burbot in Copper and Tanada lakes (2009-2011).

Tag	Archival Records	Depth (m)			Temperature (°C)		
		Minimum	Maximum	Mean (SD)	Minimum	Maximum	Mean (SD)
<b>Tanada Lake</b>							
1821	42,348	0	52	22.71 (12.34)	2.0	18.4	5.1 (4.1)
1766	34,630	0	37	2.49 (4.13)	0	16.6	4.5 (4.8)
1828	34,533	0	43	7.35 (7.32)	0.1	16.5	4.3 (4.0)
1756	42,649	0	51	13.05 (15.62)	0.1	17.6	4.3 (4.1)
1780	34,484	0	41	21.62 (7.67)	0.6	17.7	3.7 (3.1)
1755	22,782	0	52	12.06 (9.13)	0.5	17.8	5.3 (4.8)
1758	34,237	0	31	7.81 (6.98)	0.4	18.1	4.42(4.1)
1779	34,063	0	52	19.53 (13.17)	1.4	18.3	4.6 (4.1)
1803	34,072	0	52	22.71 (11.71)	0.1	17.8	4.5 (4.2)
1788	42,046	0	48	20.03 (11.63)	1.8	18.5	5.5 (4.5)
1800	42,041	0	41	8.29 (7.10)	0	18.0	5.4 (4.5)
1817	33,888	0	42	13.27 (10.68)	0	17.0	4.0 (4.0)
1824	34,013	0	31	12.94 (8.05)	0.2	18.0	4.2 (4.2)
1790	41,741	0	48	25.73 (6.98)	0.1	17.8	5.20 (4.5)
1794	33,993	0	48	25.73 (10.87)	1.5	17.6	4.10(3.7)
<b>Copper Lake</b>							
1995	44,714	0	64	28.53 (20.3)	3.4	16.2	6.2 (3.7)
2224	44,251	0	48	12.88 (11.59)	0.1	18.5	5.5 (3.7)
2063	44,330	0	57	18.71 (14.35)	0	16.5	5.3 (3.4)
2023	44,121	0	62	17.4 (17.31)	0	17.5	5.6(3.6)
2014	43,780	0	41	8.53 (10.50)	0.1	17.8	7.4 (4.2)
2024	43,363	0	58	15.51 (13.85)	0	17.5	5.6 (3.5)
2001	43,286	1	68	25.51 (19.17)	3.1	15.0	5.9 (3.3)
2096	43,542	0	51	13.91 (12.48)	0	15.5	5.3 (3.0)
2048	43,368	0	48	12.88 (12.73)	0	18.1	4.9 (4.1)

Burbot remained in the littoral zone for the entire ice-free period, where their mean daily occupancy depth was 5.70 m (SE = 0.06 m; range = 0–55 m) and the mean internal temperature of fish increased to 12.6°C (SE = 0.02°C). In September during the ice-up period, 14 of the 15 Burbot migrated to back the profundal zone, with one fish (tag 1766) remaining at a shallow occupancy depth. The mean daily occupancy depth during this period was 24.39 m (SE = 0.08 m; range = 0–56 m), and the mean internal temperature of fish was 6.0°C (SE = 0.02°C). Under isothermal conditions during the ice-cover period, recaptured Burbot displayed a variety of occupancy depths. Although initially present within the profundal zone, 80% of the Burbot were observed occupying shallow occupancy depths during the putative spawning season (February–March), while the remaining fish remained at deeper occupancy depths. The mean daily occupancy depth for the entire ice-cover period was 17.15 m (SE = 0.06 m; range = 0–50 m), and the mean internal temperature of fish was 1.5°C (SE = 0.002°C). A description of the annual average occupancy depth and internal body temperature for individual fish is provided in Appendix A.

Similar to Tanada Lake, recaptured Burbot from Copper Lake displayed variations in their movements throughout the year and had internal temperatures that ranged from 0.02–18.48°C (mean = 6.01°C; Table 2). During the ice-out period, the average daily occupancy depth was 12.80 m (SE = 0.13 m; range = 0–60 m), and the mean internal temperature of fish during this period was 9.5°C (SE = 0.03°C). Burbot remained in the littoral zone for the entire ice-free period, where their mean daily occupancy depth was 8.85 m (SE = 0.08 m; range = 0–57 m) and the mean internal temperature of fish increased to 11.5°C (SE = 0.03°C). In September during the ice-up period, all recaptured Burbot migrated back to the profundal zone, except one fish (tag 2048) that only remained there briefly before returning to a shallow occupancy depth.

The mean daily occupancy depth during this period was to 19.78 m (SE = 0.10 m; range = 0–55 m), and the mean internal temperature of fish was 6.6°C (SE = 0.02°C). Under isothermal conditions during the ice-cover period, 78% of Burbot returned to the littoral zone and remained there until after the putative spawning event. However, Burbot with tag numbers 1995 and 2001 either remained deep or at intermediate depths relative to the other fish. The mean daily occupancy depth for the entire ice-cover period was 13.15 m (SE = 0.09 m; range = 0–58 m), and the mean internal temperature of fish was 2.6°C (SE = 0.01°C). A description of the annual average occupancy depth and internal body temperature for individual fish is provided in Appendix B.

The transition of Burbot between occupancy depths during the spring ice-out period varied between lakes. In Tanada Lake, this transition occurred through a progressive increase in the amplitude of DVMs that resulted in a gradual change in depth over time (Figure 3a). In contrast, this shift in occupancy depth was abrupt in the majority of instances in Copper Lake, with fish migrating from the profundal zone to the littoral zone within a few hours (Figure 3b). Once the migration was complete, Burbot were found residing primarily in the littoral zone where activity levels were lower and DVMs dampened in amplitude.

Both Tanada and Copper lakes were stratified in July and August; as a result, internal temperature data from recaptured Burbot were used to determine thermal habitat use (THU) and occupancy depth. Thermal habitat use of Burbot between Tanada and Copper lakes indicated that recaptured fish did not display a significant difference in their internal temperatures from July through August ( $t = 0.36$ ,  $P = 0.72$ ). In Tanada Lake, Burbot occupied depths between 3 and 10 m where water temperatures ranged from 5.1 to 16.0°C (Figure 4a). In Copper Lake, fish were located between the surface and 10 m in depth, but most commonly at 3 m where water

temperatures ranged from 9.8 to 14.5°C (mean = 12.6°C; Figure 4b). The observed occupancy depths and internal temperature records of Burbot indicated that fish were primarily found at the thermocline.

The second migration that resulted in a change in occupancy depth for Burbot occurred prior to the ice-up period when surface waters reached their maximum temperatures (18.3°C in Tanada Lake and 20.8°C in Copper Lake). Within both lakes, this migration occurred through a series of progressive DVMs that increased in amplitude with increasing depth. For example, over a 10-day period in early September 2009, fish 1779 from Tanada Lake migrated from an occupancy depth of 3 m on 01 September to 30 m on 10 September (Figure 5a). Likewise in Copper Lake, fish with tag number 2063 took 10 days in late August to migrate from a residency depth of 3 to 25 m (Figure 5b). Once in the profundal zone, Burbot remained in this area until the onset of the putative spawning period. Although it was not possible to determine if fish were spawning, fish behavior (reduction in occupancy depth and an increase in activity rates) and the published literature suggested that spawning events took place between early February to late March. During this period, 10 of the 15 fish from Tanada Lake migrated to  $\leq 5$  m in occupancy depth at water temperatures that ranged from 0 to 3.2°C (mean = 1.5°C). In Copper Lake, seven of the nine fish migrated to occupancy depths  $\leq 5$  m and resided at water temperatures that ranged from 0 to 4°C (mean = 2.6°C). Following the putative spawning event, fish returned to the profundal zone. The change in daily median occupancy depth from the spawning to the post-spawning period was from 8 to 13 m in Tanada Lake and 2 to 19 m in Copper Lake.

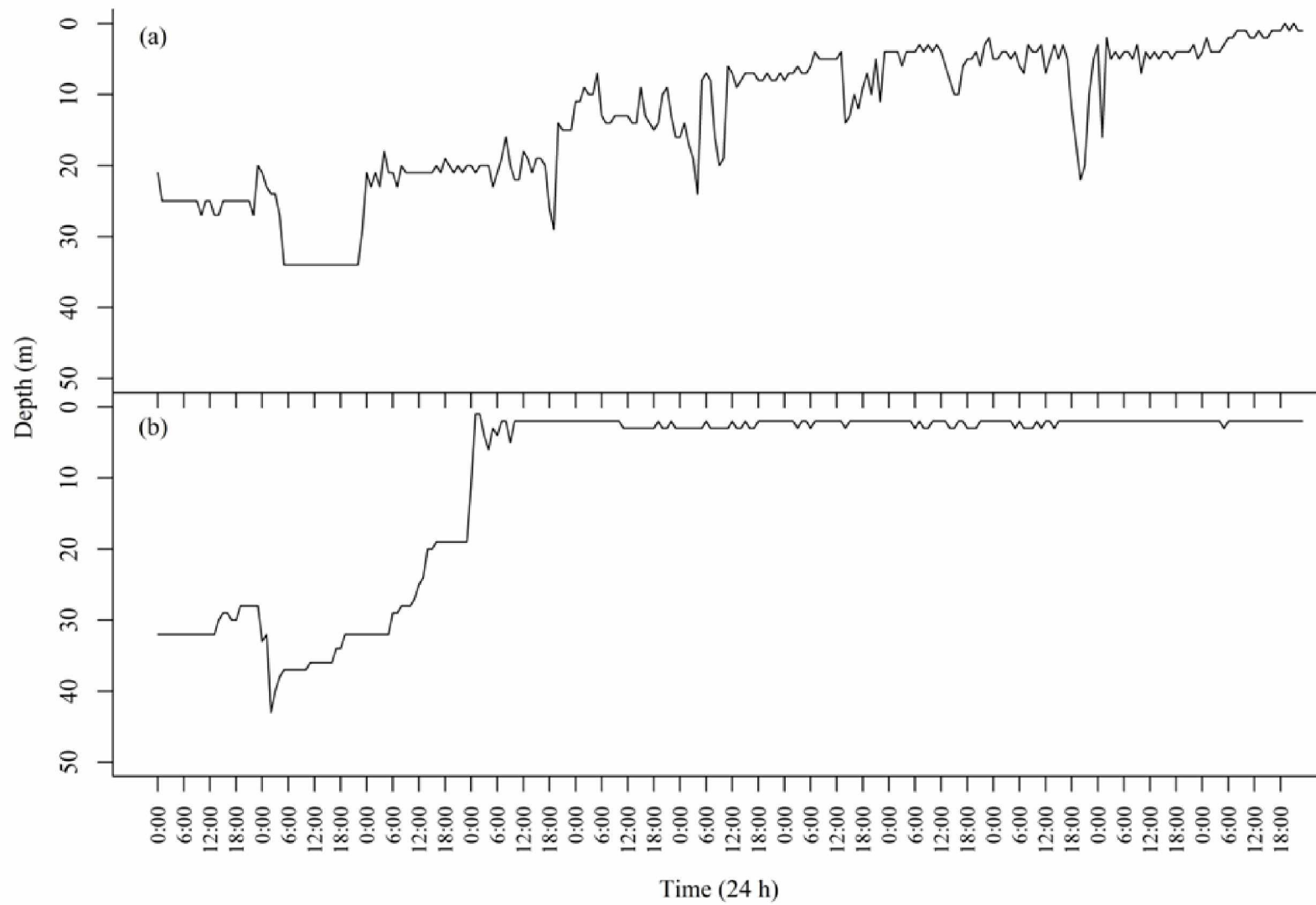


Figure 3. Burbot migrations from the profundal zone to the littoral zone over two 10-day periods from (a) 20-30 June 2010 in Tanada Lake (fish 1821) and (b) 10-20 June 2010 in Copper Lake (fish 1995).

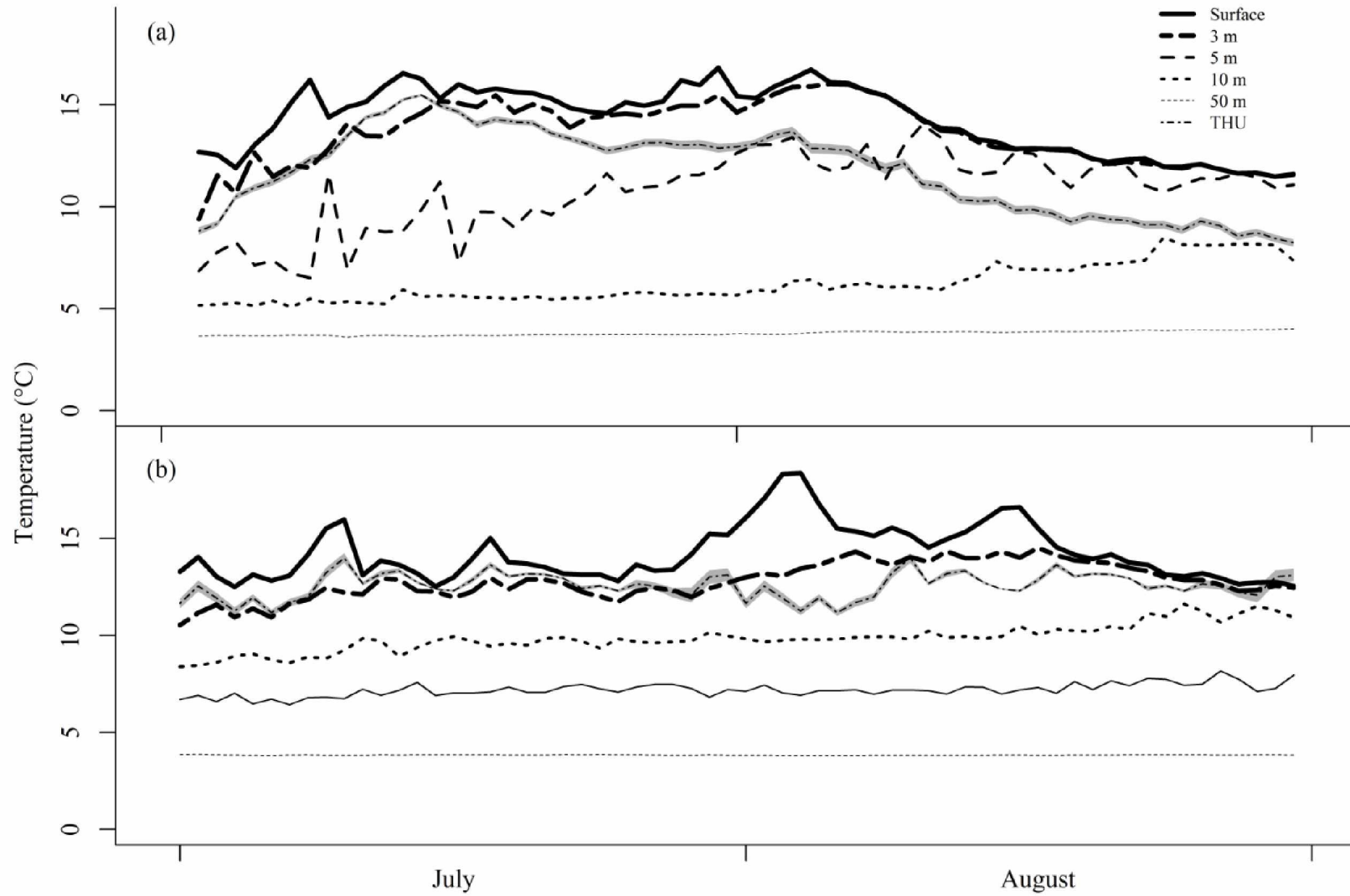


Figure 4. Mean internal temperature (THU)  $\pm$  95% confidence interval (shaded area) for recaptured Burbot in (a) Tanada Lake and (b) Copper Lake, along with available water temperatures (isoclines).

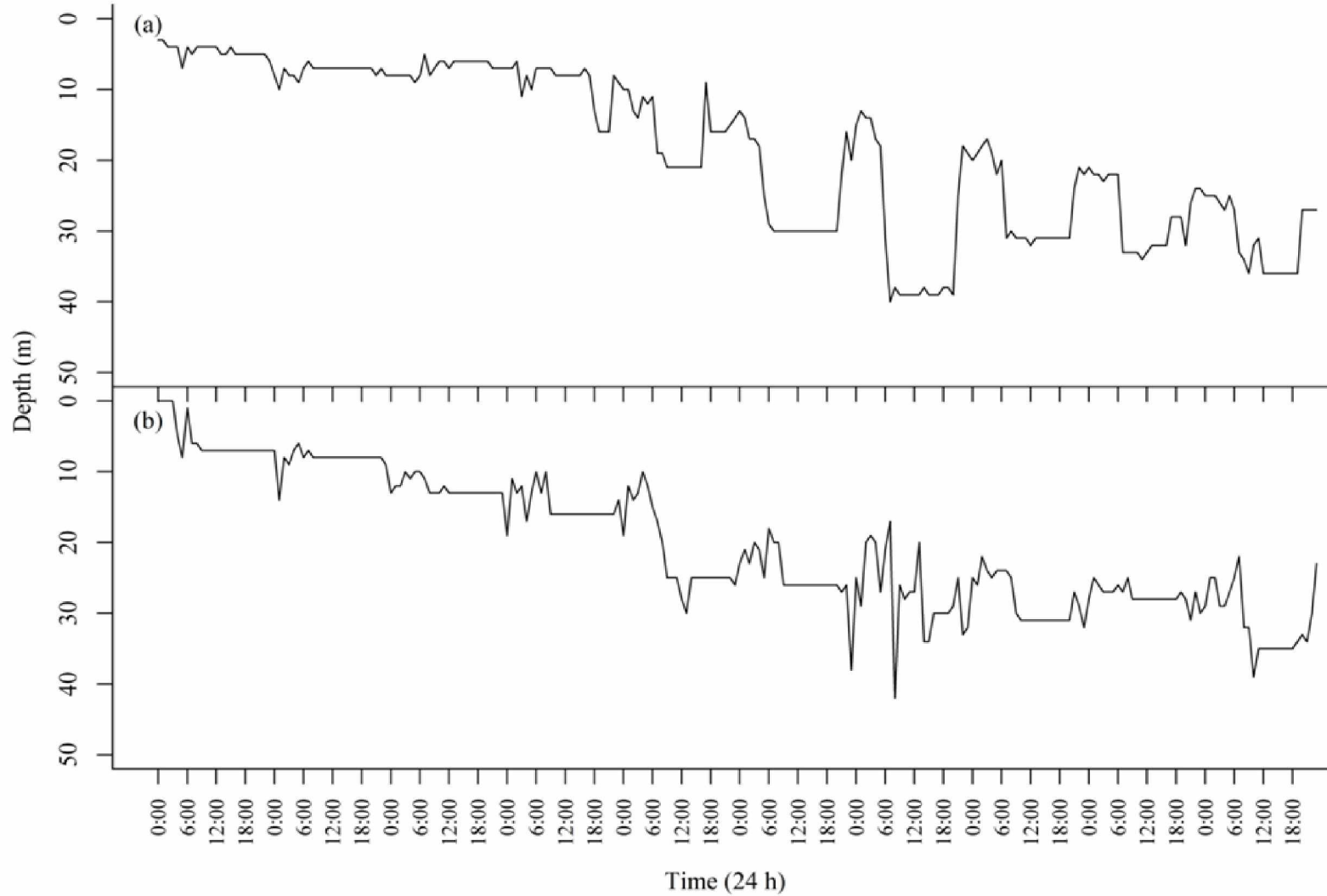


Figure 5. Burbot migrations from the littoral zone to the profundal zone over two 10-day periods from (a) 1-10 September 2009 in Tanada Lake (fish 1779) and (b) 20-30 August 2010 in Copper Lake (fish 2063).



### *Diel Vertical Movements*

The DVM rates of Burbot varied by month and time of day in both Tanada and Copper lakes (Table 3; Figure 6). The greatest DVM rates corresponded to seasonal migrations (i.e., ice-out and ice-up periods) that resulted in changes in occupancy depth. For instance, during the ice-out period in Tanada Lake, 34% of Burbot depth records in June indicated DVMs relative to 23% the previous month. In Copper Lake, the rate of DVMs were highest in both May (40%) and June (33%) relative to 28% in April. Throughout the year, DVMs consistently corresponded to the changing photoperiod, peaking during the dawn and dusk (crepuscular) periods of the day. For instance, during the ice-up period in October (the month with the greatest activity), DVMs within both Tanada and Copper lakes were greatest at 0800 and at 1700, which are times that corresponded to the onset of sunrise/sunset. The DVM rates declined but remained steady during the nocturnal period, while daylight hours contained the lowest DVM rates. During the ice-free period (when photoperiod was near constant), Burbot activity DVMs peaked at approximately 2400 hours.

Burbot occupancy depths associated with DVMs indicated that fish from both Tanada and Copper lakes occurred at shallow depths at night and deeper depths during the day (Figure 7a and b). The only exception to this pattern was during the ice-free period when, based on mean hourly occupancy depth, there was no change, suggesting that DVMs were short in amplitude and occurred throughout the day, likely due to the near constant daylight. Besides the ice-cover period when lakes were isothermal, DVMs resulted in a significant change in THU. In Tanada Lake, the mean daytime internal body temperature was  $8.6 \pm 0.2^{\circ}\text{C}$  and the nighttime internal body temperature was  $8.9 \pm 0.2^{\circ}\text{C}$  ( $z = -9.04, P < 0.001$ ). In Copper Lake, the mean

daytime internal body temperature was  $7.8 \pm 0.2^{\circ}\text{C}$  and the nighttime internal body temperature was  $8.1 \pm 0.2^{\circ}\text{C}$  ( $z = -8.71$ ,  $P < 0.001$ ).

Table 3. Monthly activity rates in recaptured Burbot from Tanada and Copper lakes, Alaska (2009-2011).

Month	Depth Records		Activity Rate (%)
	(n)	(n $\geq$ 1 m)	
<b>Tanada Lake</b>			
January	44,640	10,300	23.07
February	40,006	8,427	21.06
March	41,664	12,057	28.94
April	40,320	8,096	20.08
May	41,664	9,502	22.81
June	35,060	11,991	34.20
July	56,199	13,531	24.08
August	59,520	19,092	32.08
September	49,913	17,744	35.55
October	44,640	18,261	40.91
November	43,200	16,093	37.25
December	44,640	12,639	28.31
<b>Copper Lake</b>			
January	28,327	7,828	27.63
February	25,685	6,500	25.31
March	28,816	6,326	21.95
April	28,067	7,801	27.79
May	29,676	11,810	39.80
June	43,318	14,186	32.75
July	56,550	11,458	20.26
August	56,276	16,504	29.33
September	41,799	17,982	43.02
October	29,760	15,657	52.61
November	28,307	11,737	41.46
December	28,199	8,373	29.69

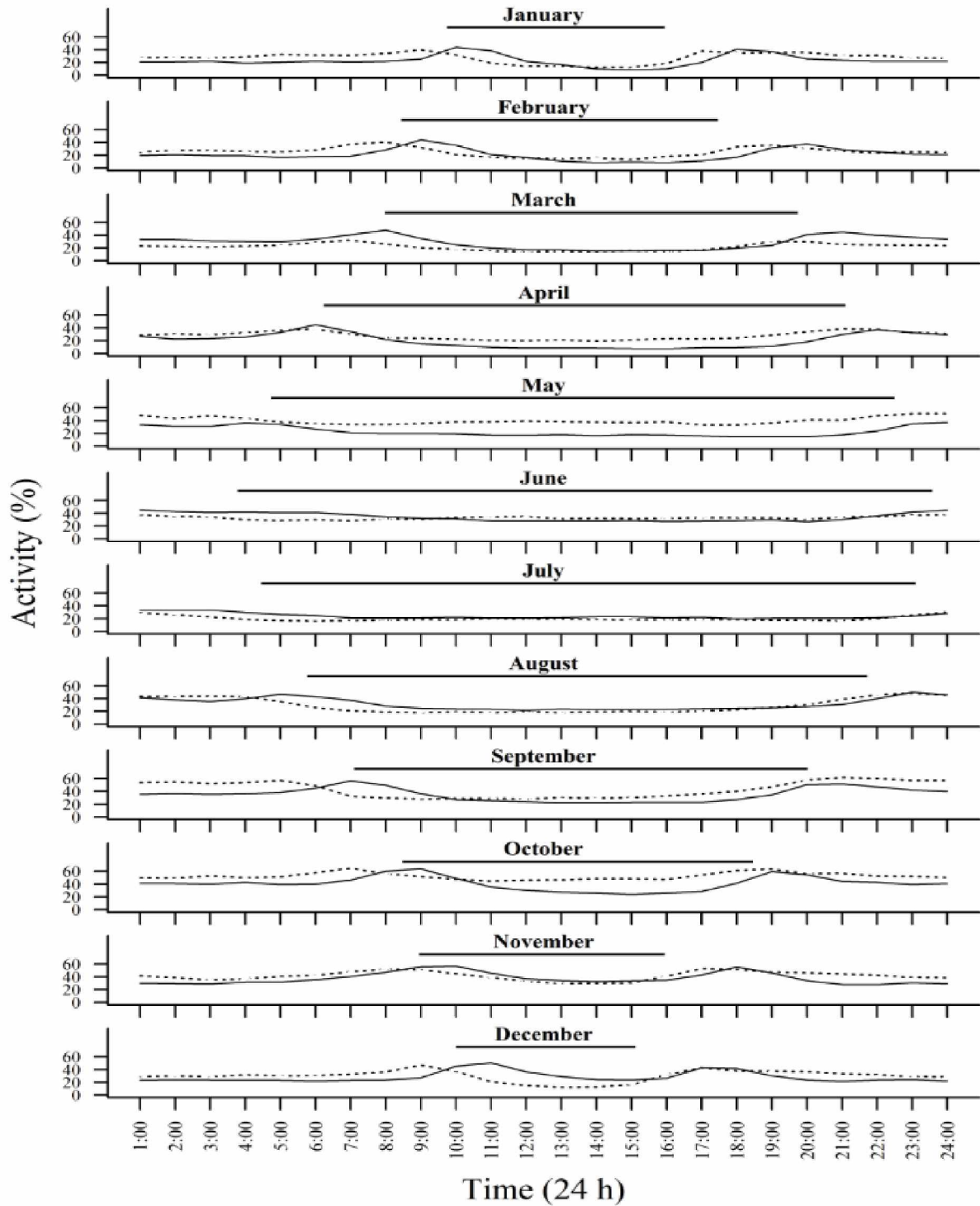


Figure 6. Hourly activity rates throughout the study period of recaptured Burbot in Tanada Lake (dotted line) and Copper Lake (solid line); bold flat lines correspond to median length of the photoperiod for the month.

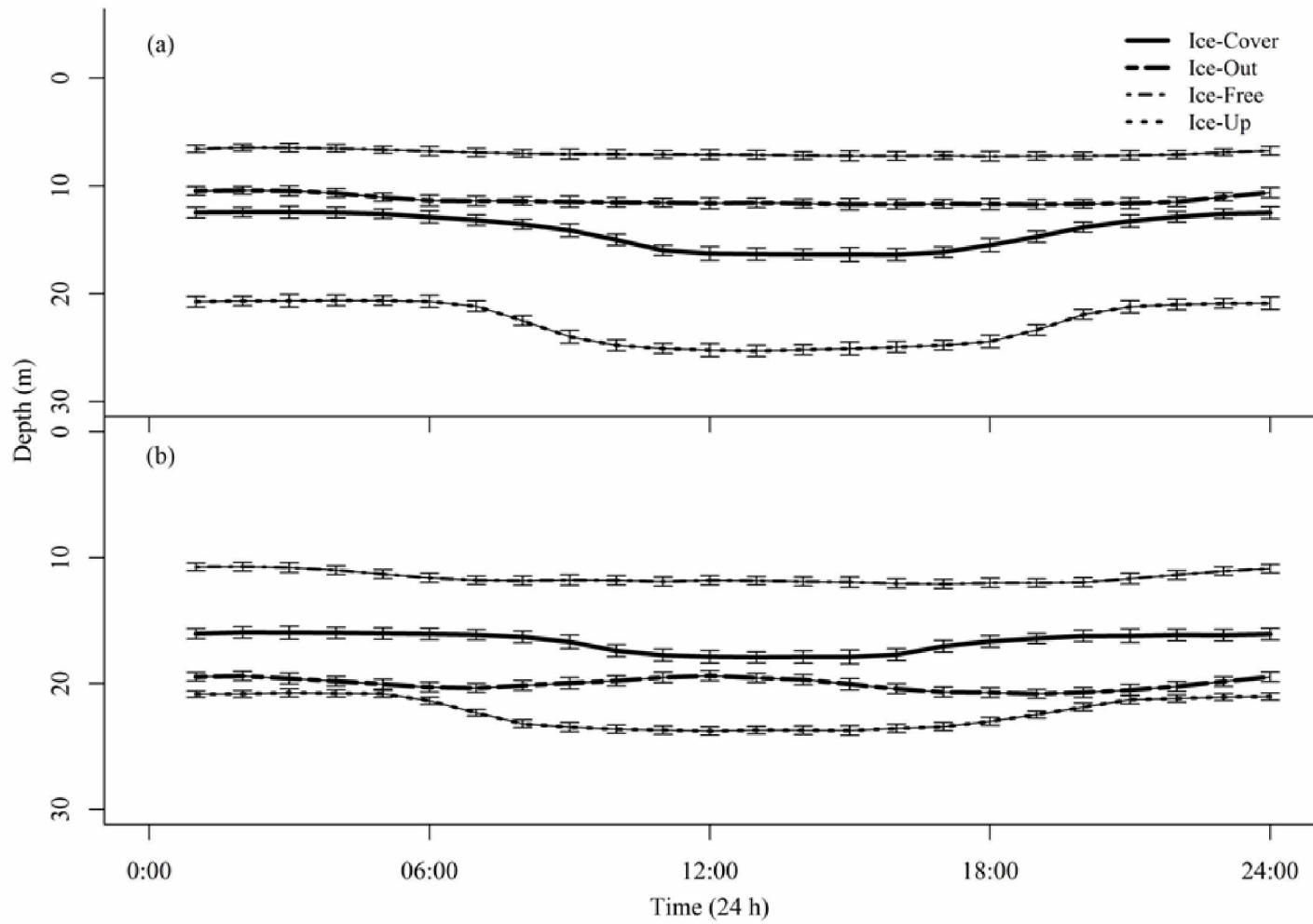


Figure 7. Mean hourly depth occupancy with 95% confidence interval (error bars) of recaptured Burbot from (a) Tanada Lake and (b) Copper Lake.

## Discussion

This study provides a detailed examination of the seasonal habitat use and DVMs of Burbot for a complete annual cycle. Burbot in Tanada and Copper lakes were largely sedentary, which is consistent with other studies conducted on this species and their marine relatives (Bergersen et al. 1993; Carl 1995; Løkkeborg et al. 2000; Neat et al. 2006). Generally speaking, Burbot were found in the littoral zone during the ice-out and ice-free periods, in the profundal zone during the ice-up period and at the onset of the ice-out period, and returned to the littoral zone again during late winter. On a finer temporal scale, DVMs corresponded to photoperiod and, despite the ice-free period when sunlight was nearly constant, Burbot were crepuscular year round. Given the benthic nature of Burbot, it was concluded that all movements follow basin bathymetry and Burbot were not migrating through the water column (Fischer 1999; McPhail and Paragamian 2000; Cott et al. 2015; Harrison et al. 2013). Based on previous studies conducted throughout North America and observations from this study it was assumed that seasonal depth preferences and DVMs were likely related to foraging success, bioenergetic efficiency, spawning, and dissolved oxygen levels (Lawler 1963; McPhail 1997; Chambers et al. 2000; Hofmann and Fischer 2002, 2003; Pääkkönen et al. 2003; Hardewig et al. 2004; Harrison et al. 2013; Cott et al. 2015).

During the spring ice-out period, fish migrated from the profundal to the littoral zone over a one-month period. This transitional period increased photoperiod and water temperature, both of which are known to trigger vertical migrations and increase activity levels of fish attempting to maximize foraging and growth by tracking prey that are also taking advantage of productive littoral habitat (TeWinkle and Fleischer 1999; Hofmann and Fischer 2003; Jensen et al. 2006). The DVMs corresponded with twilight hours, a timeframe that has been referred to as

an “anti-predation window” when both coregonids and salmonids (the predominant prey found in stomachs of recaptured Burbot; H. Scannell, UAF, unpublished data) moved to (dusk) and from (dawn) shallow water to forage at a time when predation risk from visual predators was low due to darkness (Clark and Levy 1988; Scheuerell and Schindler 2003; Mehner et al. 2007). Burbot are not visual predators and are considered nocturnal ambush predators; as a result, they are able to exploit this “anti-predation window” more effectively by taking advantage of fast-swimming prey that are adapted to visually recognize predators (Lawler 1963; Scott and Crossman 1973; Pääkkönen 2000).

In addition to prey availability, recent studies have indicated that Burbot may use DVMs to increase bioenergetic efficiency (Harrison et al. 2013; Cott et al. 2015). The current study supported the conclusion that Burbot were implementing a “hunt warm, rest cool strategy”, by remaining active in warmer waters at night but sedentary during the day in cooler water. This change in internal temperature was modest ( $\sim 0.3^{\circ}\text{C}$ ), and less than the  $0.9$  to  $1.2^{\circ}\text{C}$  range documented in Burbot from both the Kinbasket Reservoir in British Columbia (Harrison et al. 2013), and in Alexie Lake, Northwest Territories, Canada (Cott et al. 2015). However, this range was close to the  $0.4$  to  $0.9^{\circ}\text{C}$  gradient that resulted in a 4% reduction in the daily energy costs of benthic sharks (Sims et al. 2006).

The water temperatures that Burbot occupied during the ice-out period were less than the  $13.6$ – $14.4^{\circ}\text{C}$  temperature range at which maximum daily intake has been determined for this species (Pääkkönen and Marjomäki 2000). Thermal gradient experiments conducted on Burbot captured from Lake Constance, Germany, estimated a final temperature preferendum of  $14.2^{\circ}\text{C}$  and concluded that a temperature range of  $14$ – $18^{\circ}\text{C}$  optimized growth and food consumption (Hofmann and Fischer 2002). The disparity between those results and the results from the

current study may be explained by the geographical differences among study areas. Several Burbot studies examining thermal preferences have been conducted in laboratories or lakes at lower latitudes than Tanada and Copper lakes (Pääkkönen and Marjomäki 1997, 2000; Hofmann and Fischer 2002; 2003). Although Burbot from the current study migrated into water temperatures  $\geq 14^{\circ}\text{C}$ , it was a rare occurrence. Generally, this study found that the depth distribution and activity levels of Burbot occurring at water temperatures from  $2^{\circ}$  to  $12^{\circ}\text{C}$  were consistent with findings from other North American lakes (Hackney 1973; Kroneld 1976; Bernard et al. 1993; Carl 1995; Cott et al. 2015).

During the ice-free period, Burbot were mostly sedentary and associated exclusively with the thermocline instead of utilizing the colder waters of the profundal zone where metabolic costs would have been reduced (Carl 1995; Pääkkönen and Marjomäki 1997; Hofmann and Fischer 2003). This close association with the thermocline, a spatially limited area but a zone of significant interactions between predator and prey (Janssen and Brandt 1980), may reflect a change in foraging behavior. Previous studies have shown that Burbot make significant horizontal movements in lakes (Cott et al. 2015), movements that would not have been recorded by archival tags that record temperature and pressure. Horizontal movements, if significant enough, would likely still be recorded by hoop trap catch rates but would not explain why there was a 50% reduction in catches during this period (Bernard et al. 1993). A more plausible explanation is that due to the near constant photoperiod, the nocturnal hunting advantage of Burbot became diminished due to the near constant photoperiod, resulting in a shift in the forage base. During summer months, invertebrates often become an important component of the Burbot diet and given the higher energy obtained from this prey type, Burbot were able to consume less prey, resulting in a decrease in observed activity (Rudstam et al. 1995; Pääkkönen et al. 2003).

To highlight this difference in energy content among prey types, a study in Finland that examined Burbot bioenergetics found that Opossum Shrimp *Mysis relicta* had almost double the lipid content of Vendace *Coregonus albula* (7.0 versus 3.6%, respectively; Pääkkönen et al. 2003).

By the end of August, Burbot activity levels in the current study increased and DVM patterns reemerged in the presence of a decreasing photoperiod and cooler water temperatures. Given that the photoperiod during the ice-up period was similar to the ice-out period, Burbot behavior followed similar DVM patterns and fish remained within the littoral zone as has been observed by Hofmann and Fischer (2003). However, as surface waters reached their maximum temperature (~18°C), fish began to migrate to the profundal zone in late August. Fish that are adapted to colder water temperatures typically have an overall lower critical thermal maximum and, once that limit is met, activity is triggered resulting in fish migrating out of warm water (Hofmann and Fischer 2002; 2003). Additionally, limnological events (i.e., algal blooms, mixing, and turnover) likely resulted in a dispersal of Burbot prey from the littoral zone where they were congregated in spring and summer. If so, foraging efficiency would be reduced, and a migration to the colder waters of the profundal zone would have allowed Burbot to optimize growth rates due to a reduction in metabolic costs and gastric evacuation rates (Pääkkönen and Marjomäki 1997; Hofmann and Fischer 2003; Wilhaber and Lamberson 2004). Although it is unknown what ultimately triggered the migration, Burbot activity levels peaked during this period. Given that the majority of fish from both lakes made the same migration, it was clear that they preferred the benthic habitat of the profundal zone.

The observed increase in activity during fall months has been documented throughout their North American range and corresponds with water temperatures (< 5°C) in which Burbot



have been reported as having their greatest activity (Carl 1995; Paragamian and Wakkinen 2008). Burbot metabolism is well adapted to low water temperatures, and by remaining active at these temperatures, a compensatory increase in metabolic activity enables them to support simultaneous somatic growth and gonad maturation (Pääkkönen and Marjomäki 1997; Hardewig et al. 2004; Cott et al. 2015). Under the isothermal conditions of the profundal zone, activity peaked during crepuscular hours, suggesting that DVMs were not solely related to bioenergetic efficiency. More specifically, this observation was noted in British Columbia, Canada, where Burbot from a reservoir continued DVMs during winter when there was no difference in thermal regime. Based on activity rates and the availability of prey (i.e., coregonids and salmonids) that also conduct DVMs during this period, it was concluded that DVMs were likely related to foraging efficiency (Steinhart and Wurtsbaugh 1999; Hrabik et al. 2006; Neat et al. 2006; Mehner et al. 2007; Harrison et al. 2013). This strategy has been observed in other marine benthic species. For instance, Atlantic Cod and Ling *Molva molva*, both marine gadid relatives of Burbot, have been documented utilizing DVMs to increase their probability of finding prey during this same timeframe (Løkkeborg 1998; Løkkeborg et al. 2000; Neat et al. 2006). The majority of Burbot from both lakes remained within the profundal zone throughout much of the fall until early to mid-winter when fish showed a reduction in activity and migrated to shallower waters.

Beginning in early winter under isothermal conditions, there was a progressive shift in Burbot activity levels and residency depth as fish migrated from the profundal zone. It has been documented in northern latitudes that Burbot were primarily active during the day in winter and did not switch to nocturnal activity until April (Müller 1973; Kroneld 1976). I found that DVMs during this period continued to coincide with crepuscular periods despite the likelihood that

declining photoperiod and increasing ice-cover inhibited sunlight penetration. As winter progressed, there was a noticeable reduction in activity from October to January when activity rates declined in both lakes. It is not known exactly why these reductions occurred, but it may be related to the onset of spawning that is known to occur between December and March (Lawler 1963; Breeser et al. 1988; Evenson 2000; McPhail and Paragamian 2000).

In February and March, Burbot from Tanada and Copper lakes resided at depths (2–13 m deep) and water temperatures (0–4°C), both of which are consistent with previously described spawning conditions (Lawler 1963; Becker 1983; Boag 1989; McPhail and Paragamian 2000). Although it is believed that spawning took place when Burbot were residing at shallow depths, it is likely that there may have been additional factors (i.e., low dissolved oxygen levels) that prolonged their occupancy at this shallow depth beyond the estimated two to three week spawning period (Boag 1989; Evenson 2000). The acute intolerance of Burbot to low dissolved oxygen can be classified as sensitive (acute limit = 2 mg·L<sup>-1</sup>), and dissolved oxygen levels ≤ 6 mg·L<sup>-1</sup> may extend the spawning period of Burbot by up to five weeks (Chambers et al. 2000). Both lakes experienced seasonal dissolved oxygen depletions at deeper depths (M. McCormick, Wrangell-St. Elias National Park and Preserve, unpublished data). Seasonal dissolved oxygen levels approaching 2 mg·L<sup>-1</sup> were only occasionally recorded in Tanada Lake at depths approaching 50 m, close to the maximum depth of the lake. Copper Lake, however, had dissolved oxygen levels approaching 2 mg·L<sup>-1</sup> from 60 m in depth in the summer and fall 2007 to 25 m in depth in April 2010. If these dissolved oxygen levels are consistent annually, they may play an important role in determining the winter depth occupancy.

## Conclusion

This study provides clear evidence that water temperatures influenced seasonal occupancy depth selection and photoperiod influenced seasonal DVMs for Burbot. These influences need to be considered by fisheries managers in developing effective sampling protocols because study designs rely on attaining representative samples of sufficient sizes. For example, data from Tanada and Copper lakes identified that the spring ice-out period was the optimal period for sampling while adhering to protocols that restrict gear to depths  $\leq 15$  m needed to avoid decompression trauma (Bernard et al. 1993). During this period, all tagged Burbot were actively foraging (i.e., DVMs were at a seasonal maximum), which would maximize capture probabilities in baited hoop traps for the entire population. Although fish were available to sampling during the ice-free period, the reduced activity levels may result in poor capture probabilities. During the ice-up period, catch rates in Alaskan lakes generally increase again (Bernard 1993); however, in both Tanada and Copper lakes, a portion of fish resided deeper than 15 m effectively resulting in a zero probability of capture (i.e., non-random sampling) under ADF&G protocols. This observation contrasts with other studies that indicated that Burbot are equally available in spring and fall (Bernard et al. 1991; 1993). Therefore, the current study demonstrates that by monitoring environmental variables (i.e., water temperature, photoperiod, dissolved oxygen levels), fishery managers can identify optimal sampling periods for Burbot.

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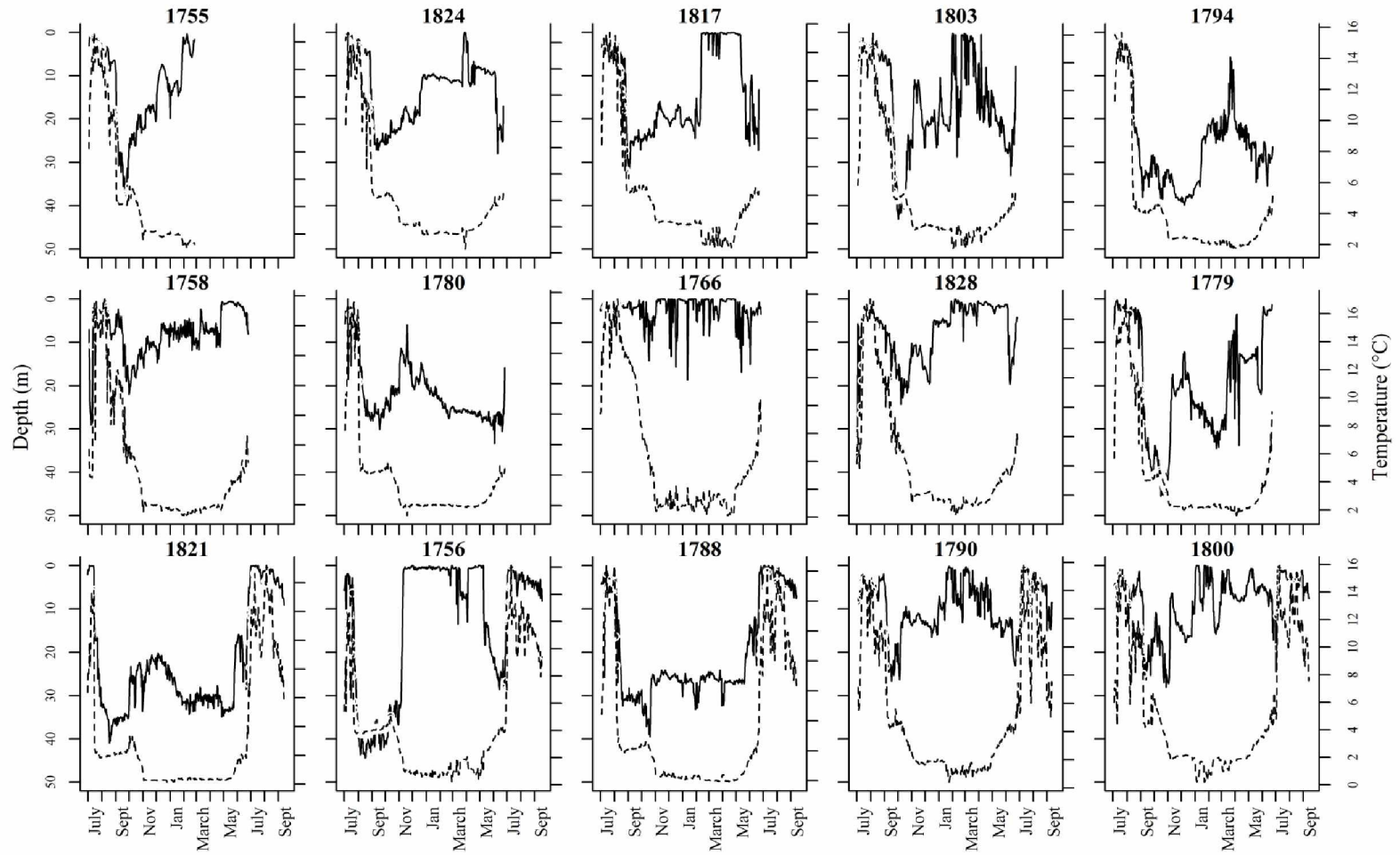
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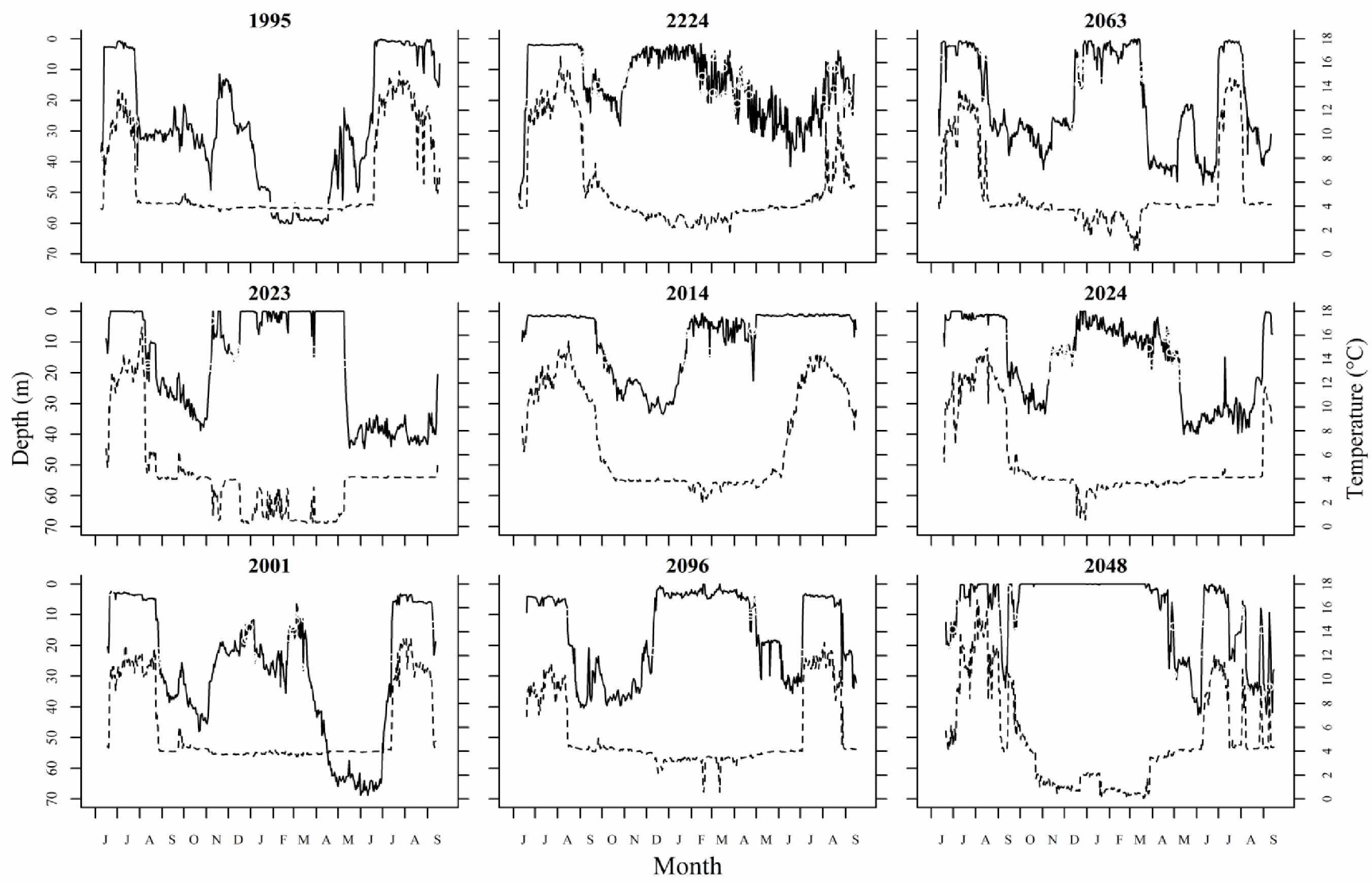
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Appendix A. Mean depth and internal body temperature of recaptured Burbot from Tanada Lake.



Appendix B. Mean depth and internal body temperature of recaptured Burbot from Copper Lake.

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Appendix C. IACUC Approval




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**Institutional Animal Care and Use Committee**  
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 19, 2009

To: Joseph Margraf, PhD  
Principal Investigator

From: Erich H. Follmann, PhD   
IACUC Chair

Re: IACUC Assurance Application

The University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC) reviewed the following Assurance at their June 9, 2009, meeting. This Assurance was approved pending receipt of a revised assurance addressing the committee's questions. The assurance received on June 17, 2009 was determined to be satisfactory; therefore I am pleased to issue approval.

Protocol#: 09-37

Title: *Vertical Movement of Burbot using Archival Tags*

Received: May 29, 2009 (orig)  
June 17, 2009 (revisions)

Approved: June 19, 2009

Review Due: June 19, 2010

*The PI is responsible for acquiring and maintaining all required permits and permissions prior to beginning work on this assurance. Failure to obtain or maintain valid permits is considered a violation of an IACUC assurance, and could result in revocation of IACUC approval.*