# Sex-specific spawning behaviour of lake whitefish in Lake Huron revealed by fine-scale acoustic telemetry

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ABSTRACT

# Sex-specific spawning behaviour of lake whitefish in Lake Huron revealed by fine-scale acoustic telemetry

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Lake whitefish (*Coregonus clupeaformis*) are ecologically, economically, and culturally significant across their range, yet little is documented about the species' spawning behaviour. Recruitment of lake whitefish has dramatically declined over the past two decades across many regions of the Laurentian Great Lakes, most notably in lakes Huron and Michigan, prompting research efforts to fill critical knowledge gaps in the life history of this species. Understanding the reproductive ecology of lake whitefish, including documenting aspects of spawning behaviour, may reveal clues about factors contributing to the declines. This study used fine-scale acoustic telemetry to characterize sex-specific movement patterns and habitat associations of lake whitefish during the spawning season. A VEMCO Positioning System (VPS) was deployed at an active spawning shoal in Georgian Bay (Lake Huron), with guidance provided by Saugeen Ojibway Nation members with local ecological knowledge about the shoal and the lake whitefish population. In the fall of 2020, 50 lake whitefish were captured and tagged at the spawning shoal; 28 of those fish were observed the following spawning season in 2021. A clear increase and decrease was observed in the presence of individuals in the study area over the spawning period. Both sexes moved into shallower waters at night and deeper waters during the day at rates of 0.162 m/h and 0.08 m/h, respectively. Decreased rates of movement and horizontal distance travelled were detected during the day leading up to a peak activity phase where 22 fish were present. At night during this peak activity phase, males moved 30.0% faster on average than females (0.204 ± 0.13

and 0.143 ± 0.10 m/s, respectively). This study provided a unique opportunity to work with local First Nations to understand lake whitefish spawning behaviour, providing insights into the reproductive ecology of a population undergoing concerning declines in recruitment and abundance.

Keywords: Two-Eyed Seeing; GLATOS; *Coregonus clupeaformis*; spawning habitat; coregonine restoration; fine-scale acoustic telemetry

# DEDICATION

To my biggest supporter, inspiration, and best friend: Dad. Thank you for being you, for all you have done, and continue to do.

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# CHAPTER 1 - GENERAL INTRODUCTION

## *Historical alterations to Great Lakes fisheries and ecosystems*

Over the past century, significant alterations to the Laurentian Great Lakes (herein Great Lakes) fisheries have occurred due to invasive species, habitat degradation, and overfishing, causing dynamic changes in commercial yields and stock health (Rennie et al. 2009, Brenden et al. 2013). Expansion of sea lamprey into lakes Erie, Huron, Michigan, and Superior from Lake Ontario in the 1920s/30s, in conjunction with overexploitation of fisheries, led various native fish species, like lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and walleye (*Sander vitreus*), to collapse in the 1950s and 60s (Bunnell et al. 2014). Non-native planktivorous pelagic fish, like alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), likely exacerbated the declines in native fish during the mid-1900s as well through predation and competition (Nalepa et al. 2005). Recoveries of key commercial species like lake whitefish occurred in the 1980s/90s in lakes Huron, Michigan and Superior, while some percid species like walleye and yellow perch (*Perca flavescens*) proliferated in the lower Great Lakes (Brenden et al. 2013). In the 1980s and later in the 1990s/early 2000s, the invasion of two efficient filter-feeding and mat-forming bivalves, collectively known as dreissenid mussels, occurred (zebra *Dreissena polymorpha* and quagga *Dreissena bugensis*), which resulted in alterations in plankton and nutrient availability, the lakebed, and water clarity. These ecosystem changes likely contributed to declines of commercial species like lake whitefish in the late 1990s/early 2000s, except Lake Superior, where commercial yields remained relatively stable (Brenden et al. 2013). By 2003, the combined commercial yield across all species and for all lakes was 19,700 mt, the lowest on record since 1914 (Brenden et al. 2013).

Lake Huron is the second largest Great Lake and has undergone particularly substantial ecosystem changes over the past century. Lake Huron has three distinct basins (North Channel, Georgian Bay, and main basin), which are primarily oligotrophic, with the exceptions of the North Channel, which is mesotrophic and inner Saginaw Bay, which is eutrophic (Stow et al. 2014, Rudstam et al. 2020). Over the past twenty years in Lake Huron, essential nutrients for primary production have been altered. For example, total phosphorus has declined, silica has increased, and carbon levels have remained stable (Barbiero et al. 2018). Decreased phosphorus is concerning as it is the main nutrient that limits primary production in the Great Lakes (Chapra and Dolan 2012). Decreased nutrient loading and the spread of dreissenid mussels have contributed to these declines in phosphorus levels (Reavie et al. 2017, Sgro and Reavie 2018, Rudstam 2020). The limitation of phosphorus in Lake Huron has contributed to changes in the distribution, composition, and declines in primary productivity, specifically in phytoplankton and zooplankton communities (Rudstam et al. 2020). The reductions in phytoplankton and zooplankton communities decrease the food available for larval fish that hatch in the spring and feed on small zooplankton throughout the spring and summer.

Lake whitefish (*Coregonus clupeaformis*) support the largest commercial fishery in Lake Huron, although fluctuations in yields have occurred in the past fifty years. Lake whitefish commercial yields recovered substantially in the mid-1980s, primarily due to declining sea lamprey populations, implementation of harvest control strategies, and high availability of prey items (Ebener et al. 2021). However, the recovery was short-lived as lake whitefish commercial yields subsequently declined in the late 1990s/early 2000s and are currently at low levels not seen since the 1970s/early 1980s (Fig. 1.1). In addition to declining yields, lake whitefish recruitment has also declined. Recruitment is generally defined as the addition of new individuals that become established into a particular portion of the harvestable fishery, where natural mortality stabilizes (Ludsin et al. 2014, Ebener et al. 2021). For lake whitefish, recruitment is typically measured at age 4 years, as this is typically the late juvenile stage when mortality stabilizes as well as the age at which fish generally become fully recruited to fisheries monitoring nets (Ebener et al. 2021). Prior to this age, and especially through the first year of life, lake whitefish can experience high levels of mortality, which can limit subsequent survival and recruitment to later life stages (Ebener et al. 2021). Unfortunately, the factors and mechanisms inhibiting the recruitment of lake whitefish are not well-known, calling for increased research on this critical topic.

### *Overview of lake whitefish biology and ecology*

Lake whitefish are a widely distributed cold-water species across Canada and the northern United States (Goodyear 1982). Collectively known as salmonids, lake whitefish are in the Salmonidae family, which also includes salmon, trout, char, freshwater whitefish, grayling, taimen, and lenok. Salmonids are typically characterized by having soft-fin rays, a dorsal adipose fin, and pelvic fins placed far back on their body. Lake whitefish are part of the subfamily Coregoninae, known as the freshwater whitefishes, characterized by having smaller mouths and weaker teeth than their cousins in the Salmoninae subfamily, including salmon and trout (Alaska Dept. of Fish and Game n.d.). The Coregoninae subfamily also includes cisco, round whitefish, and inconnu.

Lake whitefish seasonal distributions are primarily driven by temperature, prey availability, and spawning (Nester and Poe 1984, Bégout Anras et al. 1999). Adult and juvenile lake whitefish typically occupy deep, offshore waters below the thermocline during late spring, summer, early fall, and winter (Fig. 1.2), though their depth occupation varies across regions. For example, Rennie et al. (2015) compiled depth of capture data across the Great Lakes, showing lake whitefish were captured in depths between 5-219 m during summer months, though this varied among sites, lakes, locations, and years with or without dreissenid mussel establishment. Data from trawling surveys in Lake Superior found 0-3 year-old lake whitefish resided in 15-85 m, where depths during the summer were the deepest on average compared to other seasons (Selgeby and Hoff 1996). Gorsky et al. (2012) in their study of adult lake whitefish seasonal distributions in Clear Lake, Maine, indicated seasonal vertical habitat selection was primarily driven by temperature, although in the spring and fall when the thermocline dissipated, their distributions were also driven by invertebrate availability and spawning, respectively. In the fall, adults move into more nearshore regions and shallower depths to spawn (Fig. 1.2). Early work by Hart (1930) found adult lake whitefish in the Bay of Quinte remained between depths of 9-15 m during the fall spawning season, where eggs were not found deeper than 4.5 m.

There is generally less known about the early life stages of lake whitefish than the adult life stage. After being spawned in the late fall, lake whitefish embryos incubate overwinter in interstitial spaces within rocky and cobble substrates, where optimal water temperatures for the embryos range between 0.5-8 °C (Price 1940, Brooke 1975). Hatching typically occurs when water temperatures reach 6 °C in early spring after ice-out (Price 1940, Cunningham and Dunlop 2023). Temperature is important for hatchling survival, as laboratory incubation trials by Mueller et al. (2015) found lake whitefish hatchling survival decreased with increasing incubation temperatures, specifically from 55 % at 2 °C, to 38 % at 5 °C, and 17 % at 8 °C. After hatching, larval lake whitefish move to the surface where they remain suspended until wind, currents, or their locomotion transports them into shallow embayments for protection from offshore winds and strong currents (Goodyear 1982). The exact timing of the shift from surface waters to nursery areas is unknown (Ebener et al. 2021). During the shift to nursery areas, larval lake whitefish begin feeding exogenously on zooplankton after exhausting their endogenous energy reserves from their yolk sac, which can occur 12-25 days after hatching, depending on water temperature (Brown and Taylor 1992). In lakes Huron, Michigan and Ontario, larval lake whitefish have been documented to eat zooplankton and insect larvae, in particular, cyclopoid and calanoid copepods, cladocerans (e.g., *Daphnia* spp. and Bosminidae), mayfly nymphs, and chironomid larvae (Pothoven and Nalepa 2006, Hoyle et al. 2011, Pothoven et al. 2014, Pothoven 2019).

Diets of adult and juvenile lake whitefish vary regionally, but typically consist of benthic invertebrates like amphipods, *Bythotrephes* spp., mysids, chironomids, molluscs, fish, and fish eggs (Ihssen 1981, Rennie et al. 2012, Pothoven and Madenjian 2013). Traditionally, juvenile and adult lake whitefish diets consisted of a lipid-rich, primarily offshore amphipod named *Diporeia* spp. (Cook and Johnson 1974, Nalepa et al. 2005). However, *Diporeia* spp. populations declined to low levels in most regions following the spread of dreissenid mussels in lakes Michigan, Ontario, Huron and Erie, causing shifts in lake whitefish foraging patterns and diets to less nutritious shelled prey (e.g., dreissenid mussels and gastropods) (Nalepa et al. 1998, Lozano et al. 2001, Nalepa et al. 2003, Madenjian et al. 2006). From these diet shifts, subsequent declines in lake whitefish growth and condition occurred (Pothoven et al. 2001, Pothoven and Madenjian 2008, Fera et al. 2015). However, Fagan et al. (2017) determined that the loss of *Diporeia* spp. was not the only factor contributing to declines in adult lake whitefish condition in lakes Michigan, Erie and Superior, as they found no evidence relating low *Diporeia* spp. abundances to poor condition.

### *Factors affecting lake whitefish recruitment*

Many forces are likely working together to affect early life stages and recruitment of lake whitefish. A leading hypothesis for declines in recruitment is the loss of the spring phytoplankton bloom due to the establishment of dreissenid mussels, resulting in a decline of zooplankton available for larval lake whitefish during the spring and summer (Ebener et al. 2021). Additionally, Cunningham and Dunlop (2023) determined that November water levels and spawning stock biomass contributed to variation in larval densities, but dreissenid mussel presence was the only consistent factor that explained the declines in larval densities in the Fishing Islands, Lake Huron between pre- and post-dreissenid mussel invasion. Other factors that can affect variation in survival of early life stages and subsequent recruitment of lake whitefish include larval length, adult density, winter ice cover, wind, dreissenid mussel density, temperature, and density-dependent effects (Claramunt et al. 2010, Ebener et al. 2021, Cunningham and Dunlop 2023). However, little is known about how the magnitude or combinations of these factors might affect lake whitefish recruitment. To address these uncertainties, Ebener et al. (2021) outlined a critical research priority for lake whitefish that focuses on understanding the productive capacity of reproductive habitat and how the spawning substrate (if affected by dreissenid mussels) might affect egg and larval survival in the Great Lakes.

### *Understanding spawning behaviour is important*

Understanding spawning behaviour is crucial to predicting a fishery's productivity and future outcomes. For example, by looking at where and when fish spawn, we can better protect or restore critical spawning habitat or implement spawning closures that are accurate to the duration of the spawning period. Additionally, by examining the spawning population, we can better predict the reproductive potential of a population, which is especially important for a population with a low abundance (Rand and Fukushima 2014). Considering climate change, understanding how spawning behaviour responds to the warming of water temperature is critical in predicting changes in reproductive potential, distributional changes, and the timing of spawning (Lynch 2010, Lynch et al. 2015). For example, a study in the Experimental Lakes Area in northwestern Ontario noted that stratification is shifting to later in the year, which has likely delayed lake trout spawning over time (Guzzo and Blanchfield 2017). Spawning strategies can also influence a species' vulnerability to collapse. For example, species that spawn for a brief period may be more vulnerable to environmental changes than those with an extended spawning period, as their window for spawning is shorter, leaving a greater chance for failure if adverse conditions arise (e.g., from temperature changes, temperature waves, and storms). Additionally, species that display various degrees of iteroparity within populations will likely find a balance between reproductive investment (the energy invested into gonad development and reproductive behaviour) and post-spawning survival (Birnie-Gauvin et al. 2021). For example, a study by Aykanat et al. (2019) noted that smaller, more mature Atlantic salmon (*Salmo salmar*) were more likely to display iteroparity as less energy would be required for each reproductive event (Biggs et al. 2021).

Quantifying various reproductive traits can be helpful in understanding spawning behaviour and lead to effective management strategies. Knowing the sex ratio coupled with where males and females are while spawning are useful for management decisions surrounding closures during the spawning season (Morgan and Trippel 1996). For example, Morgan and Trippel (1996) found that Atlantic cod (*Gadus morhua*) on the Grand Banks of Newfoundland and southern Scotian Shelf formed separate sex-dominated shoals during spawning and acknowledged that spawning ground closures, which affect only certain sections of a stock area, might have indirect effects that could lead to unequal sex-specific fishing pressure. Additionally, by quantifying reproductive behaviours, we can estimate the energetic costs of spawning, which is important to understand the bioenergetics of populations (i.e., how much energy is required to sustain population growth and abundance) (Tentelier et al. 2020).

### *Spawning behaviour of lake whitefish*

Considering lake whitefish's economic and ecological significance, we know surprisingly little about their spawning behaviour. Lake whitefish typically spawn in the fall between mid-October – early/mid-December, depending on site, at water temperatures <10 °C (Goodyear 1982, Hart 1930; Fig. 1.2). Spawning occurs in shallow water (generally <5 m), over rocky and cobble shoals that can include honeycomb-shaped rock (Hart 1930, Scott and Crossman 1973, Goodyear et al. 1982, Bodaly 1986). Most historical spawning sites in the Great Lakes, as provided by Goodyear (1982), are within the lakes. However, spawning can also occur in tributaries such as the Detroit, Menominee, and Fox rivers (Roseman et al. 2007, Ransom et al. 2021). Lake whitefish are broadcast spawners that, like lake trout, but unlike many other Salmonidae spp., do not provide parental care (Martin 1957, Esteve et al. 2007). Lake whitefish are sexually size dimorphic, where females are typically larger than males at the same age, and both sexes can develop tubercles in the fall in preparation for spawning (Morbey 2018, Bégout Anras et al. 1999). Lake whitefish in lakes Huron and Michigan have exhibited some spawning site fidelity among populations through evidence of mark-recapture and distinct genetic stocks (VanDeHey et al. 2009, Ebener et al. 2010). Additionally, recent evidence in Lake Erie indicates that some spawning reefs of lake whitefish may be reproductively isolated, but further evidence is needed to define distinct spawning stocks (Euclide et al. 2022).

Most research detailing lake whitefish spawning behaviour has been conducted on inland lake populations. Particularly, Bégout Anras et al. (1999) studied the movement and habitat use of lake whitefish during spawning in a small, boreal lake in Ontario. Bégout Anras et al. (1999) found that adult lake whitefish mean distance travelled and swimming speed decreased leading up to peak spawn. Additionally, over their two-year study, Bégout Anras et al. (1999) found that lake whitefish swimming speeds ranged from 15.3-3.8 cm/s and distances between 10-3 km/day for about three weeks leading up to and during spawning. Research describing other *Coregonus* spp. spawning behaviour has been published, but mostly from European lakes or from laboratory observations. For example, Eckmann (1991) studied the pelagic spawning behaviour of European whitefish (*Coregonus lavaretus*) in Lake Constance, Germany, using hydroacoustics and found that during dawn and dusk, fish moved up to 50 m in amplitude, ascending at dusk and descending at dawn. Additionally, laboratory experiments revealed that both European vendace (*Coregonus albula*) and multiple Siberian *Coregonus* spp. (*C. peled*, *C. pidschian*, *C. muksun*, *C. tugun*, and *C. migratorius*) displayed various degrees of pair / communal spawning where, in some cases, one or two males participated in a spawning event with a female (Karajalainen and Marjomäki 2018, Semenchenko and Smeshlivaya 2021). Furthermore, Semenchenko and Smeshlivaya (2021) observed multiple body orientations during spawning events among the five whitefish species including vertical, horizontal, and a combination of both orientations while both sexes released gametes. However, sex- and diel-specific differences in spawning activity metrics (swimming speed, distance moved, vertical displacement) and spatial occupation over the spawning period across regions have yet to be evaluated for lake whitefish in the Great Lakes.

### *Acoustic telemetry: General overview*

Acoustic telemetry has become a worldwide method for studying fish movements, where it became a notable technology among aquatic tracking studies in the 1990s (Hussey et al. 2015). Generally, acoustic telemetry comprises two components: acoustic transmitters and acoustic receivers. Acoustic transmitters (also known as ‘tags’) are small devices that emit an acoustic signal at pre-determined rates and frequencies, depending on the make and model, that can be surgically implanted into fish. Acoustic receivers are larger devices typically moored into the bottom of a study system (ocean, lake, estuary, tributary) that captures and records the acoustic signal from the tags and stores information like date, time, and unique transmitter ID (called a ‘detection’). There are generally two types of acoustic telemetry: active and passive. Active acoustic telemetry involves real-time tracking of tagged animals from a surface vessel using a receiver or hydrophone (Meese and Lowe 2020). Passive acoustic telemetry consists of using stationary receivers that will record a tagged animal if the animal is in range of that receiver. Most commonly, passive acoustic telemetry consists of deploying receivers into widely-spaced grids across areas of interest to answer questions involving critical niche areas, seasonal patterns, and stock structure (Hussey et al. 2015). Additionally, receivers can be deployed with overlapping detection ranges (i.e., the distance of how far a receiver can detect a transmitter) in a line, or across a boundary or passageway as a gate, to answer questions involving migration routes (Hayden et al. 2014, Jung et al. 2015). Another form of acoustic telemetry involves closely-spaced receivers with overlapping detection ranges deployed as a grid, which can calculate geographic positions of tagged animals, providing useful information on fine-scale behaviours, movements, and detailed home-ranges. A well-known type of fine-scale acoustic telemetry is called a VEMCO positioning system (VPS), developed by Innovasea Ltd. (based out of Bedford, Nova Scotia, Canada).

### *VEMCO Positioning System*

The VPS can be applied to finer-scale objectives, such as identifying spawning areas, creating utilization distributions, and quantifying locomotory metrics. What sets the VPS apart is its ability to calculate geographic positions of fish (latitude/ longitude coupled with time, date, and transmitter ID), rather than simply obtaining detections (time, date, and unique transmitter ID). This technology allows researchers to calculate movement metrics like distance travelled, distance to the nearest site of interest, and swimming speed, or create heatmaps of activity (Bégout Anras et al. 1999, Binder et al. 2018, Dahl and Patterson 2020).

Understanding the detection range of acoustic receivers within a VPS system is necessary before deploying a VPS array, as the receivers require a particular arrangement to calculate positions (Kessel et al. 2013). For a VPS to calculate positions, at least three receivers must be in the detection range of each other. This is because the algorithms of a VPS are based on a three-receiver time difference of arrival of the tag signal, which measures differences in transmission detection times at pairs of time-synchronized receivers and converts them to distance differences using the signal propagation speed (Smith 2013, Roy et al. 2014). Therefore, understanding the appropriate spacing for receivers within each system is critical in calculating fish positions. However, many factors can influence a receiver's detection range and efficiency (i.e., the ability of a receiver to detect a tag transmission). Some of these factors include receiver depth and orientation, time since deployment, wind speed, thermocline, type of transmitter, slope, substrate, and anthropogenic, biological and environmental noise (Kessel et al. 2013, Huveneers et al. 2016, Klinard et al. 2019, Wells et al. 2021).

VPS fish positions also have an associated error with each fish position named Horizontal Positioning Error (HPE). HPE is calculated based on various factors, including transmitter depth, receiver-measured positions (i.e., synctags), signal arrival time, and salinity (Smith 2013). Typically, the higher the HPE, the less accurate your fish position is. HPE can be challenging to interpret as it is unitless. However, in a typical VPS, receivers have tags associated with them, called synctags, to assess the measured error experienced at each receiver throughout deployment ($HPE_m$). The relationship between HPE and $HPE_m$ of synctags can determine an appropriate HPE cut-off for a study's associated fish positions, which aids in data interpretation and setting project goals, as such data can be used to account for positional errors associated with each fish position.

### *Indigenous Ecological Knowledge in fisheries science – General overview*

Indigenous Ecological Knowledge (IEK), also known as Traditional Ecological Knowledge (TEK), is a category of Indigenous Knowledge (IK) relating to Indigenous generational knowledge of the natural world, the environment, and living beings (Berkes 2018). Berkes (2018) defines IEK as "a cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment". In academic scholarship, IK has been identified as having four orientations: ecological, critical, relational, and collaborative, where each operates under different assumptions (Latulippe 2015). IEK is typically qualitative in practice and has a worldview that there are multiple ways of knowing (Denny and Fanning 2016). It is important to note that each Indigenous community has its own perspectives and ecological knowledge, and generalization should be avoided whenever possible (Warren et al. 1995, Berkes 2018).

In early ecological western science literature, IEK was rarely mentioned compared to western scientific methods. According to Berkes (2018), the earliest publications including IEK for resource management in Canada was a study that estimated Canada goose (*Branta canadensis*) populations with the Cree of James Bay in the nineteenth century (Barnston 1861). Early work by Fikret Berkes with the Chisasibi

Cree fishery of James Bay may be some of the earliest documented and published fisheries research that involved Indigenous peoples in Canada (Berkes 1977, Bekes 2018). Only in the 1990s did publications begin to mention IEK in scientific literature, but, as Jessen et al. (2021) reveal, research involving IEK is increasing.

### *Bridging knowledge systems – Two-Eyed Seeing*

Dr. Albert Marshall, a Mi'kmaq elder, conceptualized Two-Eyed Seeing and describes it as "learning to see from one eye with the strengths of Indigenous knowledges and ways of knowing, and from the other eye with the strengths of mainstream knowledges and ways of knowing, and to use both these eyes together, for the benefit of all" (Bartlett et al. 2012, Reid et al. 2021). Two-Eyed Seeing emphasizes that western science and IEK are not competing with one another but work together as independent, yet interwoven knowledges, to create a more holistic view of science and nature. The "two eyes" of Two-Eyed Seeing are equal, where one eye is not more important than the other. Two-Eyed Seeing persists as a co-partnership, co-learning, and co-production of knowledge between the two eyes, where the framework's purpose is not to integrate or validate the other eye's knowledge systems (Armitage et al. 2011, Almack et al 2023).

Two-Eyed Seeing bridges Indigenous and non-Indigenous knowledge systems to gain a more comprehensive understanding of the world. Reid et al. (2021) outlined multiple Indigenous conceptualizations for bridging knowledge systems. Some of these frameworks include: *Kaswentha* (Haudenosaunee for "Two Row Wampum"), *Ganma* (seawater and freshwater together) of the Yolngu people of northeastern Australia and *Waka-Taurua* (Māori for "Double-Canoe" and *Etuaptmumk* (Mi'kmaw for "Two-Eyed Seeing") (Reid et al. 2021). Collectively, these frameworks keep both knowledge systems separate, indicating that each system maintains its own identity. However, only Two-Eyed Seeing places a responsibility on the holder of knowledge to act on learned knowledge, directing the framework into applied situations (Hatcher et al. 2009, Reid et al. 2021).

Although not a well-known concept in academia, Two-Eyed Seeing is becoming a more widely used framework in ecological, health, and educational studies across Canada (Hatcher et al. 2009, Marshall et al. 2015). In fisheries research, the Two-Eyed Seeing framework is relatively new. Still, the framework is becoming an increasingly recognized conceptual model in academia, appearing in projects presented at conferences and publications across Canada (Bingham et al. 2021, Reid et al. 2021, Duncan et al. 2023, Almack et al. 2023). For example, Abu et al. (2020) applied Two-Eyed Seeing in the Saskatchewan River Delta by collaborating with the Cumberland House community to assess the effect of anthropogenic stressors on various aquatic features, including fish abundance. In the Great Lakes, a study by Duncan et al. (2023) is one of the first true applications of Two-Eyed Seeing in a fisheries context. Duncan et al. (2023) investigated Saugeen Ojibway Nation Ecological Knowledge (SONEK) of lake herring (*Coregonus artedi*) and lake chub (*Coregonus* spp.) to address the lack of information about ciscoes in Saugeen Ojibway Nation (SON) traditional territory (Lake Huron) through both mapping interviews and contemporary sampling. The project by Duncan et al. (2023) paved the way for another Two-Eyed Seeing project that investigates the role of lake trout in the declines of lake whitefish, done in collaboration between SON and the Ontario Ministry of Natural Resources and Forestry (MNRF) (Almack et al. 2023). Although there are many published examples of projects that work together with

Indigenous communities on fisheries-related issues, they do not appear to be examples of true Two-Eyed Seeing, which collaborates on all aspects of a project.

### *The Saugeen Ojibway Nation and lake whitefish*

Declines of lake whitefish (*dikameg* in Anishnaabemowin) populations in Lake Huron concern Indigenous communities around the lake, including the Saugeen Ojibway Nation (SON). SON is comprised of two sister First Nations, the Chippewas of Nawash Unceded First Nation and the Chippewas of Saugeen First Nation, located on the Bruce Peninsula along the shores of Georgian Bay and the main basin of Lake Huron (Fig. 1.3). SON have cared for the lands and waters of their traditional territory and have harvested lake whitefish for subsistence, trade, economy, and ceremony since time Immemorial (Almack et al. 2023, Duncan et al. 2023, Gobin et al. 2023). SON have an inherent right to fish commercially and for subsistence within their traditional territory. This right was reaffirmed in a significant court case in Ontario in 1993 (R.v. Jones 1993). The SON rely on lake whitefish as a source of protein for their communities. However, the declines in lake whitefish abundance over the past two decades have exacerbated barriers to accessing this traditional food (Lowitt et al. 2018).

### *Bringing it all together: Two-Eyed Seeing research to investigate lake whitefish movements in Lake Huron*

Filling critical knowledge gaps about lake whitefish and identifying the cause(s) of the declines in Lake Huron are a priority for SON and provincial and federal agencies, which have led to several important collaborative projects. Two of the projects important for my thesis are the Together with Giigoonyag project and the Bima’azh project, which have begun investigating various aspects of lake whitefish ecology to better understand,

and address, lake whitefish declines. These projects were primarily born out of community meetings held with the SON Fisheries Assessment Program, where community members shared their views and thoughts on lake whitefish population dynamics and declines within their territory (Gobin et al. 2023). A central theme community members discussed at these meetings was “assisting reproduction and stocking,” which included several recommendations about increasing the reproductive success of lake whitefish (Gobin et al. 2023). However, many additional themes arose during these community meetings, including harvesting, invasive species, stocking of other species, habitat and water clarity, and people and the community, to name a few (Gobin et al. 2023).

Together with Giigoonyag (TWG) translates to ‘together with the fishes’ in Anishnaabemowin. The TWG project is a multi-agency, multi-year project in collaboration with three levels of government: a First Nation (SON) and provincial (MNRF) and federal (Parks Canada) governments. The TWG project aims to provide invaluable information about lake whitefish and lake trout, and build mutually respectful relationships among Indigenous communities and government agencies. Specifically, the project aims to assess movement patterns within and between basins of Lake Huron (Georgian Bay, the North Channel, and the main basin), understand the contribution of spawning populations to commercial and Indigenous fisheries in various regions, identify the use of key migration corridors, and assess spawning sites. Many different sampling techniques are used to achieve the TWG goals, including acoustic telemetry, larval sampling, plankton sampling, spawning shoal habitat mapping, offshore index netting (sampling offshore fish populations), and nearshore index netting (sampling nearshore fish populations).

Bima’azh translates into ‘to follow or to track along a path’ in Anishnaabemowin. The Bima’azh project is a collaborative, community-based initiative that uses a Two-Eyed Seeing approach to address community concerns about lake whitefish. Specifically, the objectives of Bima’azh were to provide SON community members with opportunities to learn about lake whitefish reproductive habitat and spawning behaviour, using both Saugeen Ojibway Nation Ecological Knowledge (SONEK) and smart technologies (i.e., western science-based technology). Bima’azh is led by the SON fisheries assessment program and Collective Environmental (an environmental consulting company) and is in collaboration with the MNRF. Bima’azh was funded by the Great Lakes Observation System’s Smart Great Lakes program and made use of funding and fieldwork conducted through the TWG project. Bima’azh funds purchased an underwater remotely operated vehicle to study spawning habitat and substrate and receivers for use in the VPS study to investigate the fine-scale spawning behaviour of lake whitefish. My research focuses on the western science eye of the Bima’azh and Together with Giigoonyag projects, to fill key western science knowledge gaps in the movement ecology of lake whitefish during the spawning season.

### *Thesis Overview*

My thesis aims to assess the sex-specific spawning behaviour of adult lake whitefish, including quantifying the spatial occupation, movements, and depth associations at a spawning shoal in Georgian Bay, Lake Huron, that is important to SON. In my data chapter, I describe the occupancy of lake whitefish over the spawning period using visual heatmapping. To assess the temporal variations in presence of lake whitefish during the spawning season, I visualize the number of individuals present throughout the spawning period and plot the presence of each fish within the study area over time using an abacus plot. Additionally, to quantify lake whitefish movements over the spawning period, I calculated movement metrics like lake depth displacement, horizontal distance moved, and horizontal rate of movement. In the general discussion, I summarize my main findings, present an overview of potential implications, and reflect on the research results.

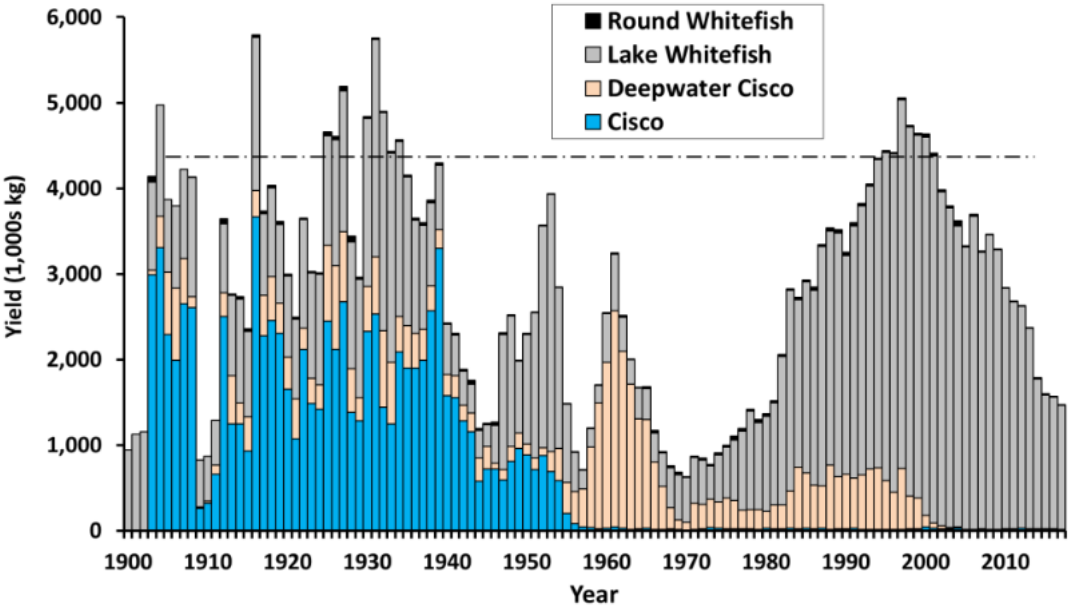

Figure 1.1 Total annual commercial yield of coregonines from Lake Huron, 1900- 2017. The dashed horizontal line indicates the Great Lakes Fishery Commission Fish Community Objective of 3.8 million kg. Figure by Cottrill et al. (2020).

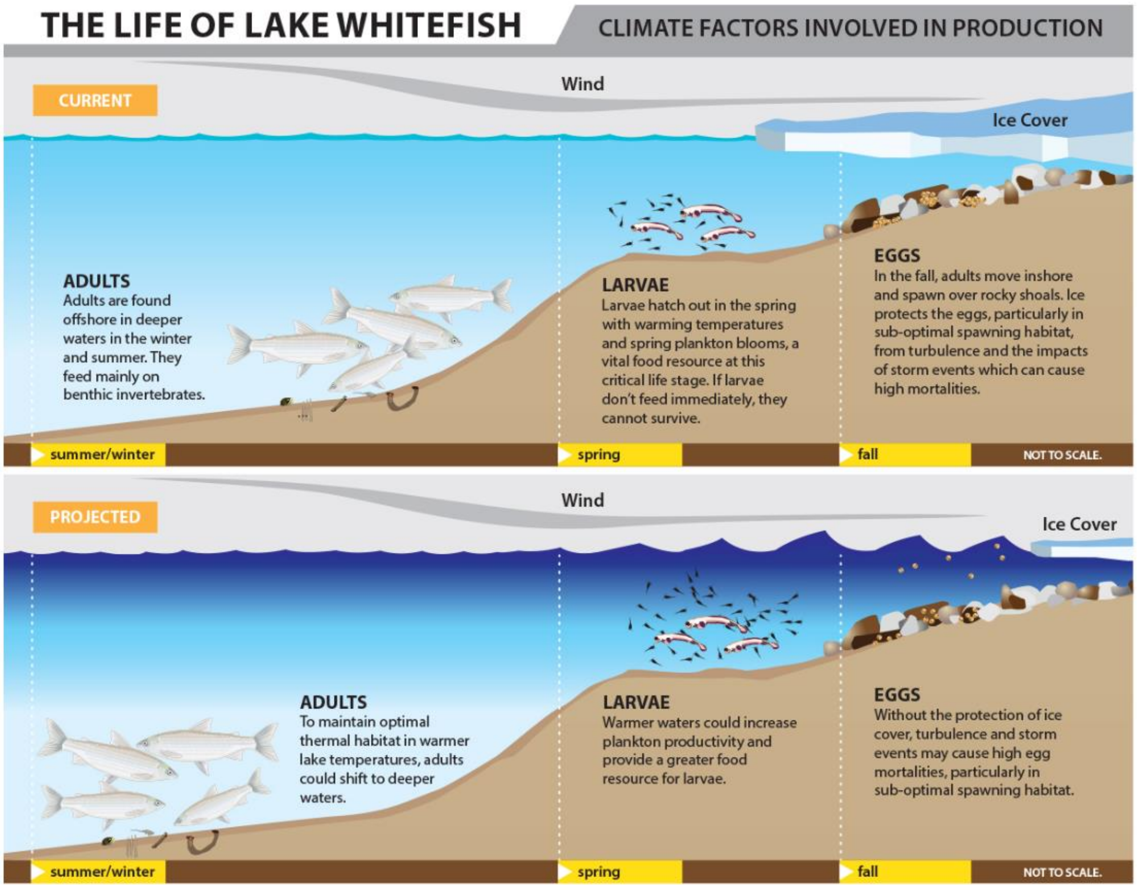

Figure 1.2. Life cycle of lake whitefish. Figure by Michigan Sea Grant (MICHU-13-206).

Figure 1.3. Map of Saugeen Anishinaabekiing – Traditional Territory of the Saugeen Ojibway Nation comprised of the Chippewas of Nawash Unceded First Nation and the Chippewas of Saugeen First Nation. Figure by the Saugeen Ojibway Nation Environmental Office.

# CHAPTER 2: SEX-SPECIFIC SPAWNING BEHAVIOUR OF LAKE WHITEFISH IN LAKE HURON REVEALED BY FINE-SCALE ACOUSTIC TELEMETRY

## Abstract

Lake whitefish (*Coregonus clupeaformis*) are ecologically, economically, and culturally significant across their range, yet little is documented about the species' spawning behaviour. Recruitment of lake whitefish has dramatically declined over the past two decades across many regions of the Laurentian Great Lakes, most notably in lakes Huron and Michigan, prompting research efforts to fill critical knowledge gaps in the life history of this species. Understanding the reproductive ecology of lake whitefish, including documenting aspects of spawning behaviour, may reveal clues about factors contributing to the declines. This study used fine-scale acoustic telemetry to characterize sex-specific movement patterns and habitat associations of lake whitefish during the spawning season. A VEMCO Positioning System (VPS) was deployed at an active spawning shoal in Georgian Bay (Lake Huron), with guidance provided by Saugeen Ojibway Nation members with local ecological knowledge about the shoal and the lake whitefish population. In the fall of 2020, 50 lake whitefish were captured and tagged at the spawning shoal; 28 of those fish were observed the following spawning season in 2021. A clear increase and decrease was observed in the number of individuals present in the study area over the spawning period. Both sexes moved into shallower waters at night and deeper waters during the day at rates of 0.162 m/h and 0.08 m/h, respectively. Decreased rates of movement and horizontal distance travelled were detected during the day leading up to a peak activity phase where 22 fish were present. At night during this peak activity phase, males moved 30.0% faster on average than females (0.204 ± 0.13

and 0.143 ± 0.10 m/s, respectively). This study provided a unique opportunity to work with local First Nations to understand lake whitefish spawning behaviour, providing insights into the reproductive ecology of a population undergoing concerning declines in recruitment and abundance.

Keywords: Two-Eyed Seeing; GLATOS; *Coregonus clupeaformis*; spawning habitat; coregonine restoration; fine-scale acoustic telemetry

## Introduction

Spawning behaviour is a crucial component in the life history of fishes and can be used to help predict reproductive resilience in populations (Biggs et al. 2021). Relating spatiotemporal aspects of spawning, such as where, when, and for how long a population spawns, can provide insights into the population's vulnerability to harvest or other stressors during periods of population decline (Sadovy De Mitcheson and Erisman 2012, Biggs 2021). Additionally, characteristics of spawning populations, such as sex ratios and the number of spawning individuals, can be important for quantifying reproductive potential, aiding in stock assessments (Methot Jr and Wetzel 2012). Furthermore, species that are diverse and adaptable with where they spawn, may show increased resilience to environmental changes and spawning habitat degradation (Roseman 2007, Gatch et al. 2021). At a finer scale, quantifying the sex-specific movement and activity rates of fish can also help us understand the energetic costs of spawning behaviour, which can be used in bioenergetics models (Rudstam et al. 1994). More broadly, describing the migratory behaviour of spawning stocks is important in formulating harvest strategies (Ebener et al. 2008, Li et al. 2014).

Lake whitefish (*Coregonus clupeaformis;* dikameg in Anishnaabemowin) are an important species from an economic, cultural, ecological, and subsistence perspective in the Great Lakes and across the species range. In Lake Huron specifically, lake whitefish abundances have declined over the past 25 years. These declines have raised concerns from commercial fishermen, Indigenous communities, and fisheries management agencies over the loss of a sought-after commercially harvested species, which also are an energy linkage between nearshore and offshore ecosystems (Brenden et al. 2010, Cottrill et al. 2020, Gobin et al. 2023). In addition to the declines in abundance, lake whitefish have also undergone reductions in yield, growth, condition, and recruitment in many parts of the Great Lakes (Rennie et al. 2009, Herbst et al. 2013, Fera et al. 2015, Gobin et al. 2015, Ebener et al. 2021). Several factors have been hypothesized to have led to these declines. The invasion of dreissenid mussels in Lake Huron (Zebra *Dreissena polymorpha* and quagga *Dreissena bugensis* mussels) is linked to the loss of *Diporeia* spp., an important prey item for adult lake whitefish. Since this invasion, lake whitefish switched to consuming dreissenid mussels, which have a lower energy density, contributing to declines in lake whitefish body condition and growth (Pothoven et al. 2001, Pothoven and Madenjian 2008). Dreissenid mussels are also hypothesized to have contributed to the declining recruitment of lake whitefish through their filtering feeding abilities, reducing the amount of primary production and, subsequently, zooplankton available for larval lake whitefish (Higgins and Vander Zanden 2010, Ebener et al. 2021, Cunningham and Dunlop 2023). Concerns have also been raised that invasive or nuisance species (e.g., dreissenid mussels, *Cladophora* spp., and round goby) are diminishing the quality of spawning habitat or reducing survival of embryonic life stages (Ebener et al.

2021, Gobin et al. 2023. A more complete understanding of lake whitefish reproductive ecology, including examining spawning behaviour, may help provide insights about factors affecting lake whitefish recruitment.

Most literature on lake whitefish spawning in the Great Lakes originates from historical studies, where sex- and diel-specific details of behaviour are generally not alluded to. Lake whitefish are described as being broadcast spawners that spawn between late October to early December, depending on temperature and site (Goodyear 1982). Spawning typically occurs in shallow water of <5-10 m, over rocky and cobble shoals that can include honeycomb-shaped rock (Hart 1930, Scott and Crossman 1973, Goodyear et al. 1982, Bodaly 1986). Lake whitefish spawning generally occurs at water temperatures <10 °C (Hart 1930, Nester and Poe 1984). Lake whitefish are sexually size dimorphic, where females are typically larger than males at the same age (Morbey 2018). Regarding other phenotypic differences, males can develop tubercles on their bodies in the fall in preparation for spawning, though this has also been noted for females in inland lakes (Bégout Anras et al. 1999). Mark-recapture and genomic studies have shown that lake whitefish typically stay in, or adjacent to, their management unit of tagging in lakes Huron, Michigan, and Superior, and distinct spawning stocks are present in Lake Huron (VanDeHey et al. 2009, Ebener et al. 2010, Ebener et al. 2021). Mark-recapture data published by Ebener et al. (2021) revealed that at least a proportion of tagged lake whitefish showed spawning site fidelity in Lake Huron, returning to the spawning site where they were tagged in subsequent years (Ebener et al. 2010, Ebener et al. 2021). Studies of finer-scale movements are restricted to inland lakes (Bégout Anras et al. 1999, Gorsky et al. 2012, Whitaker and Wood 2021). For example, Bégout Anras et al. (1999)

found lake whitefish swimming speed and distance travelled decreased until a peak in activity during spawning, although sex-specific comparisons were not available. To our knowledge, fine-scale sex- and diel-specific information like biometrics, distances travelled and spatial activity before, during and after spawning, has not been published for lake whitefish in the Great Lakes.

Acoustic telemetry represents a useful tool to fill knowledge gaps in our understanding of fish movement and behaviour (Hussey et al. 2015, Binder et al. 2018). Worldwide, acoustic telemetry tends to be used to understand general animal movements, which typically encompasses large spatial receiver arrays to characterize seasonal migrations, passage through systems, and use of protected areas (Matley et al. 2022a). However, understanding spawning behaviour tends to include smaller receiver arrays, or arrays where geographic positions can be calculated to visualize fish paths (Dean et al. 2014, Binder et al. 2018). Specifically, the VEMCO Positioning System (VPS; Innovasea Ltd., Bedford, NS, Canada) has been deployed to describe movement patterns, habitat associations, and behaviours of various marine fishes. For example, VPS has been used to evaluate the habitat use of reef fish (Dahl and Patterson 2020, Banks et al. 2021), invertebrates (Scheel and Bison 2012, Coates et al. 2013), and temperate fish like Atlantic cod (*Gadus morhua*) and Atlantic sturgeon (*Acipenser oxyrhynchus oxyrhynchus*) (Reubens et al. 2013, McLean et al. 2014, Whitmore and Litvak 2018). In the Great Lakes, VPS usage is far less widespread, as there are relatively few examples using this technology to study fine-scale movements of fishes (Meckley et al. 2014, Binder et al. 2016a,b, Binder et al. 2018, Withers et al. 2021). A notable example of a VPS array in the Great Lakes deployed to study spawning behaviour is Binder et al.'s

(2016a, 2016b, 2018) study of lake trout in the Drummond Islands of Lake Huron. Using a combination of fine-scale bathymetry and a VPS array, Binder et al. (2018) identified new lake trout spawning habitat, which included gravel and rubble areas at the base of large boulders where egg deposition occurred. To our knowledge, no study has used a VPS array to study the fine-scale spawning behaviour of lake whitefish in the Great Lakes.

The purpose of this study was to quantify sex-specific movement patterns of lake whitefish at the Little Port Elgin spawning shoal (in Georgian Bay, Lake Huron) during the 2021 spawning season. In 2020, 50 lake whitefish were tagged at the Little Port Elgin shoal, and a VPS array was deployed before the spawning season of 2021 to observe the spawning behaviour of any returning tagged fish. Specifically, we compared the dates of arrival and departure from the study area, spatial use of the spawning shoal and surrounding area, associations with lake depth, distances travelled, and rates of movement between males and females throughout both the day and night over the duration of the spawning period. Importantly, our study was done in collaboration with, and using guidance from, the Saugeen Ojibway Nation (SON), two sister First Nations with extensive local ecological knowledge of the spawning shoal and surrounding waters. SON, which includes the Chippewas of Nawash Unceded First Nation and Chippewas of Saugeen First Nation, located on the Bruce Peninsula between Georgian Bay and Lake Huron, have harvested lake whitefish for thousands of years for food, economy, and cultural purposes (Almack et al. 2023, Duncan et al. 2023, Gobin et al. 2023). SON members have raised concerns about declining lake whitefish abundance in their traditional territory and identified that understanding more about the reproductive behaviour and spawning habitat of lake whitefish was a priority (Gobin et. al 2023). In our study, we took inspiration from the Two-Eyed Seeing approach, where Indigenous Ecological Knowledge and Western Science are used to conduct research (Reid et al. 2021, Almack et al. 2023). SON community members were involved with project conception and SON harvesters captured the fish that were tagged, helped co-design the VPS array, and aided in interpreting results. With our study, we aim to fill important knowledge gaps on the spawning behaviour of lake whitefish, such as how males and females differ in their movement patterns, to better understand the reproductive ecology of this highly valued fish species.

## Methods

### *Study area and bathymetry mapping*

The study area is a partly sheltered bay, known as Port Elgin Bay, on the eastern side of Cape Croker in Georgian Bay (Ontario), offshore of Neyaashiinigmiing, Chippewas of Nawash Unceded First Nation (Nawash) (Fig. 2.1). Port Elgin Bay includes an active spawning shoal (the Little Port Elgin or LPE shoal) fished by Nawash since time Immemorial. The LPE shoal consists of a main spawning shoal (main LPE shoal) at 2 - 5 m depth, as well as other locations within the study area, such as an adjacent “finger” to the main shoal (near Stn 8) in slightly deeper waters (5 - 10 m), where spawning is also thought to occur (Fig. 2.2). The main LPE shoal is approximately 1 km x 0.1 km in size (44.899883 ˚N, 81.021666 ˚W, Fig. 2.2). Waters surrounding the LPE shoal are influenced by the greater Georgian Bay currents and winds, and strong undertows are present in deep waters (~70 m) east of the LPE shoal towards Hay Island. The lakebed surrounding the Bruce Peninsula is mainly composed of post-glacial dolomite, which, over time, has formed rocky and small-medium cobble substrates in waters surrounding Cape Croker (Cowell 1976). Nawash has described parts of the LPE shoal as being ‘honeycomb rock’, a flat rocky substrate with small circular holes that give the lakebed a dimpled texture. Other substrate types are also present in the study area, for example, sandy flats are at the southern edge of our study site beyond the main shoal (Fig. 2.2).

Fine-scale bathymetric mapping was completed in the study area by the Ontario Ministry of Natural Resources and Forestry (MNRF) in the summer of 2020 to inform the VPS array design (Fig. 2.2). The surveyed area was roughly 2.1 km x 2.9 km at the widest points, with recorded depths ranging from 2 -77 m. Mapping was completed using a Kongsberg M3 multibeam sonar unit and Hemisphere Vector VS330 for positional information (GPS, heading, pitch and roll). The multibeam was run using M3 software (in Profiling – Bathy mode) and data were recorded with Hypack + Hysweep (Appendix A, A1).

### *Fish Sampling and tagging*

Sampling of adult lake whitefish (n = 50; 22 females, 28 males; Appendix B, Table B1) occurred at the main LPE shoal over one week during the spawning season (21 – 27 November 2020). Lake whitefish were captured using short-set (~ 2 hrs) gill nets set and retrieved at nighttime by a SON harvester and crew using a ‘punt’ commercial fishing vessel (Fig. 2.2, Appendix C; Fig. C1). Live fish were transferred to a Bonar holding tank (2.5 x 3.5 ft) on the vessel to transport to the surgery location onshore, ~800 m north on the Nawash government dock (44.91895 ˚N, -81.014683 ˚W, Fig. 2.2).

Before surgeries, fish were transferred to a large holding tank (~34 $ft^3$) onshore (~1 m from the lake) for observation. The holding tank was continuously fed with freshwater from the lake. Individual fish deemed healthy (e.g., swimming upright, no signs of injury) were removed from the holding tank for each surgery. Surgeries occurred in a mobile tagging station set up in a trailer on the dock, where a semi-controlled environment provided optimal handling and surgical conditions **(**Appendix C, Fig. C2**)**. Individuals were anaesthetized in a buffered 120 ppm solution of tricaine methanesulfonate (MS-222) until loss of mobility, reduced gill movement, and loss of fin mobility occurred. Fish were measured before surgery for fork length (mm), total length (mm), and round weight (g; 5 fish were not measured for weight). Only fish greater than 500 mm fork length underwent surgery to ensure an adequate tag-to-fish size ratio, which is typically no more than 2% of a fish's body weight (Winter 1983).

Tagged lake whitefish had fork lengths ranging from 548 – 692 mm (609.60 ± 37.29 mm) and round weights ranging from 1.85 – 5.35 kg (3.30 ± 0.69 kg) (Appendix B, Table B1). To determine if there was a significant difference between the round weight and fork lengths of males and females, two-sample Wilcoxon tests were performed, accounting for the non-normality of the data. Fork lengths were not significantly different between males and females on the fish remaining in the dataset after HPE-filtering (see *Data filtering* below; p = 0.4976, n = 23, W = 49), but females were significantly heavier than males (p = 0.04377, n = 22, W = 26) (Fig. 2.3).

Following measurements, fish were placed into a cradle for immobilization and freshwater was irrigated slowly over the gills. In total, 50 individual fish were implanted with V16 tags from Innovasea (Bedford, NS, Canada), including 40 V16-4x-69 kHz (16 x

68 mm, 24 g in air) and 10 pressure (that provides a depth reading) V16P-4x-69 kHz (16 x 71 mm, 26 g in air) tags set to a nominal delay of 120 seconds. Tags were surgically inserted through a ~50 mm ventral incision slightly off mid-line, anterior of the pelvic fins. Fish were sexed visually, either prior to surgery (if a fish was expelling eggs or milt) or following incision (visual inspection of gonads). FLOY cinch tags were inserted (~2 cm anterior of the adipose fin) as a visual marker in case of later capture by harvesters. Incisions were closed using 2-3 box sutures depending on the incision size. Following surgeries (average surgery was 3.8 ± 0.77 min), fish were placed back into the holding tank for post-surgery monitoring (average time 11.6 ± 11.84 min) and assessed for condition (deemed excellent, great, very good, good, fair, okay, or poor), then released off the side of the dock.

### *VPS array design*

All receivers used in our study were VR2AR – 69 kHz receivers manufactured by Innovasea Ltd. (Bedford, NS, Canada). Two receivers ("sentinel" receivers) were placed in the study site during tagging in 2020 and were left out until they were incorporated into the VPS array in mid-October 2021 (Fig. 2.2). One sentinel receiver was placed at the gill netting location (Receiver ID: 549910) and the other sentinel receiver was placed just off the dock where the fish were released in 2020 (Receiver ID: 549915). These receivers were meant to provide information on the fate of tagged fish (for example, to determine if a fish immediately died following the surgery and if fish returned to Port Elgin Bay over time) and were part of a broader acoustic telemetry array deployed in Lake Huron.

The VPS array was designed using a Two-Eyed Seeing approach (Reid et al. 2021), where both local Indigenous knowledge and Western science were used to determine receiver placement. In this study, we refer to the Indigenous Ecological Knowledge of SON as SONEK (Saugeen Ojibway Nation's Ecological Knowledge) to recognize that the knowledge is specific to the First Nation from which it is derived. VPS positions are calculated from raw detections using hyperbolic positioning algorithms (Smith 2013). These algorithms are based on the time-distance-of-arrival of transmissions among receivers at fixed locations with synchronized clocks (Smith 2013, Meckley et al. 2014, Roy et al. 2014). At least three receivers are needed to 'triangulate' positions to calculate a geographic longitude and latitude location paired with a datetime stamp. The spatial extent of the main spawning shoal and study area were determined using the bathymetric map and SONEK of spawning habitat and spawning locations. Before receiver deployment, range tests were completed to assess detection range within the study area and to help inform appropriate receiver spacing (Appendix D, D1). Consultation with experts working with the Great Lakes Acoustic Telemetry Observation System (GLATOS) noted that we likely had a >1 km detection range in the study area (T Binder, C Vandergoot, and C Holbrook, personal communication). From this information, we created multiple potential designs for the VPS array and brought these to SON harvesters for input. SON harvesters noted two concerns: first, the receivers were too close, which might interfere with fishing activity on the shoal, and second, receivers would be difficult to see, resulting in the potential for entanglement with fishing gear. To accommodate these concerns, the array design was modified so receivers were placed further apart (although not compromising tag detectability) and we added a visual flag above the water surface to the receiver mooring design. Receivers were anchored with either 60- or 100-lb concrete blocks connected to the receiver with a chain and aircraft cable and with a rope running up to an 11-inch diameter subsurface plastic float. A small 10-lb mushroom anchor attached to the main anchor with a rope was marked at the surface with a flag (Appendix C, Fig. C3). The mushroom anchor was placed 2-10 m from the main anchor to prevent entanglement with the receiver. Overall, the receivers were placed no more than ~750 m (ensuring triangulation of detections), but no less than 500 m, apart (addressing harvester concerns of fishing interference).

Eleven receivers (designated as stations, ‘Stn’ 1-11) were deployed on 15 October 2021 at the study site as part of a VPS array and removed on 18 January 2022, for a total of 96 days in the water (Fig 2.2). The receivers were placed in depths ranging from ~ 5 m (Stn 2) to ~ 36 m (Stn 3). Receivers were programmed to collect hourly environmental information, including noise (dB), temperature (°C), and the number of detections with internal synctags, programmed to the same configuration as the tags implanted in the lake whitefish (see Appendix A, A2 for details).

### ***Data filtering***

From the 50 fish tagged in 2020, we analyzed the movement patterns of those fish that returned to the LPE spawning shoal and were detected on the VPS array in 2021. All analyses were conducted in R 3.6.4 (R Core Team 2022) and QGIS 3.20.1 (QGIS Development Team 2022). Initial pre-processing of detection data was completed by Innovasea Ltd.

Two fish (Fish IDs 4285 and 64620) that were detected on the VPS receivers during the VPS deployment did not have positions calculated and were filtered out of the fish positional data (herein positional data) (Appendix C, Fig. C4). Positional data were then filtered for the 50 fish that were tagged as part of this study ($n_{positions}$ = 143,338), of which removed 14,800 positions, leaving 26 fish ($n_{males}$ = 15, $n_{females}$ = 11) in the dataset. Statistical analyses were only based on data collected between 15 October – 22 December, as males were no longer in the study area after 22 December 2021.

Horizontal positioning error (HPE), calculated by Innovasea Ltd. during pre-processing from the algorithms to calculate fish positions, was provided for sync and animal tags as a relative, unitless estimate of error sensitivity (Smith 2013). An actual measured error estimate ($HPE_m$) was provided for synctag positions only, which produces a horizontal distance (m) associated with each synctag position. Typically, a significant relationship between HPE and $HPE_m$ for synctags indicates that fish positions can be filtered by a specific HPE value that is set based on project goals (Meckley et al. 2014). To filter positions using HPE, we followed Coates et al. (2013) and Tom Binder (personal communication), which involved binning HPE values (bin width = 1 - 200) and calculating the corresponding 90th percentile of $HPE_m$ (see Appendix A, A3 for more details). Based on project objectives, we determined that 10 m was an acceptable error level for each fish position. For synctag positions, a 90th percentile of $HPE_m$ at 10 m corresponded to HPE 14 for fish positions. Filtering by HPE 14 resulted in 79.4% of fish positions being retained in our dataset for further analyses (n = 113,879). However, this filtering resulted in a loss of three females in the dataset (Fish ID 64622, $n_{positions}$ = 1; Fish ID 64619, $n_{positions}$ = 1; Fish ID 4282, $n_{positions}$ = 24), leaving a total of 23 fish in our analyses. Three of the fish remaining in our dataset after filtering had depth tags.

Two fish were captured (and removed) by harvesters mid-December in both 2020 and 2021 (Fish IDs: 64602, 64592, respectively) and one fish was not detected at all post-release (Fish ID: 64588). Fish ID 64592 was used in our analyses because we had over 2800 positions before the fish was harvested. One fish (Fish ID: 4282) with a depth tag was assumed dead, or the tag expelled, in mid-January 2021 because it was detected on a single sentinel receiver for an extended period and its depth remained unchanged; that fish was removed from the dataset post-HPE filtering (Appendix C, Fig. C4).

### ***Data visualization and heatmapping***

To assess how environmental variables affect the total number of detections, mean daily noise (dB), temperature (°C), and number of detections were plotted against time. To assess the temporal presence-absence of fish over the study period in 2021, an abacus plot was created to visualize the positions of individual males and females. Day and night designations for each position were calculated by the sunrise() function in the *maptools* package, where day is sunrise to sunset and night is sunset to sunrise (Bivand and Lewin-Koh 2022). Heatmaps depicting the percentage and the number of individual males and females detected during the day and night were created using the position_heat_map() function in the *glatos* package (Holbrook et al. 2021). Mirroring the positional error, the study area for the heatmaps was divided into 10 m x 10 m grid cells.

### ***Lake depth analysis***

To quantify the extent to which males and females differed in their depth associations during the spawning season, the movement patterns of fish relative to the depth of the lake were examined. For those depth analyses, we first estimated depth of the lake at each fish position by interpolating the contour lines of the bathymetry map in

QGIS. The *TIN interpolation* tool was used to interpolate between contour lines at 1 x 1 pixel resolution and the resulting raster was converted to a scalar PC Raster map using *PCRaster* tool for further analysis. Fish positions were overlaid onto the bathymetry raster and the tool *Sample raster values* was used to obtain the lake depth at each unique fish coordinate. (See Appendix A, A4 for details.)

Mean daily lake depth was calculated per individual and averaged per sex and diel period to characterize changes over the study period. We then calculated the average lake depth displacement (m) per individual per hour for both day and night, representing the average hourly change in vertical lake depth (m) for each individual fish between day and night. These data were calculated by taking the mean lake depth per hour and then subtracting the mean lake depth from the next consecutive hour for each individual. If there was greater than 1 h gap between the consecutive hours, these data were omitted from the dataset before calculating displacement as we wanted to calculate only consecutive hourly displacement values within individuals. We averaged the lake depth data per hour to account for unequal timesteps between consecutive positions. Positive mean lake depth displacement values indicated that, on average, tagged fish were moving into shallower lake depths, while negative lake depth displacement values indicated that, on average, fish were moving into deeper lake depths. We then plotted the mean hourly lake depth displacement by day, sex, and diel period.

Three fish had depth tags which allowed an examination of the depth of the fish within the water column (i.e., the depth of the tagged fish as opposed to the depth of the lake over which the tagged fish was detected). For these depth-tagged fish, we compared the depth of the fish in the water column (explanatory variable) to the depth of the lakebed (response variable) using linear regression.

### *Distance travelled and rate of movement*

To quantify movement, the horizontal distance travelled (m; hereby ‘distance’) and horizontal rate of movement (m $s^{-1}$; hereby ‘rate of movement’) were calculated for each lake whitefish. Following procedures by Dahl and Patterson (2020), the Euclidean distance (i.e., horizontal distance; m) travelled between consecutive VPS positions was calculated as:

$$d(X,Y) = \sqrt{(X_2 - X_1)^2 + (Y_2 - Y_1)^2},$$

where $X$ and $Y$ are the local coordinates (in meters; derived from geographic longitude and latitude) for two sets of consecutive positions (1 and 2). Rate of movement (m $s^{-1}$) was calculated as:

$$Rate\ of\ movement = \frac{d(X,Y)}{(t_2 - t_1)},$$

where $t_1$ represents the time at the first position and $t_2$ represents the time at the next consecutive position.

For analyses calculating distance (m) and rate of movement (m/s), positional data were further filtered to remove consecutive timesteps that were greater than 3600 seconds ($n_{positions}$= 112,349). Filtering by time in this way mitigates potential overestimation of distances and rate of movement measurements that may occur when an individual leaves and then re-enters the array. A similar strategy was used by Dean et al. (2014) in their study of sex-specific spawning behaviour in Atlantic cod (*Gadus morhua*), where they created ‘bursts’ of individual fish positional data, which included no more than 1 h between consecutive positions to account for periodic movements outside of their array.

Rate of movement was averaged per hour per individual over the study period to account for unequal timesteps between consecutive positions. To elucidate movement patterns, rates of movement were averaged per sex and diel period for each day of the year (DOY). Total distances were calculated by summing the distance moved per individual per diel period per day and visualized by plotting averages for each sex against DOY. Additionally, to determine the distances (km) travelled for males and females during the day and night, total distance values were summed for each individual, averaged by sex and diel period, and displayed in boxplots.

### ***Statistical analyses of receiver performance and environmental variables***

A linear model was used to determine the effect of DOY on the mean daily temperature for each receiver. To assess the relationship between detections and environmental variables, two linear mixed models were developed using the *lmerTest* package (Kuznetsova et al. 2022), with daily detections as the response variable and daily noise (dB) and daily temperature (°C) as explanatory variables (Table 1). DOY and receiver were added as random variables to account for variability across days and for repeated sampling. The p-values for fixed effects were calculated from F-tests based on a Kenward-Roger approximation. Histograms of residuals and quantile plots were used to assess the normality of residuals. The models satisfied all assumptions of normality and variance.

### ***Statistical analyses of movement variables***

Linear mixed models created with the *lmerTest* package (Kuznetsova et al. 2022) were used to examine the extent to which variation in key movement variables (lake depth displacement, rate of movement, and total distance) were explained by sex and diel period (Table 2). Full models were developed for these three movement variables (i.e., the dependent variables). In the full model for lake depth displacement (m), hour of the day was added as a random effect to account for hourly variation. Individual fish was left out because this variable explained no additional variation in an earlier version of the model we ran. Predictions for the lake displacement models were reported as a vertical rate of movement in m/h. To account for repeated sampling among individuals and variation among each hour and day, random effects included individual fish, as well as hour nested within DOY in the full model for rate of movement (m/s). In the full model for total distance (m), individual fish and DOY were added as random effects. Additionally, the number of positions used to calculate each movement value was added as a covariate for both the rate of movement and total distance models.

Alternative (sub) models that included all possible combinations of explanatory variables were compared using their Akaike Information Criteria (AIC) values to choose the model of best fit (see Appendix E, Tables E1-E3 for model details). For all full and alternative models, the p-values for fixed effects were calculated from F-tests based on a Kenward-Roger approximation. For tests where Kenward-Roger could not be used due to issues with calculating degrees of freedom, Satterthwaite approximation was used instead (*lmerTest*). A p-value of $\leq 0.05$ was used to assess significance. Assumptions of normality and homogenous residuals were evaluated for each model by plotting model residuals using quantile-quantile plots and histogram plots with supplementary Levene’s tests (*car* package; Fox and Weisberg 2019). We assessed independence of residuals using autocorrelation function plots.

To test whether the mean total distance travelled over the duration of the spawning season significantly differed between males and females, we ran a two-sample Wilcoxon test of the total distances travelled by each individual with sex as the explanatory factor.

## Results

### *Annual movement patterns of fish detected on a sentinel receiver*

We noted several patterns in tagged fish in 2020-2021 detected on the sentinel receiver placed near the gill netting location (Receiver ID: 549910) during tagging in November 2020 and left in the water year-round. Only sentinel receiver ID: 549910 was used to report patterns over time as it was closest to the main LPE shoal and we wanted to avoid reporting duplicate detections due to the possibility of overlapping detection ranges between both sentinel receivers. First, 46% of fish (n = 23; $n_{males}$ = 13, $n_{females}$ = 10) were detected in the area for 1-3 months after tagging in 2020 before leaving the area; of those fish, 7 ($n_{males}$ = 6, $n_{females}$ = 1) returned and were detected on the VPS array in 2021 (Appendix C, Fig. C5). However, one of these was Fish ID 64592 that was harvested in mid-December 2020. Second, 20% (n = 10; $n_{males}$ = 4, $n_{females}$ = 6 females) of individuals were more resident in nature, either having relatively higher detections compared to other fish and/or were detected most months from tagging onwards; of those, 9 ($n_{males}$= 3, $n_{females}$ = 6) were detected on the VPS array in 2021. The remaining tagged fish (n = 16; $n_{males}$ = 11, $n_{females}$ = 5) returned to the area at various times throughout 2021; of those fish, 12 ($n_{males} = 7$, $n_{females} = 5$) returned and were detected on the VPS array in 2021.

### ***Environmental conditions and VPS performance***

During the VPS deployment (i.e., the entire time during which the VPS array was in the water), temperature (°C) consistently and significantly declined over time ($p < 0.0001$; Table 1), while no differences in temperature among receivers were observed (Fig. 2.4). There were two noticeable drops in temperature in late October and mid-November of 2021, which appeared to correspond to precipitation events (rain, ice showers) and declines in air temperature that were recorded 1-2 days prior on a nearby weather buoy (Wiarton, Ontario; 44° 44’ 39” N, 81° 06’ 31” W; operated by Environment and Climate Change Canada). In general, higher mean daily noise (dB) was associated with fewer mean daily detections (Fig. 2.4). Mean daily noise (dB) and temperature (°C) were significant predictors of mean daily tag detections ($p < 0.0001$, $p = 0.013$, respectively; Table 1). However, these models should not be used to infer detection probability, as they lack accountability for other variables that affect detection probability, such as wind, water currents, depth, anthropogenic noise, and substrate type (Kessel et al. 2013).

In total, 256,752 positions were calculated on the VPS array, of which 62% were fish positions (158,138) and 38% were synctag positions (98,614). Receivers placed in shallower water had fewer synctag positions calculated (7513 at Stn 11 to 10,524 at Stn 7) and fewer fish detections (55,124 at Stn 2 to 126,603 at Stn 5) than those set in deeper waters (Appendix C, Fig. C6, C7). However, this pattern could be the result of receivers placed in deeper water having a higher sampling volume than those in shallower water.

Synctag detections decreased as the number of fish detections increased, likely because of increased tag collisions as more fish with tags entered the array (Appendix C, Fig. C8).

### ***Patterns of occupancy on the VPS array***

The remaining results only include HPE-filtered data. The number of individual fish positions detected on the VPS array ranged from 121 (Fish ID: 64600) to 23,805 (Fish ID: 64605). On average, individual females had approximately 48% more positions calculated than males, but positions were more variable among females (7203 ± 9242.76 for females and 3750 ± 1877.07 for males). Two female fish (Fish ID: 64605, Fish ID: 64601) accounted for nearly 75.4% of the total female positions (23,805 and 19,652, respectively). Additionally, despite having twice the number of males than females, total positions for each sex were near equal (female positions = 57,629; male positions = 56,250).

To determine patterns of individual occupancy during the spawning season, we plotted the daily number of individuals detected on the VPS array. We found that fish occupancy resembled a bell-shaped curve, where there was an increase and subsequent decrease in the number of individuals detected on the array (Fig. 2.5, Table 3). To aid in the description of the results, we divided the curve into five stages (pre-activity; escalation; peak activity; de-escalation; post-activity). Before November 1, there were few individuals present and the slope of the relationship between the number of individuals and date was flat, indicating little change in number of fish arriving in the study area (‘pre-activity’). In general, the pre-activity stage included fish that were detected in the study area for a few days, hours, or once, and then left (Fig. 2.6). During the pre-activity stage, individuals of both sexes appeared for short periods of time and then left, except for two females (Fish ID: 64605 and 64601), which were present for almost the entire VPS deployment period. Between the pre-activity stage and November 24, there was a steady positive increase in the number of individuals over time (‘escalation’), and these fish were detected in the area for more extended periods of time than during the pre-activity stage (Fig. 2.5, 2.6). The height of activity (‘peak activity’) lasted for approximately one week between 25 November – 1 December, where as many as 22 fish were present per day and the number of individuals remained steady over time. After December 1, there was a decline in the number of individuals (‘de-escalation’), which ended when the number of individuals detected per day flattened and remained relatively constant (‘post-activity’). The slope of the relationship between number of individuals and date appeared steeper during the de-escalation stage than during the escalation stage, indicating that fish left the area quicker than they arrived. In the post-activity stage, no males were detected after December 22, whereas three females were still detected until retrieval of the VPS array on 18 January 2022.

The following paragraphs describe the spatial patterns of occupancy of lake whitefish during each stage of activity. During the pre-activity stage, no lake whitefish were present on the main LPE shoal (Fig. 2.7). Instead, during the pre-activity phase, males and females were mainly in deeper waters east of the main LPE shoal during the day, with females tending to be more dispersed. Both sexes were more concentrated at night during pre-activity, particularly along a 25-30 m depth ridge that runs north-south parallel to the shoreline.

There were three distinct areas used during the escalation stage (Fig. 2.8). First, males and females were concentrated along the same 25-30 m depth ridge during the escalation stage as used during the pre-activity phase, although males tended to use the deeper ridges (30-35 m) more than females at night. Second, fish appeared concentrated in the southern portion of the study area during the escalation stage, which is a gradually sloped and sandy region (Fig. 2.2). Third, males were using the main LPE shoal, where up to 53% of males were present in some grid cells (Fig. 2.8). Weekly heatmaps indicated males began occupying the main LPE shoal during 5 – 11 November, three weeks before peak activity (Appendix C, Fig. C12). However, congregations of males (which we define here as > 2 individuals per grid cell) on the shoal did not occur until the following week (12 – 18 November), when, in some grid cells, six individuals were detected. The week of 12 – 18 November was also the same week when water temperatures were consistently 10 °C or less (Fig. 2.4; Appendix C, Fig. C13). Conversely, females did not appear to congregate on the LPE shoal during the escalation stage.

During peak activity, there were clear differences between sexes in their spatial positions. Males no longer used the shelf areas north of the main LPE shoal and were found only in the shallower sandy substrate and on the main LPE shoal (Fig. 2.9). Females were still present along some of the shelf areas but were not concentrated on the main LPE shoal like males.

During the de-escalation stage, females were more concentrated on the main LPE shoal and the areas adjacent to the shoal at night, where males were also found (Fig. 2.10). During the first week of the de-escalation stage (3 – 9 December, as revealed by examining weekly heatmaps), females were concentrated on the ‘finger’ off the main LPE shoal (near to station 8; Fig. 2.2), whereas males were not (Appendix C, Fig. C16).

However, in the second week of the de-escalation stage (10 – 16 December), males were present in the ‘finger’ area, but females were not (Appendix C, Fig. C17).

During the post-activity stage, males were present only for the first two days (Fig. 2.11), while females were no longer present in either the sandy or LPE shoal area and they had returned to the shelves north and adjacent to the LPE shoal and shoreline (Fig. 2.11).

### ***Lake depth***

Both sexes occupied relatively deeper lake depths approximately two weeks before and two weeks after peak activity (11 November – 18 December 2022; Fig. 2.12). Although, at night, males tended to use greater lake depths than females during pre-activity (Fig. 2.12). A notable change occurred over 10 – 11 November (mid-escalation stage) at night when males generally moved into shallower lake depths than females and remained in locations where lake depths were ~3 m shallower than females until mid-December (Fig. 2.12). No visible sex-specific patterns in lake depth usage were observed during the day, as daily lake depths were highly variable and both sexes tended to occupy similar depths.

For the three fish that had depth tags, there was a statistically significant and strong positive relationship between the depth of the fish as determined from the depth tag and the estimated depth of the lake where the fish was located ($p<0.0001$, Appendix E, Fig. E1). Thus, the depth of the lake where fish were located was strongly related to the depth of the fish itself.

We found that lake whitefish moved into shallower waters at night and deeper waters during the day during the VPS array study period (Fig. 2.13). Depth displacements were less extreme about a week leading up to, during, and about a week after peak activity, which was particularly evident between ~07h00 - 08h00 local time (Fig. 2.13). Typically, movements into deeper waters occurred around dawn (~07h00 - 08h00 local time) and into shallower waters during sunset (~17h00 - 18h00 local time). Daytime vertical displacements for both sexes were more variable during the day than at night. On average, the vertical rate of movement of males was approximately 55.4% faster at night (0.137 ± 2.76 m/h and 0.06 ± 2.07, respectively) and 15.0% faster during the day (0.073 and 0.062, respectively) than females. Overall, diel period had a significant effect on lake depth displacement ($p = 0.034$, Table 1). Specifically, our model predicted that night had a positive effect on displacement, indicating movement into shallower lake depths at a vertical rate of movement of 0.162 m/h on average. In contrast, day had a negative effect on displacement, indicating fish were moving into deeper lake depths during the day at an average vertical rate of movement of 0.08 m/h (Table 1).

### ***Distance moved***

Between October 15 and December 22, males and females travelled similar total distances (mean of 247.67 km for females and 245.97 km for males; $p = 0.254$, $W = 290$; Fig. 2.14). Individual total distances travelled were variable, with distances ranging from 6.3 km (Fish ID: 64600) to 640.73 km (Fish ID: 64605) for females and 44.4 km (Fish ID: 4287) to 453.2 km (Fish ID: 64623) for males (Fig. 2.14). Overall, there was a significant interaction between diel period and sex on total distance moved ($p < 0.0001$, Table 1), with females moving an average 1.26 km less than males at night (1.04 km and 2.30 km, respectively for each sex). During the day, on average, females moved more than males (2.69 km and 2.04 km, respectively). Mean daily total distance moved during the day decreased gradually leading up to peak activity (25 November – 1 December 2022). for both sexes during the day but only for males at night (Fig. 2.15).

### *Rate of movement*

Between October 15 and December 22, the average rate of movement for all individuals was 0.161 (± 0.108) m/s. The average rate of movement per day for both sexes decreased gradually until a week after peak activity (Fig. 2.16; Appendix C, Fig. C23). During the day, average rates of movement were 14.4% higher for females than males (0.216 ± 0.105 and 0.188 m/s ± 0.103 m/s, respectively). The opposite was observed at night when the mean rate of movement was 29.5% higher for males than for females (0.171 ± 0.116 and 0.120 ± 0.09 m/s, respectively). There was a significant interaction between sex and diel period on mean rate of movement ($p < 0.0001$, Table 2), where the model predicted females were moving on average 0.057 m/s slower than males at night and 0.006 m/s faster than males during the day (Table 1). For the pre-activity and escalation stages, mean rates of movement were lower at night than during the day for both sexes (Appendix B, Table B2). Conversely, during peak activity, de-escalation, and post-activity stages, male rates of movement during the night were faster than during the day. Specifically, during peak activity, mean rate of movement during the day and night was 0.184 (± 0.09) and 0.143 (± 0.10) m/s, respectively, for females and 0.173 (± 0.09) and 0.204 (± 0.13) m/s, respectively, for males (Appendix B, Table B2). Overall, rates of movement were fastest during dawn (06h00 - 08h00 local time) and dusk (18h00 - 20h00 p.m.), although this was more pronounced for males than females (Appendix C, C23).

## Discussion

At an active spawning shoal in Georgian Bay (Lake Huron), lake whitefish displayed obvious patterns of diel movements and sex-specific behaviour during the spawning season. Both sexes moved into shallower waters at night and deeper waters during the day, as indicated by depth displacement patterns and the significance of diel period in our linear mixed model (Fig. 2.13). While the total distance travelled over the spawning season was similar for males and females, both sexes travelled less during the day in the lead-up to peak activity. Males furthermore showed a similar decrease in distance travelled at night leading up to peak activity whereas females did not. Rate of movement depended on whether the fish was male or female and whether it was day or night, with males moving faster at night and females moving faster during the day. We also found that lake whitefish used other areas in addition to the main spawning shoal during the study, including the southern portion of Port Elgin Bay, characterized by a sandy bottom, and depth ridges that run parallel to the shoreline. Thus, using the VPS array allowed us to characterize aspects of lake whitefish movement during the spawning season not previously described. Information gathered by our study, including habitat usage, arrival times on the shoal, and how the sexes differ in their movement could be helpful for future efforts in understanding factors contributing to variation in reproductive output, larval production, habitat use, and recruitment.

We found a distinct increase and subsequent decrease in the number of lake whitefish present at our study site in Port Elgin Bay, indicative of the duration and timing of the spawning season of lake whitefish at this particular spawning shoal. In the Great Lakes, the duration of lake whitefish spawning activity for a population typically depends on location, is related to temperature, and has been characterized as lasting for about two weeks to a month, depending on site (Goodyear et al. 1982). However, these previous observations are largely anecdotal and based on fisheries catches rather than being based on a quantitative analysis of spawning fish. In our study, we found that lake whitefish were already present in Port Elgin Bay, near the spawning shoal, 18 days before the escalation stage. The increase and subsequent decrease in individual occupancy in the area (i.e., the escalation and de-escalation phases) had a duration of about 1.5 months (2 November – 19 December; Fig. 2.6), clearly longer than the previously described 2-4 weeks by Goodyear et al. (1982). Additionally, congregations of 2 or more males began the week of November 12 when water temperatures were consistently 10 °C or less. Male presence on the main LPE shoal was last observed the week of 10 – 16 December, about a month after males began congregating. Older publications have noted the onset of spawning for lake whitefish to occur at water temperatures <6 ºC in Lake Huron (Nester and Poe 1964, Scott and Crossman 1973) and <10 ºC in Lake Ontario (Hart 1930).

Although we cannot pinpoint the exact timing and location of spawning events from our VPS study alone, our results show similarities to previous studies reporting on the timing and duration of spawning for lake whitefish. For example, in a study by Bégout-Anas et al. (1999), where lake whitefish were tracked using acoustic telemetry in a small lake in the Experimental Lakes Area (lake 226), spawning activity occurred for about three weeks and at peak intensity for about one week. In a telemetry study in Clear Lake, Maine, lake whitefish occupied depths of <5 m during October and November, presumably for spawning, although fine-scale movement information was not collected (Gorsky et al. 2012). Defining the spawning period and how it varies with environmental conditions is critical for assessing and implementing harvesting strategies, especially regarding closures during the spawning season.

The spawning period may contract or lengthen or shift earlier or later depending on environmental conditions such as temperature or demographics of the population such as number of spawning adults. For example, increased water temperatures may lead to a warmer summer and fall, resulting in delayed spawning of lake whitefish. Wahl and Loffler (2009), in their study of natural reproduction conditions of European whitefish (*Coregonus lavaretus*) in Lake Constance, Germany, estimated that a 1 °C increase in mean November temperature may lead to a spawning delay of 3.8 days. Additionally, a study of lake trout habitat in the Experimental Lakes Area in northwestern Ontario, noted that stratification was shifting later in the year, which, in turn, had likely delayed lake trout spawning over time (Guzzo and Blanchfield 2017). Given the declines in lake whitefish spawning stock biomass across most regions in Lake Huron (Cottrill et al. 2020), it is crucial to understand if variation in the number of spawning adults affects the length of the spawning period. Depending on mating strategies during times of low population abundance, the spawning period may lengthen if it takes longer for individuals to find mates or contract if they skip spawning to conserve energy. Understanding factors that affect the duration and timing of the spawning period will need long-term environmental and acoustic telemetry monitoring across multiple spawning locations for cross-site comparisons.

Male and female lake whitefish differed in the distances they travelled and the rate at which they moved during the day versus the night. Overall, the daily decrease in the rate of movement and total distance moved during the day leading up to peak activity was similar to results found by Bégout Anras et al. (1999) in their study of movement and habitat use of lake whitefish during spawning in a small, boreal lake in Ontario. Bégout Anras et al. (1999) found that for adult lake whitefish, mean distance travelled and swimming speed decreased leading up to peak spawn, although sex and diel comparisons were not made. Interestingly, we found female distance travelled neither increased nor decreased, and both sexes' movement rates increased at night leading up to peak activity, contrasting results from Bégout Anras et al. (1999). This difference may mean Bégout Anras et al. (1999) masked diel effects in their study, indicating the importance of diel period when conducting movement analyses on fish. Although the total distance covered over the study period was similar between sexes in our study, females were estimated to move less on average at night (1.04 vs. 2.30 km) and more during the day than males (2.69 vs. 2.04 km). Similarly, females tended to exhibit faster horizontal movement rates during the day, while males had faster horizontal movement rates at night (0.216 m/s and 0.188 m/s; 0.171 m/s and 0.120 m/s, respectively). These differences could arise, for example, if males are searching more actively for females on the shoal at night. This has been observed in brook trout (*Salvelinus fontinalis*) in Scott Lake, Ontario, where males were highly mobile and revisited spawning sites multiple times in search of mating opportunities (Blanchfield and Ridgeway 2022). Although we cannot speak directly about male-male competition, the overlapping space use observed for males coupled with a higher occupancy of the main shoal than females in our study may indicate there is endurance rivalry in males (the ability to stay reproductively active throughout the spawning season), which has been documented in other salmonids, like arctic charr (*Salvelinus alpinus*) (Johnson 1980, Esteve 2005). Differences in the rates of movement between the sexes also have implications for bioenergetics, for example, in understanding how the reproductive costs of spawning vary between males and females (Koch and Wieser 1983). Lake whitefish bioenergetic models (e.g., Rudstam et al. 1994; Madenjian et al. 2006, 2013), which rely on laboratory-derived parameters, or make assumptions based on estimates collected for other species, would benefit from having field-based sex-specific rates of movement measured during the spawning period, such as those provided by our study.

We found that both sexes of lake whitefish moved into shallow waters during the night and into deeper waters during the day. However, males moved more quickly both during the night into shallower depths and during the day into deeper depths than did females. The sex-specific vertical rate of movement estimates mirror our heatmap results as males were generally observed to move onto the main LPE shoal more often, and in higher concentrations, than females during the spawning period. Gorsky et al. (2012) found lake whitefish exhibited strong diel vertical migrations, where tagged fish had higher vertical velocities during daylight hours than during nighttime hours; this result is mirrored by our lake depth displacements, where both sexes exhibited larger amplitudes of displacement during the day versus the night (Fig. 2.13). Understanding the vertical depth associations of lake whitefish may be important for defining the spawning period. In the Binder et al. (2016) study of lake trout spawning site fidelity in Lake Huron, the spawning period was defined by male lake trout moving from deep offshore water into shallower nearshore water, where males tend to arrive earlier and are in higher numbers than females on spawning shoals.

Evidence of spawning site fidelity was observed among our tagged male and female lake whitefish. More than half of the fish tagged during the spawning season at our study site in 2020 returned to the study area during the spawning season in 2021, which was observed for both males and females. Interestingly, 20% of tagged lake whitefish remained in the study area almost year-round. In contrast, other lake whitefish left for an extended period or for repeated, shorter durations before returning in 2021 during the spawning season. This indicates that lake whitefish not only show spawning site fidelity but that individuals in this population show residency at this site year-round. A quantitative analysis of spawning site fidelity for lake whitefish based on telemetry would require additional years of data, as is the case, for example, if running Cormack-Jolly-Seber models which require at least three years of data (Binder et al. 2016b, Hayden et al. 2018). Evidence of spawning site fidelity has been shown previously for lake whitefish in Lake Superior and Lake Michigan; for example, multiple fish have been recovered at the same spawning site on the same day 1-4 years after tagging (Ebener and Copes 1985; Walker et al. 1993; Ebener et al. 2010; Ebener et al. 2021). There is also evidence of stock structure of lake whitefish within the Great Lakes that indicates distinct spawning populations. Having this stock structure means that at least some proportion of fish show spawning site fidelity. For example, Stott et al. (2012) identified four genetically distinct spawning populations of lake whitefish in the northern main basin of Lake Huron. A limitation of our VPS study is that we could not determine the fate of fish tagged in 2020 that did not return to Port Elgin Bay in 2021 (note that this information is forthcoming from a lake-wide acoustic telemetry array that has been deployed; see https://glatos.glos.us/map. Thus, these missing fish could have died, went elsewhere to spawn, or did not spawn. However, the benefits of a VPS are that we can, with greater certainty, state that the fish that return to a spawning location are likely there to spawn as their movements and residency within the spawning area can be tracked. A combination of genetic analysis and acoustic telemetry will provide a powerful tool for further understanding stock structure and identifying unique spawning populations in the Great Lakes. Such knowledge will support critical management decisions related to harvest allocation (Ebener et al. 2021).

We found evidence that lake whitefish used various locations other than the main spawning shoal within Port Elgin Bay during the spawning season. From our heatmapping, both sexes used deep ridges (~25-30 m) that run parallel to shore, which connect the southern and northern sections of the study area, although females tended to also use these areas during peak activity and one week thereafter, whereas males did not (Fig. 2.9; Appendix C, C17). Regarding shoal use, males concentrated on the main LPE shoal at night from two weeks before pre-activity (12 –18 November) until two weeks after peak activity (10 –16 December). Females, on the other hand, were positioned on the shoal only during peak activity and the subsequent week and appeared to show less spatial overlap among each other (3 – 9 December). These results concur with lake trout mating strategies observed in the Great Lakes, where males tend to be captured more significantly and congregate more on spawning sites than females (Muir et al. 2012). Male congregations are consistent with a bet-hedging strategy where males maximize their encounters with females by remaining at a high-quality spawning site while awaiting the arrival of females (Leggett 1977, Krebs and Davies 1993). During the day, males and females in our study tended to favour areas that SON community members identified as being sandy substrate, particularly over the escalation to de-escalation stages. According to a local SON harvester, lake whitefish use these sandy areas for feeding (as they are productive and have food); as spawning approaches, females rub their bellies on the substrate to loosen up their eggs. The use by lake whitefish of areas and habitats beyond the main spawning shoal is important information for management. This information could support, for example, efforts towards habitat restoration or protected area designations to aid in a population's rehabilitation.

There were limitations in this study that we would like to acknowledge. First, we provided results from only one spawning period at one spawning location with a relatively small and male-dominant sample size (15 males and 8 females). Multiple years of observations from more than one spawning site would be needed to corroborate the behaviours we observed and to build a more broadly applicable lake whitefish spawning behaviour conceptual model, like what was done for lake trout **(**Binder et al. 2021, Marsden et al. 2021). Second, obtaining a higher proportion of females during sampling should be a priority for future studies of spawning behaviour, as two females in this study dominated most female positions calculated in our telemetry array (~75%). Third, we do not know precisely where and when lake whitefish spawned, including whether they spawned at all or where embryos might have settled. Our heatmaps give us an idea of where potential spawning hotspots were; however, there was roughly 10 m of error surrounding our positions owing to the criteria for HPE filtering and based on the size we set for our grid cells. Future studies should consider using divers (Binder et al. 2018), egg mats (Marsden et al. 2001), or ROVs (Pacunski et al. 2008), to not only confirm spawning, but to begin characterizing the spawning habitat that lake whitefish are using.

Fortunately, we had Saugeen Ojibway Nation Ecological Knowledge to help interpret some of these spatial patterns and to identify the location of the main spawning shoal in our study. Ebener et al. (2021) recommended that an important step in understanding lake whitefish recruitment would be understanding the productive capacity, quantity, and distribution of lake whitefish spawning habitat. Coupling a VPS study like ours with detailed substrate mapping and sampling of early life stages (e.g., eggs, larvae) would provide a way for quantifying the productive capacity of a spawning shoal as a function of key variables such as how much spawning habitat is available. Finally, because our horizontal distances were calculated based on Euclidean straight-line distancing, our values underestimated the true distance travelled, which is a common issue with summing the straight-line displacement between discretely sampled locations (Rowcliffe et al. 2012). Methodologies exist to combat this underestimation issue, such as using high residency positioning systems (Guzzo et al. 2018) or data analysis methods where time-movement modelling frameworks can estimate movement rate and distance travelled at a higher accuracy than traditional methods (Noonan et al. 2019).

Working in close collaboration with the SON, fine-scale acoustic telemetry allowed us to quantify the movement and space use of male and female lake whitefish during the spawning season. As Brenden et al. (2010) recommended, by taking a fine-scale look at spawning locations, researchers can tease out factors affecting lake whitefish recruitment. Our detailed examination of sex-specific movements during the spawning season will hopefully lead to future work aimed at understanding linkages between spawning behaviour, environmental conditions, habitat quality, and recruitment. Future work, for example, could characterize substrate, habitat quality (e.g., whether dreissenid mussels are present), and the presence of egg predators, all of which could influence embryo survival and recruitment (Ebener et al. 2021). The significant declines of lake whitefish in many regions of the Great Lakes threaten the ecosystem services that these fish provide. Understanding the causes of these declines and identifying potential management actions are priorities for natural resource management agencies and First Nations (Ebener et al. 2021, Almack et al. 2023). As shown for many aquatic species (Dean et al. 2014, Binder et al. 2018, Dahl and Patterson 2020, Withers et al. 2021), fine-scale acoustic telemetry offers promise for filling significant knowledge gaps on the spawning behaviour and habitat use of fish as they face stressors like invasive species, climate change and overexploitation.

# CHAPTER 3: GENERAL DISCUSSION

Lake whitefish are an important economic, ecological, and cultural species, yet we know surprisingly little about their spawning behaviour. Economically, lake whitefish support one of the largest commercial fisheries in the Great Lakes, where in Lake Huron specifically, they represented 65-77% of the total commercial yield between 2011-2017 (Cottrill et al. 2020). Ecologically, lake whitefish are a key linkage between benthic and pelagic ecosystems, facilitating energy flow between nearshore and offshore regions (Rennie et al. 2009). Culturally, Indigenous communities hold a deep connection to lake whitefish around the Great Lakes, as they are an important subsistence fishery and important in ceremonial practices (Almack et al. 2023).

Despite declines in lake whitefish yield and recruitment since the 1990s in all Great Lakes except Lake Superior, and despite the economic and ecological importance of lake whitefish, we know little about the species' spawning behaviour. Most information on lake whitefish spawning behaviour is derived from historical studies (Loftus 1980, Goodyear 1982), or has been gathered from inland lakes (Bégout Anras et al. 1999, Gorsky 2012), without accounting for sex-specific differences. Through my thesis research, I was able to fill some of the existing knowledge gaps by quantifying the degree to which males and females differ in their diel movement patterns at an active spawning shoal in Georgian Bay during the spawning season of 2021. Important next steps in this work would be to examine trends in spatial movements and temporal presence over multiple spawning seasons and at other spawning shoals within the Great Lakes.

The goal of my thesis was to evaluate the sex-specific spawning behaviour of lake whitefish using fine-scale acoustic telemetry to update our current understanding of this crucial part of the species' life history. Specifically, I compared the dates of lake whitefish arrival and departure from the study area, spatial use of the spawning shoal and surrounding area, associations with lake depth, distances travelled, and rates of movement between males and females during both the day and night over the duration of the spawning period. I determined there was a clear increase and decrease in the occupancy of individuals in the study area for about 1.5 months between 2 November – 19 December 2022, where 22 of 23 returnees were present at a peak activity period for one week's time. Additionally, I observed distinct diel vertical movements throughout the spawning period, where fish moved into shallower waters during the day and deeper waters at night. Furthermore, I determined that there was a significant interaction between sex and diel period for both rate of movement and total distance travelled, where males tended to move faster and for longer distances than females during the night, and females moved faster and for longer distances during the day. I also determined that at night during the period of peak activity, males tended to congregate in shallow, shoal areas whereas females occupied sandy substrate and were rarely observed in congregations. However, during the day at peak activity, both sexes occupied similar areas, including sandy substrate and depth ridges that run parallel to the shore. These findings indicate that lake whitefish in Port Elgin Bay during the spawning period use multiple habitats over roughly a month and a half, providing information that may be relevant to managers for protecting spawning fish or their habitat during the reproductive season.

Habitat degradation is one of the main causes of biodiversity loss (Brooks et al. 2002). By densely covering the bottom of lakes, the proliferation of dreissenid mussels in the Great Lakes may be reducing the availability of quality habitat and may act as a behavioural deterrent for spawning fish (Furgal et al. 2018). Lake whitefish spawning substrate tends to be described as cobble and rocky substrates, where honeycomb-shaped rock is frequently mentioned as well (Hart 1930, Scott and Crossman 1973, Goodyear et al. 1982, Bodaly 1986). The divots and interstitial spaces in these rocky and cobble substrates provide embryos with protection from wind, currents, and predators, as well as a sufficient oxygen supply while they incubate overwinter (Gunn 1995, Schaefer 2019). However, dreissenid mussel colonization in the Great Lakes may degrade the spawning habitat of lake whitefish, by inhibiting the penetration of embryos into the interstitial spaces and potentially damaging the embryos through their sharp shells. Evidence by Marsden and Chotkowski (2001) in their study of spawning lake trout on fouled vs. newly constructed artificial reefs in Lake Champlain, has shown zebra mussel colonies may discourage lake trout from spawning, damage eggs, and increase egg vulnerability to large-bodied predators. Unfortunately, we do not know whether dreissenid mussel colonization affects lake whitefish embryo survival, egg deposition, or adult decisions of where to spawn (Ebener et al. 2021). An updated understanding of the status of lake whitefish spawning grounds is needed to assess the extent of dreissenid mussel colonization at individual spawning shoals and whether there is an associated impact on lake whitefish recruitment. The map of spawning shoals in the Great Lakes by Goodyear et al. (1982) was published before the dreissenid mussel invasion. Substrate mapping would be useful in both identifying and describing contemporary lake whitefish spawning habitat as a step towards understanding how poor-quality spawning habitat may contribute to a lack of recruitment across the Great Lakes.

A potentially important variable not considered in this study is how the lunar cycle might affect the spawning behaviour of lake whitefish. SON members have identified an interest in further examination of the role of the lunar cycle in the timing of lake whitefish spawning. Lunar synchronization of spawning is well-known for marine reef species, where the phase of the moon can cue spawning, gonadal development, and the production of reproductive hormones (Takemura et al. 2010). For example, tiger groupers (*Mycteroperca tigris*) typically spawn within 2-10 days following the full moon (Starr et al. 2018), whereas rabbitfish (Saganidae) spawn in relation to the new moon (Takemura et al. 2010). How the lunar cycle affects the spawning behaviour of freshwater fish is less well-known, although some studies do exist. Binder et al. (2010) in northern shore Lake Ontario tributaries found no evidence that the lunar cycle was related to the migratory activity of spawning-phase sea lamprey. Conversely, spawning activity of a closed population of lake sturgeon in Black Lake, Michigan increased in relation to the onset of the new moon (Forsythe 2012). Although no studies to my knowledge have focused on how the lunar cycle affects lake whitefish spawning specifically, Ransom et al. (2021) noted peaks in lake whitefish densities and spawning activity occurred with periods of full and new lunar illumination in the Fox and Menominee Rivers, Lake Michigan. Next steps for my dataset could be to visualize the rate of movement, distance moved or heatmaps in relation to the lunar cycle. However, a proper analysis on how the lunar cycle affects spawning behaviour of lake whitefish would require additional years of data.

Another variable that could affect the timing or duration of lake whitefish spawning is temperature. From my study, it appears that spawning may have occurred when temperatures fell below 10°C, generally similar to previous lake whitefish spawning temperatures reported within the Great Lakes (Goodyear 1982). Considering the warmer water temperatures occurring as a result of climate change, understanding how temperature may affect the spawning behaviour of lake whitefish is critical for predicting future fluctuations in the timing, or length, of the spawning period. Although no conclusions regarding fish biometrics are made in relation to temperature, I did obtain detailed temperature data across Port Elgin Bay that, if paired with multiple years of data, could be used to predict the onset of spawning of lake whitefish as a function of temperature and to better understand how changes in temperature might affect the bell-shaped activity curve.

An aspect missing from my thesis was a specific analysis of lake whitefish behaviour during the crepuscular period. Although I observed heightened rates of movement and larger lake depth displacements during dawn (06h00 – 08h00) and dusk (18h00 – 20h00) through my lake depth displacement analyses (Fig. 2.14), I did not include crepuscular times as an explanatory variable in my modelling of distance, rate of movement or lake depth displacement. Many species, including Atlantic sturgeon (*Acipenser oxyrhynchus oxyrhynchus*), lionfish (*Pterios* spp.), Atlantic cod (*Gadus morhua*), and yellow perch (*Perca flavescens*) display heightened activity during crepuscular times, mainly due to predator avoidance, foraging, or a combination of both (Reubens et al. 2013, McLean et al. 2014, McCallister et al. 2018, Matley et al. 2022b). Increased activity during crepuscular periods has also been observed for coregonids.

Gjelland et al. (2004) quantified the average swimming speed of European whitefish and cisco and found that during periods of twilight and low incident light, swimming speeds were higher than during darkness (16-18 and 8-10 cm/s, respectively). Given that the lake whitefish tagged in my study were large adults, it is unlikely the increased activity during crepuscular periods was because of predator avoidance, but rather, primarily from movement onto spawning shoals and feeding. For future analyses or visualizations of movement, it may be beneficial to include crepuscular times as explanatory variables to see if more variation can be explained by the movement models.

Saugeen Ojibway Nation Ecological Knowledge (SONEK) was a crucial component of this study. SONEK guided the objectives, methods, and helped with the interpretation of the findings. Local knowledge was critical for capturing spawning fish for tagging and aiding in the design of the VPS array. I was fortunate to be able to speak directly with an experienced SON harvester and discuss my results with them. This helped immensely with the interpretation of some of my observations of movement. For example, the harvester shared that females were known to use the shallow, sandy area to the south of the main shoal to rub their bellies on and loosen eggs, which helped me to better understand my heatmaps showing females occupying this area. Indigenous perspectives and involvement are often left out of research studies such as mine (Berkes 2018). The Two-Eyed Seeing framework is a way to help guide collaboration and bridge between Indigenous and non-Indigenous knowledge systems (Almack et al. 2023). I have shared my results with SON members, including at a Pow-Wow and community meeting, and at seminars and meetings attended by SON members engaged in the research. Moving forward, the results from this project should continue to be shared with SON members in conjunction with some of the other aspects of the Bima'azh and Together with Giigoonyag projects, including the SONEK parts of these studies. Seeing as both SONEK and western science are equal parts of these projects, both perspectives should be included when interpreting results.

While no direct links were made between spawning behaviour and factors that affect lake whitefish recruitment, my thesis highlights the value of using fine-scale acoustic telemetry in conjunction with Indigenous Ecological Knowledge to study sex-specific spawning behaviour. Through the integration of bathymetric mapping and fine-scale telemetry, I was able to add to our knowledge of sex and diel-specific movement and spatiotemporal activity of lake whitefish during the spawning period, which could have management implications. For example, I found lake whitefish used multiple habitats other than the spawning shoal. Therefore, if the protection of spawning shoals is considered a management action, a boundary beyond spawning shoals should be considered for protection as well. Additionally, I found an increased presence of lake whitefish for about 1.5 months in Port Elgin Bay, providing an indication of the span of the spawning season at that location. Therefore, if fishing closures are implemented, the duration of spawning should be used to guide those efforts. A long-term and cross-site dataset would further increase our understanding of reproductive productivity and stock resilience of lake whitefish while they continue to face declines in recruitment and impacts from climate change and invasive species.

Table 1. Final models to assess the relationships between independent variables of day (n = 96), mean daily temperature (n = 1056; °C), and mean daily noise (n = 1056; dB) and dependent variables (mean daily temperature (°C) and mean daily detections (n = 1056) across all receivers during deployment. Bolded p-values represent a significant result ($p<0.05$).

| Final models with main and (random effects) | Variables / Parameters | Estimate (Direction of effect) | Std. Error | F-value | P-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| Mean Temperature ~ Day | Intercept | 299.5 | 12.65 | - | - | |
| | Day | $-1.816 \times 10^{-7}$ (-) | $7.724 \times 10^{-9}$ | 54.481 | **<0.0001** | 0.852 |
| Mean detections ~ Mean temperature + (1\|Receiver) + (1\|Day) | Intercept | 66.421 | 5.422 | - | | |
| | Mean Temperature | 1.129 (+) | 0.450 | 6.282 | **0.0133** | 0.705 |
| Mean detections ~ Mean noise + (1\|Receiver) + (1\|Day) | Intercept | 116.400 | 6.645 | - | - | |
| | Mean Noise | -0.183 (-) | 0.025 | 54.481 | **<0.0001** | 0.700 |

Table 2. Final models to assess the relationships between various independent (sex; diel period; number of positions) and dependent (mean hourly lake depth displacement in m/h, n = 12,788; total distance in m; n = 1370; rate of movement in m/s; n = 13,107) variables. Hour (hour of the day), Day (each day of the study period), and Individual fish (unique IDs of the fish) were included, but varied, as random variables among the models. Bolded p-values indicate a significant result ($p<0.05$).

| Final models with main and (random effects) | Variables / Parameters | Estimate (Direction of effect) | Std. Error | F-value | P-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| Mean hourly lake depth displacement ~ Diel + (1\|Hour) | Intercept | -0.077 (-) | 0.276 | - | - | |
| | Diel | 0.239 (+) | 0.110 | 4.716 | **0.030** | 0.220 |
| Total distance ~ Sex + Diel + Number of positions + Sex:Diel + (1\|Day) + (1\|Individual fish) | Intercept | 2041.533 (+) | 246.503 | - | - | |
| | Sex | 646.999 (+) | 328.788 | 0.947 | 0.341 | 0.512 |
| | Diel | 255.243 (+) | 119.283 | 40.277 | **<0.0001** | |
| | Sex:Diel | -1902.521 (-) | 204.386 | 86.648 | **<0.0001** | |
| | Number of positions | 21.914 (+) | 1.169 | 351.461 | **<0.0001** | |
| Rate of movement ~ Sex + Diel + Number of positions + Sex:Diel + (1\|Day/Hour) + (1\|Individual fish) | Intercept | 0.214 (+) | 0.007 | - | - | |
| | Sex | 0.006(+) | 0.007 | 12.303 | **0.002** | 0.449 |
| | Diel | -0.028 (-) | 0.008 | 498.644 | **<0.0001** | |
| | Sex:Diel | -0.063 (-) | 0.003 | 363.200 | **<0.0001** | |
| | Number of positions | -0.009 (-) | 0.003 | 16.788 | **<0.0001** | |

Table 3. Description of stages of occupancy in Port Elgin Bay between 15 October 2021 – 18 January 2022. Includes dates (number of days), stage characteristics, cumulative number of individuals, ratio of males to females, and ratio of number of telemetry positions between males and females.

| Stage | Date (number of days) | Stage characteristics | Cumulative number of individuals observed (during each stage) | Number of individuals male:female | Number of telemetry positions male:female |
|---|---|---|---|---|---|
| ‘Pre-activity’ | 15 Oct – 1 Nov 2021 (18) | Few individuals present and relatively little change in occupancy over time | 19 | 12:7 | 3980:10863 |
| ‘Escalation’ | 2 – 24 Nov 2021 (23) | A steady increase in occupancy over time | 22 | 15:7 | 29040:17991 |
| ‘Peak activity’ | 25 Nov – 1 Dec 2021 (7) | Maximum number of individuals present and little change in occupancy over time | 22 | 15:7 | 6042:4468 |
| ‘De-escalation’ | 2 – 19 Dec 2021 (18) | A steady decrease in occupancy over time | 20 | 15:5 | 17090:7255 |
| ‘Post-activity’ | 20 Dec 2021 – 18 Jan 2022 (30) | Few individuals present and relatively little change in occupancy over time | 4 | 1:3 | 98:17052 |

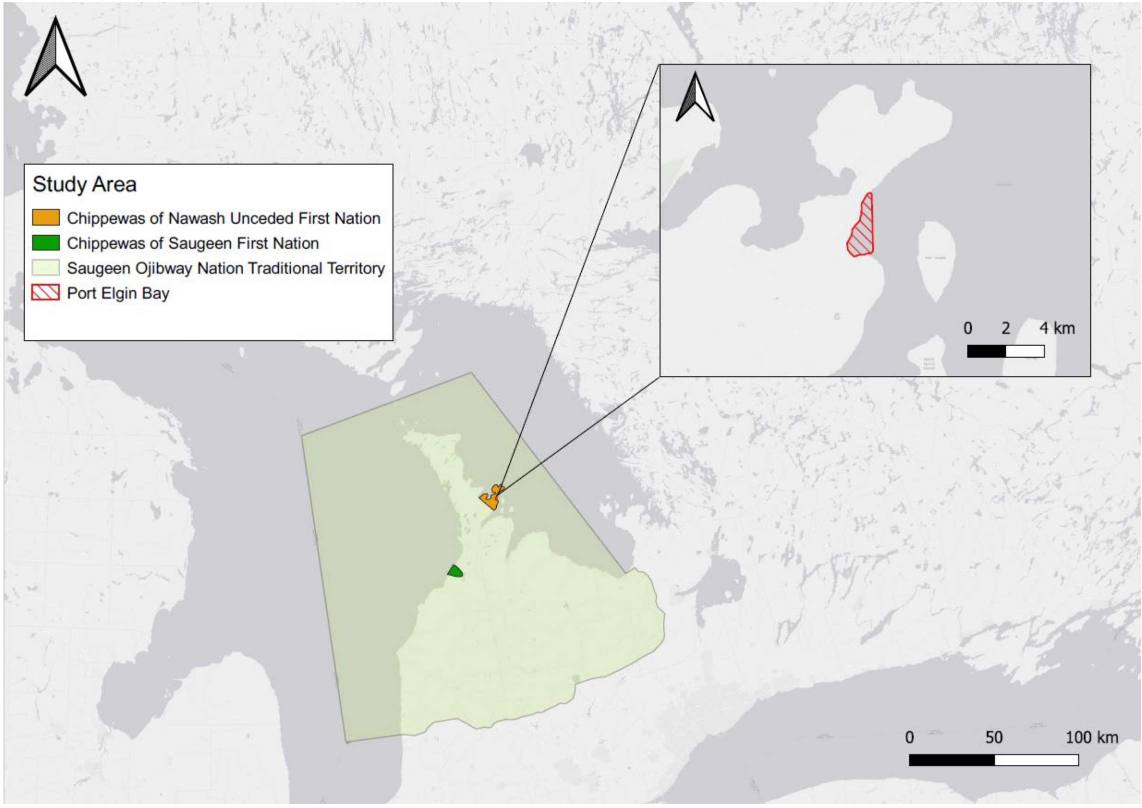

Figure 2.1. Map of the study area, Port Elgin Bay (red shading), located in Georgian Bay, Lake Huron. Port Elgin Bay is offshore of the community of Neyaashiinigmiing of the Chippewas of Nawash Unceded First Nation. Chippewas of Saugeen First Nation is the sister First Nation to the Chippewas of Nawash Unceded First Nation, collectively known as the Saugeen Ojibway Nation.

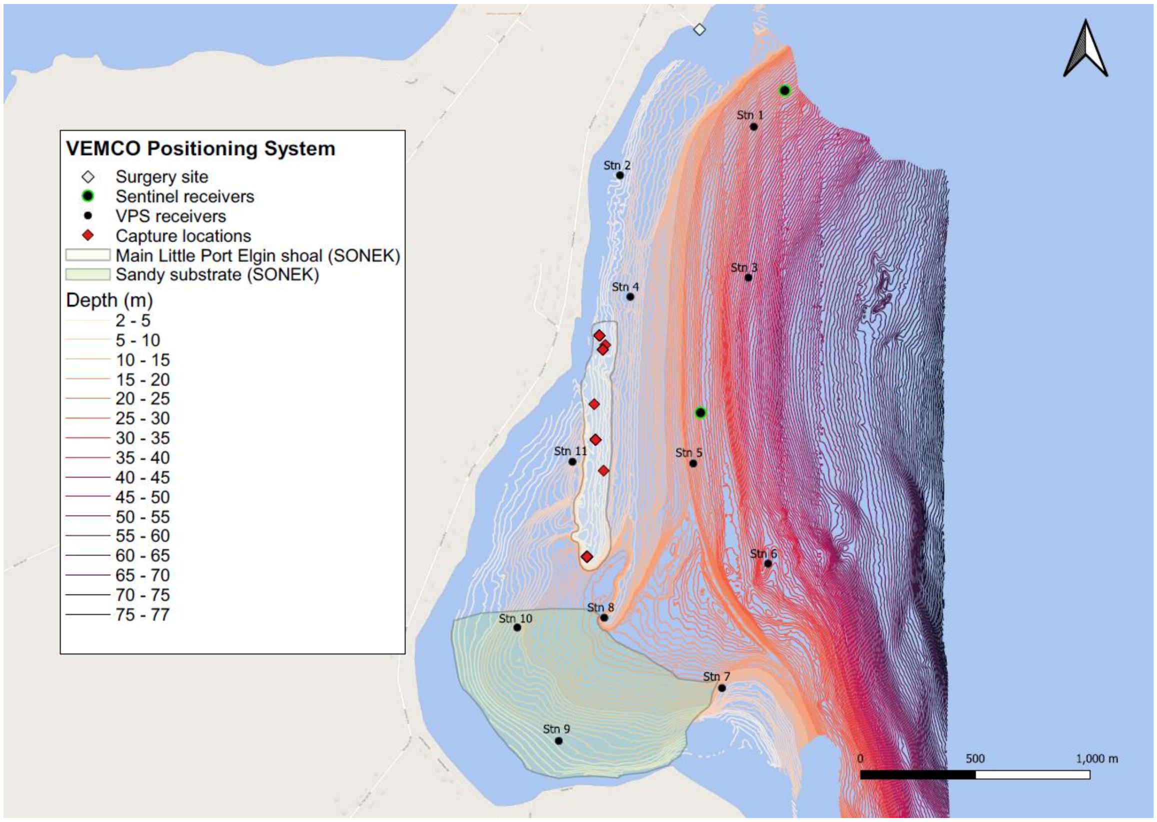

Figure 2.2. Map of the VEMCO Positioning System (VPS) study area in Port Elgin Bay (Georgian Bay, Lake Huron) showing VPS receivers, lake whitefish capture locations, surgery site, and sentinel receivers. Sandy substrate (green) and the main spawning shoal (white) within Port Elgin Bay are shown as polygons. The polygons were informed by Saugeen Ojibway Nation Ecological Knowledge (SONEK).

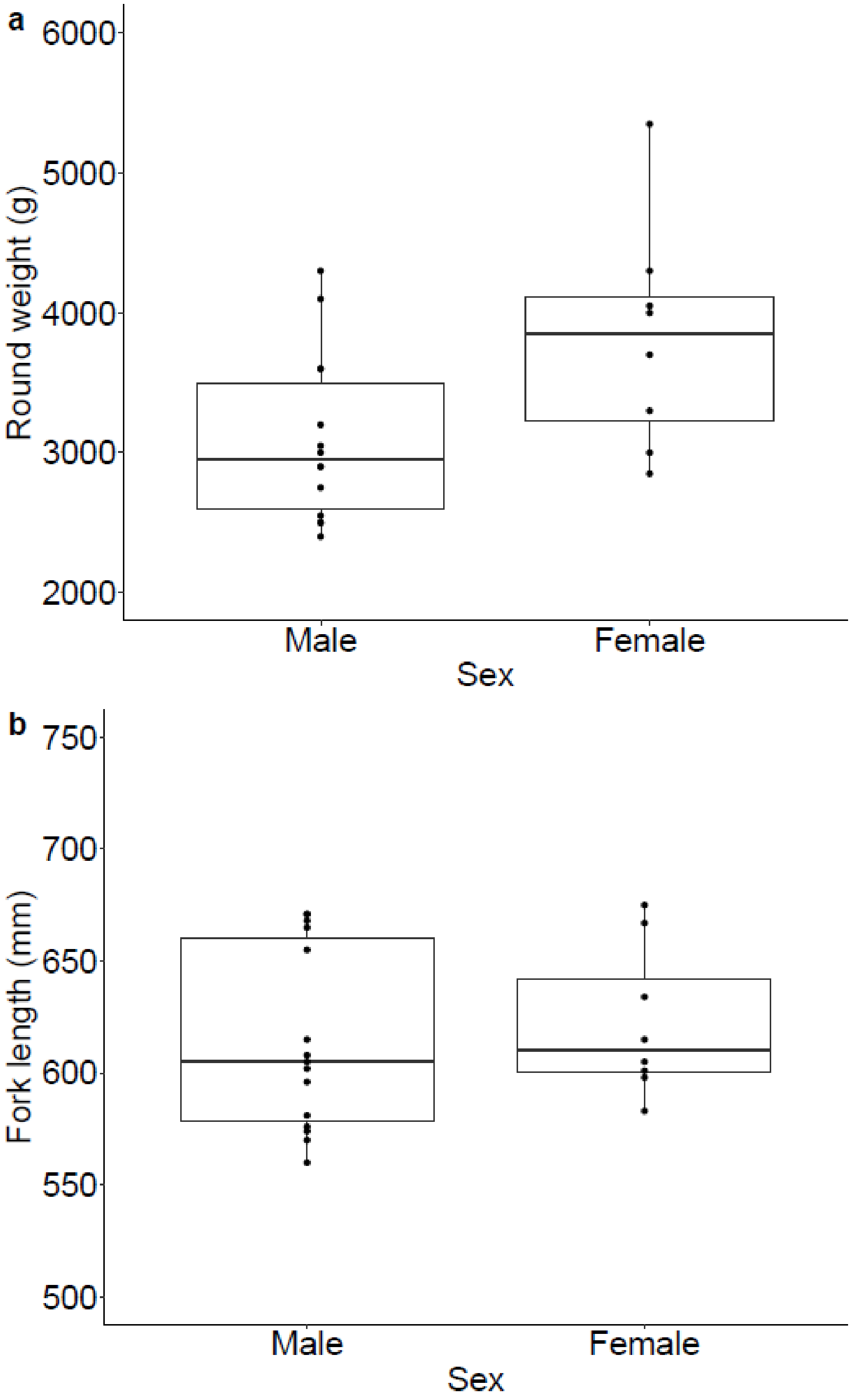

Figure 2.3. Boxplots depicting the median and upper and lower quartiles of round weight (a) (g) and fork length (b) (mm) of male ($n_{fl} = 15$; $n_{rw} = 14$) and female (n= 8) lake whitefish.

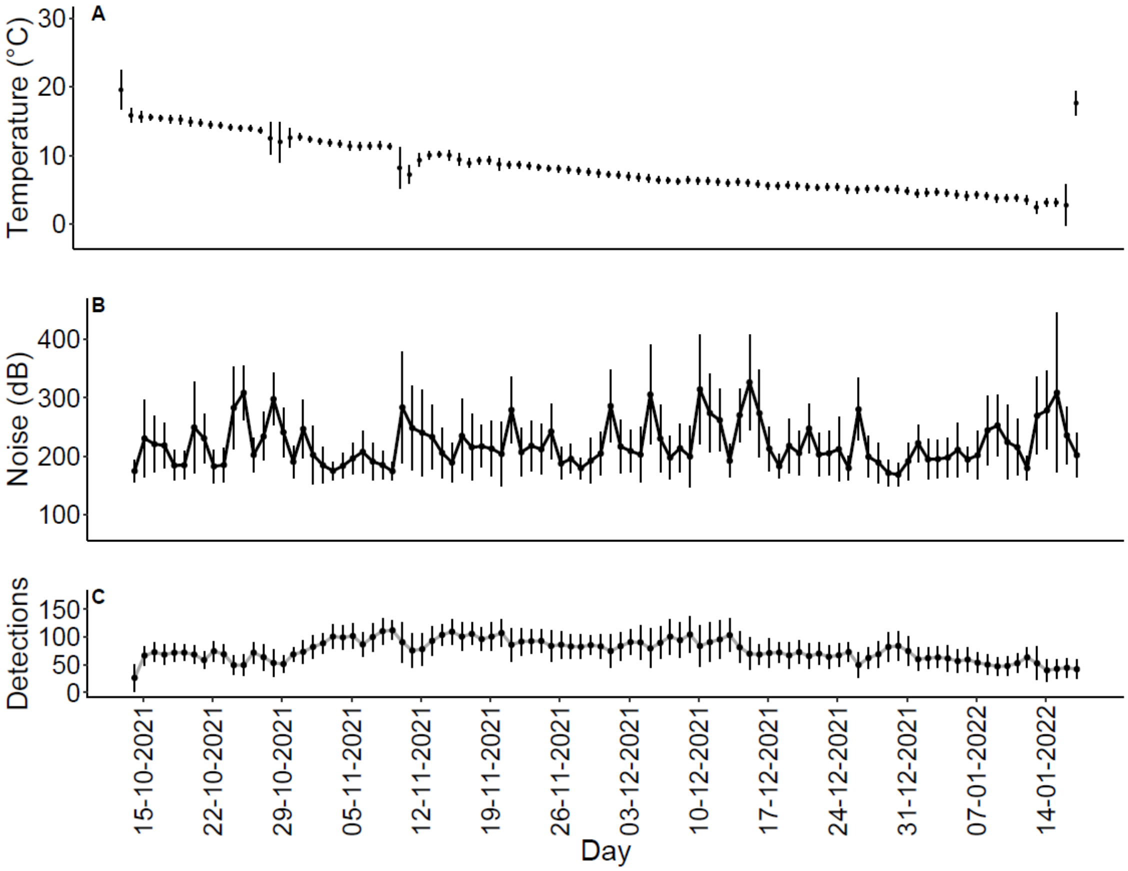

Figure 2.4. Mean daily temperature (°C) (a), noise (dB) (b), and detections (c) measured at 11 receivers in Port Elgin Bay, Lake Huron. Values were recorded on receivers once per hour.

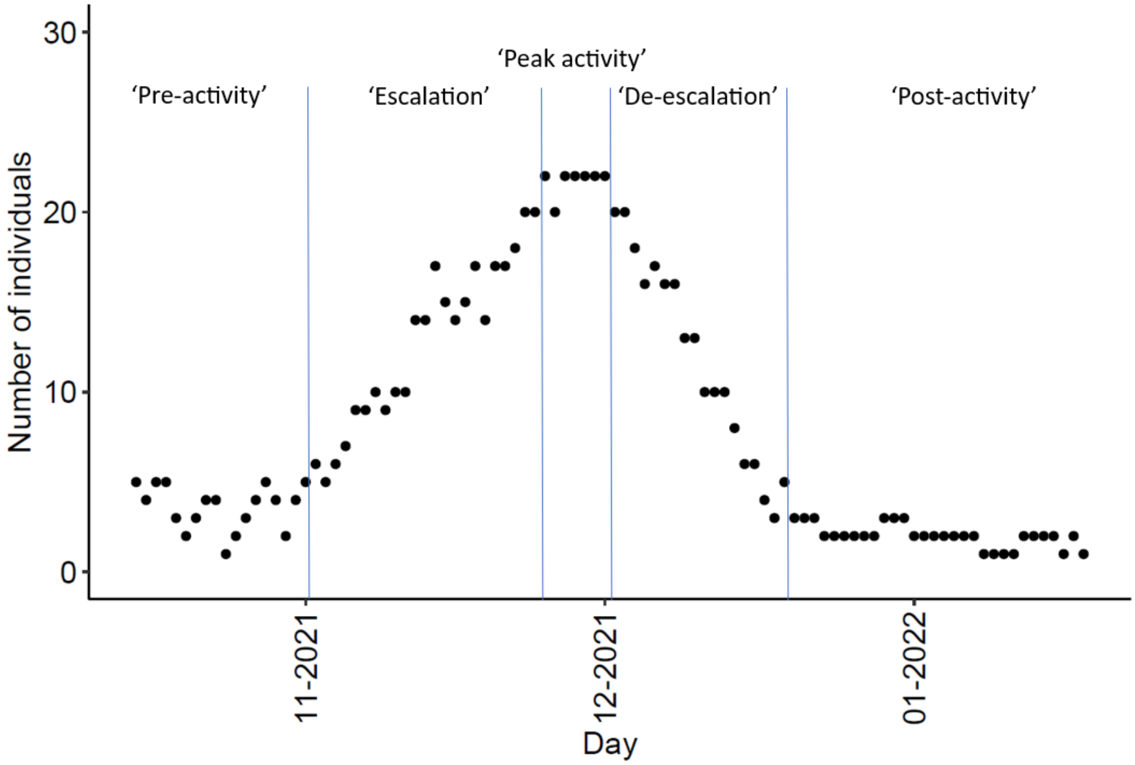

Figure 2.5. The number of individuals detected per day during the VEMCO positioning system deployment, in Port Elgin Bay, Neyaashiinigmiing, Ontario, Canada. Five stages of activity are depicted based on patterns of occupancy.

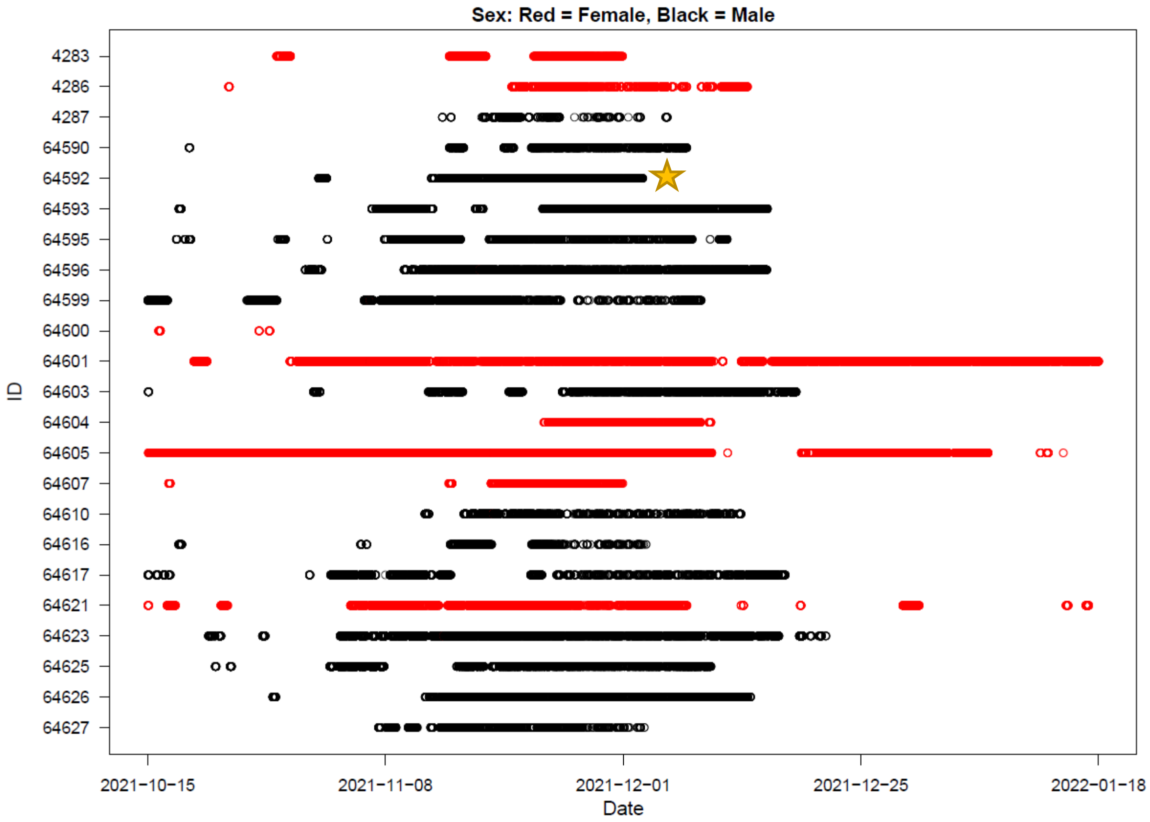

Figure 2.6. Abacus plot displaying the presence-absence of individual lake whitefish (ID are the fish’s unique identifier) over the study period (15 October 2021 – 18 January 2022). Each open circle represents one position. Red represents females and black represents males. The yellow star represents the date when Fish ID 64592 was harvested.

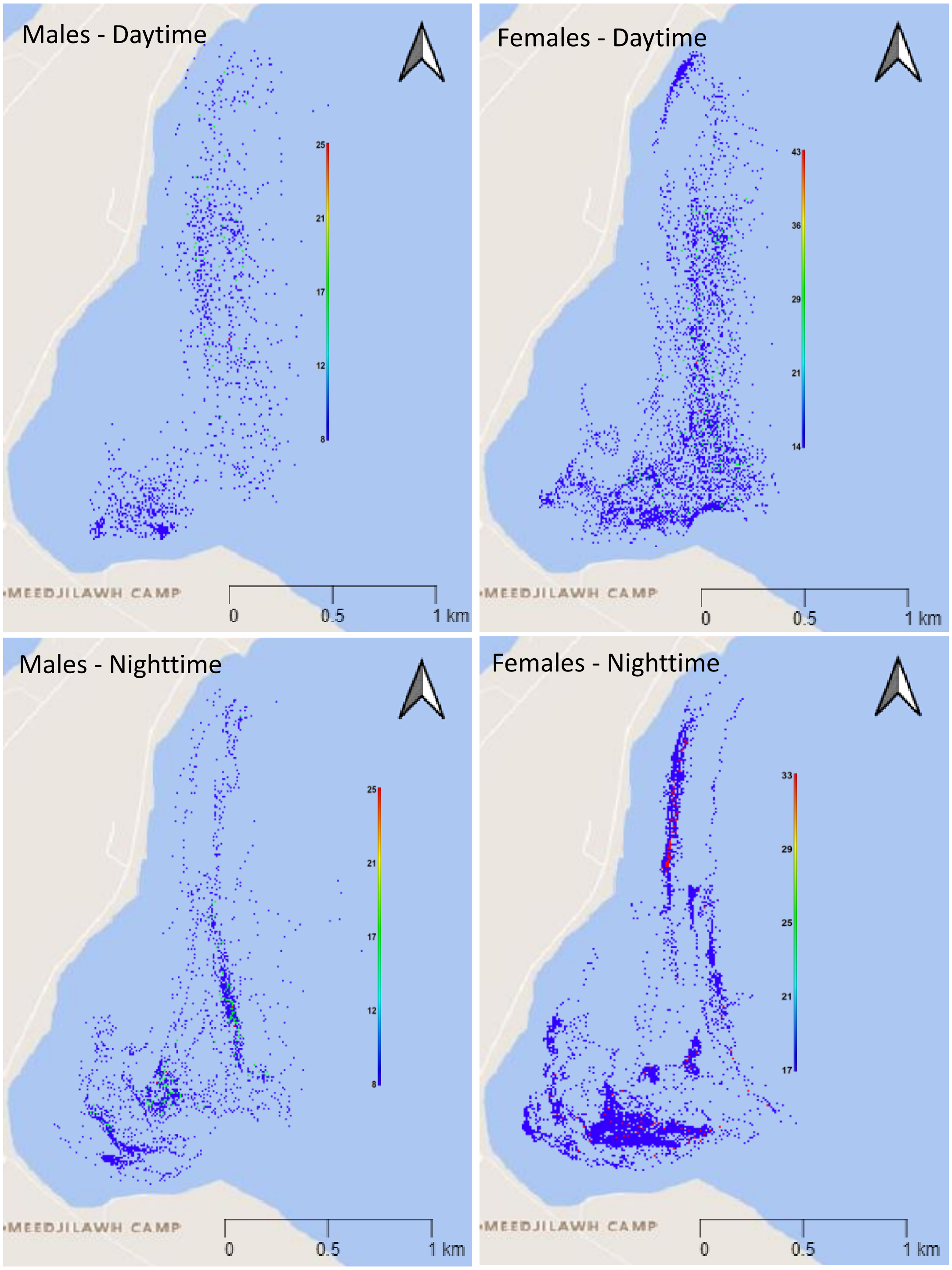

Figure 2.7. Heatmap displaying the percentage of male (n = 12) and female (n = 7) lake whitefish in each grid cell (10 m x 10 m) in the study area during the pre-activity stage (15 October - 1 November 2021).

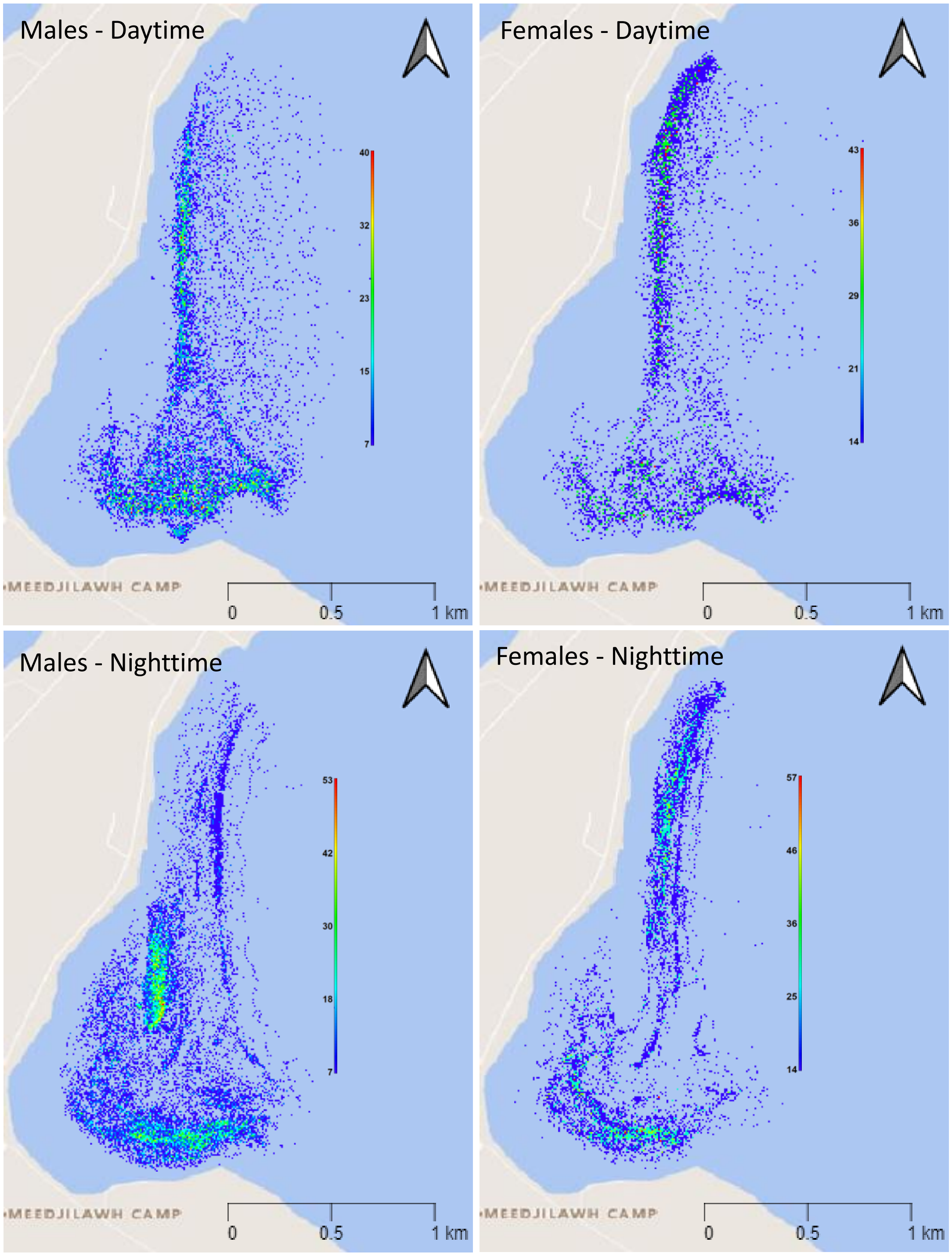

Figure 2.8. Heatmap displaying the percentage of male (n = 15) and female (n = 7) lake whitefish in each grid cell (10 m x 10 m) in the study area during the escalation stage (2 - 24 November 2021).

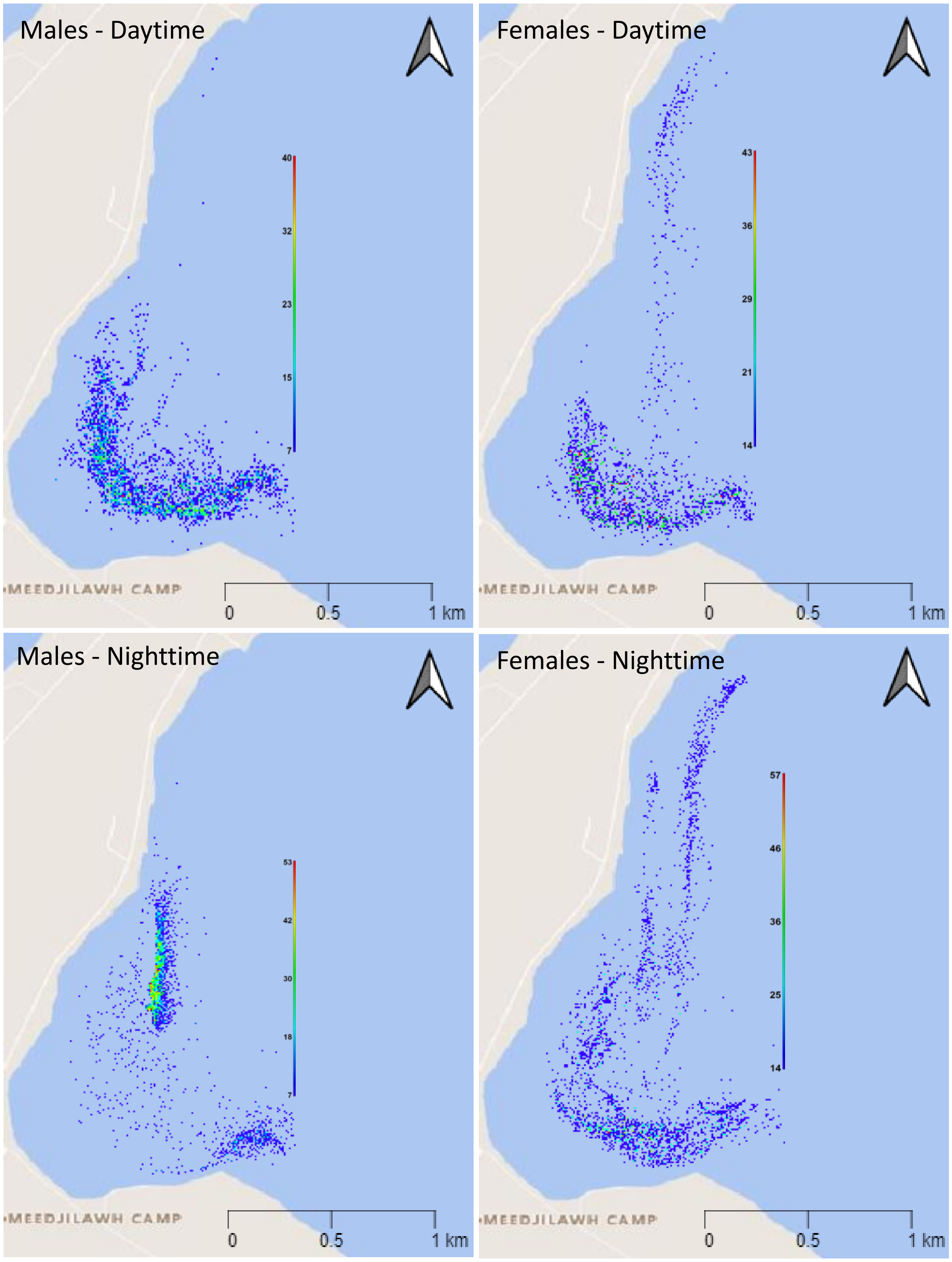

Figure 2.9. Heatmap displaying the percentage of male (n = 15) and female (n = 7) lake whitefish in each grid cell (10 m x 10 m) in the study area during the peak activity stage between 25 November – 1 December 2021.

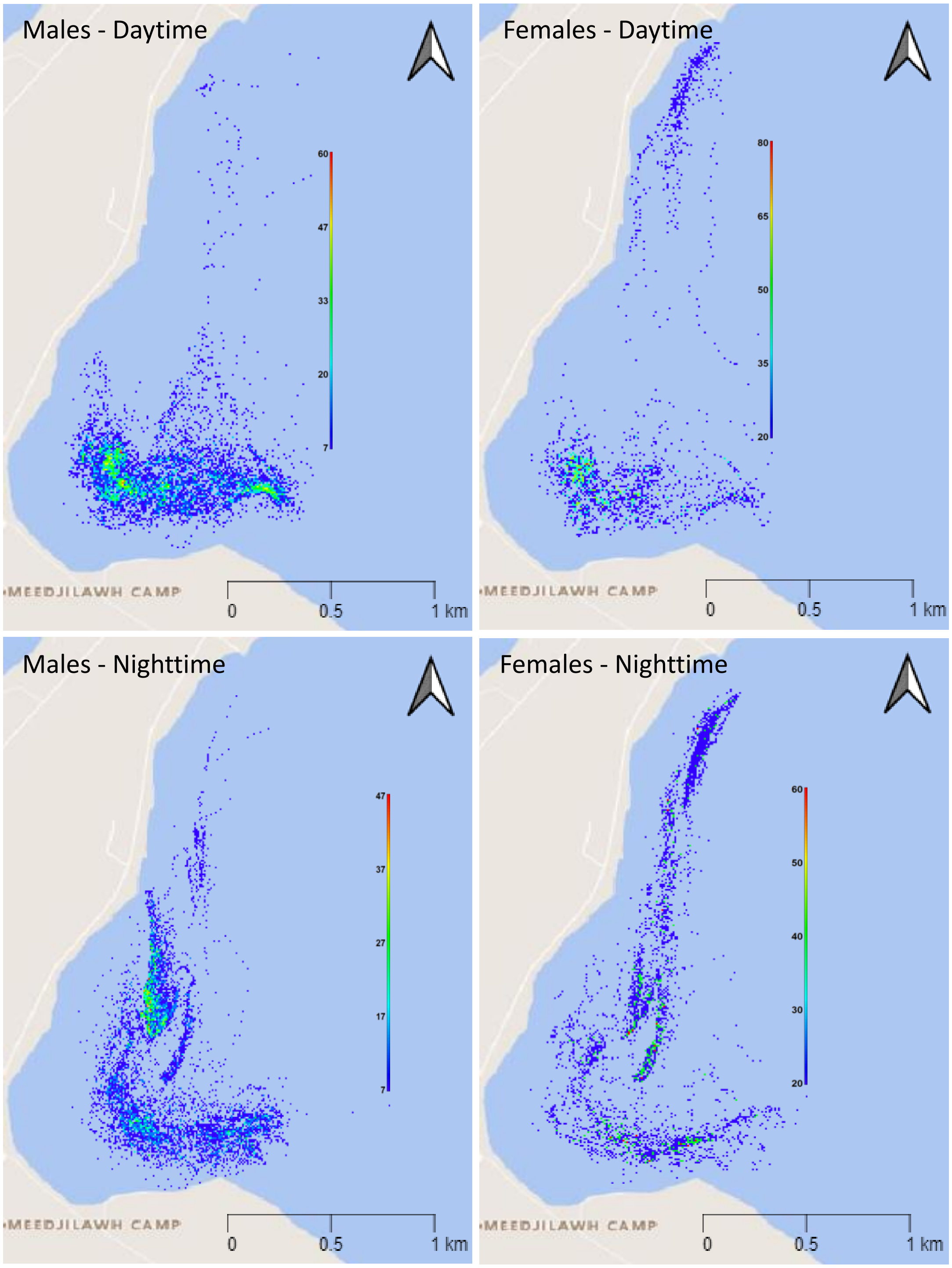

Figure 2.10. Heatmap displaying the percentage of male (n = 15) and female (n = 5) lake whitefish in each grid cell (10 m x 10 m) in the study area during the de-escalation stage between 2 – 19 December 2021.

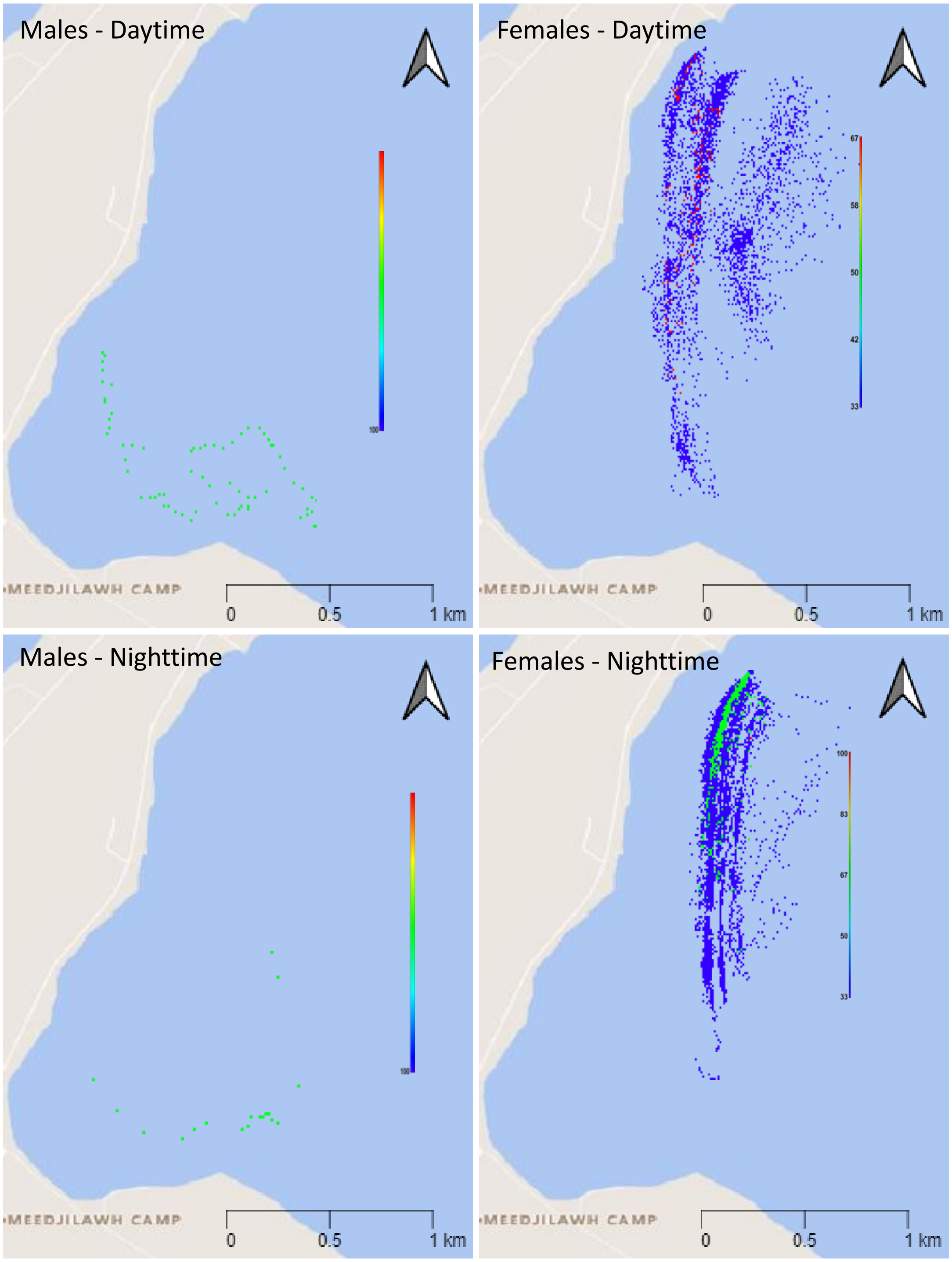

Figure 2.11. Heatmap displaying the percentage of male (n = 1) and female (n = 3) lake whitefish present in each grid cell (10 m x 10 m) in the study area during the post-activity stage between 20 December 2021 – 18 January 2022.

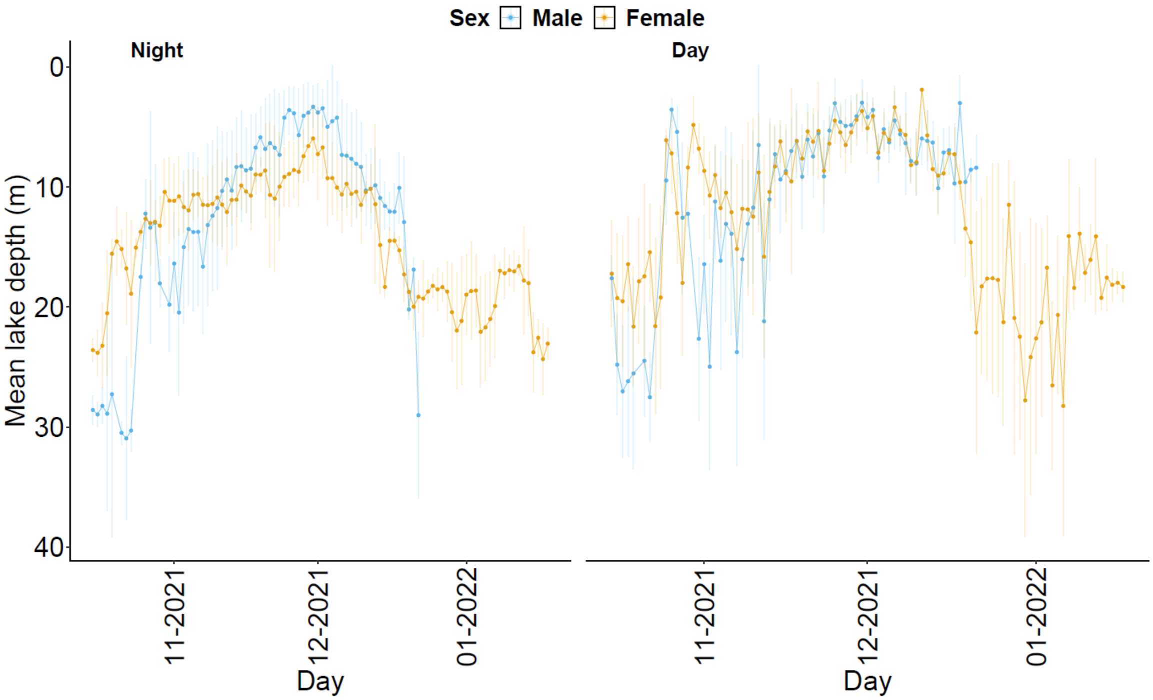

Figure 2.12. Mean daily lake depth (m) between 15 October 2021 – 18 January 2022 at individual fish positions. Males (15) are blue and females (8) are orange.

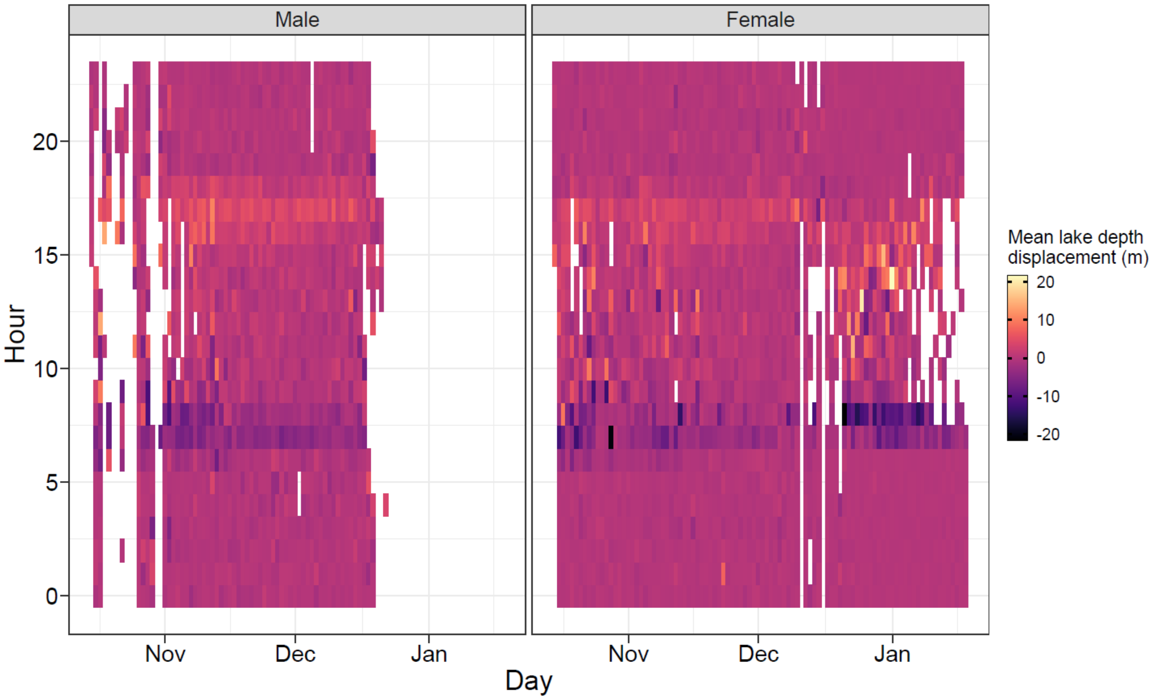

Figure 2.13. Mean lake depth displacement (m) per hour, over the study period (15 October 2021 – 18 January 2022) based on 15 males and 8 females. Positive displacement (yellow hues) indicates fish were moving into shallower lake depths and negative displacement (purple hues) indicates fish were moving into deeper lake depths.

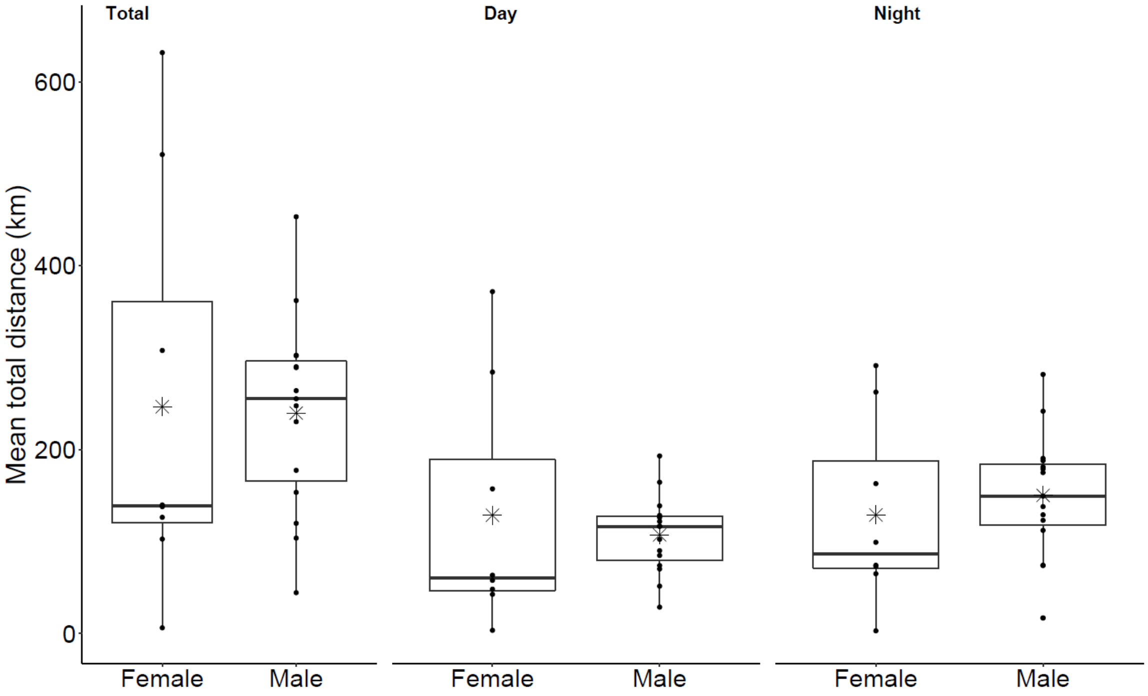

Figure 2.14. Mean total distances travelled for each sex and separated by diel period between 15 October – 22 December 2021. Total represents the combination of both day and night total distances. The upper and lower sides of the box represent the upper and lower quartiles. The whiskers represent minimum and maximum values (within 2.5x the interquartile range). An outlier is indicated as a dot plotted beyond the whiskers for male total distance at night. The asterisk (*) represents the mean, whereas the bolded line represents the median.

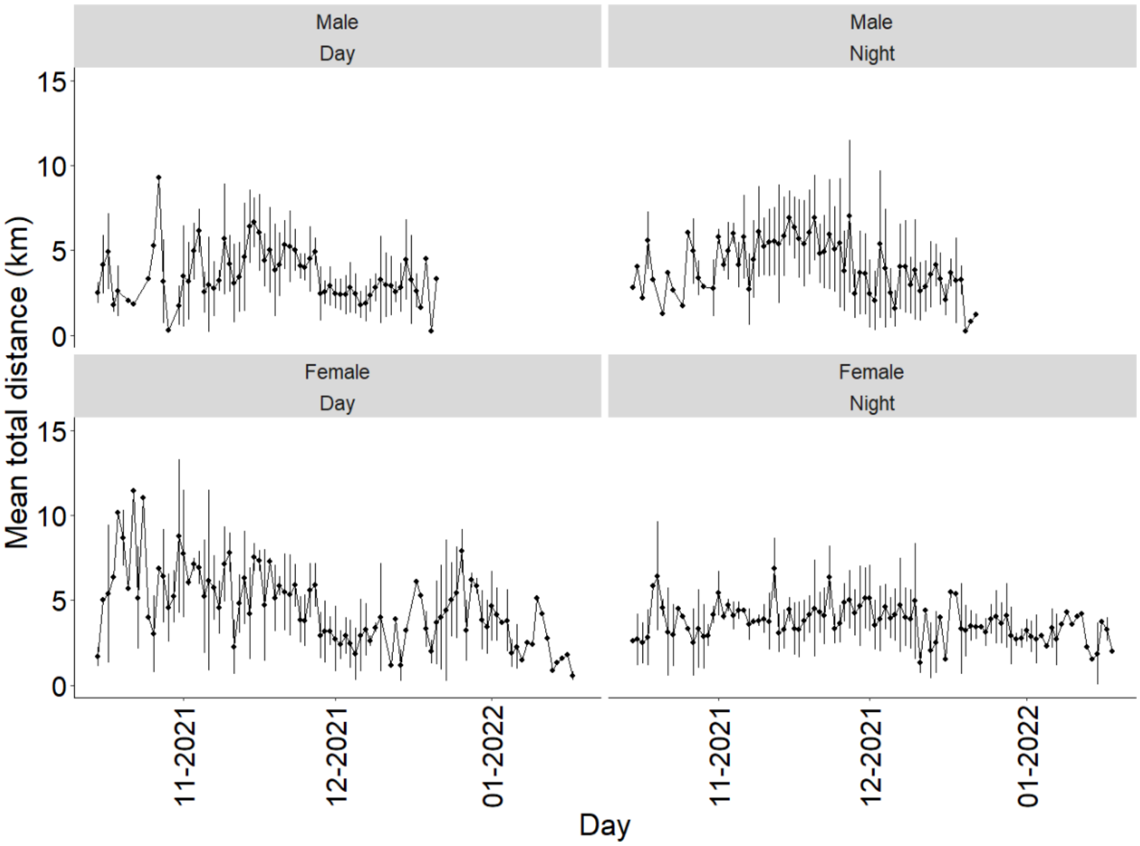

Figure 2.15. Mean total daily distance moved per sex and diel period over the study period (15 October 2021 – 18 January 2022) based on 15 males and 8 females. Error bars represent the standard deviation.

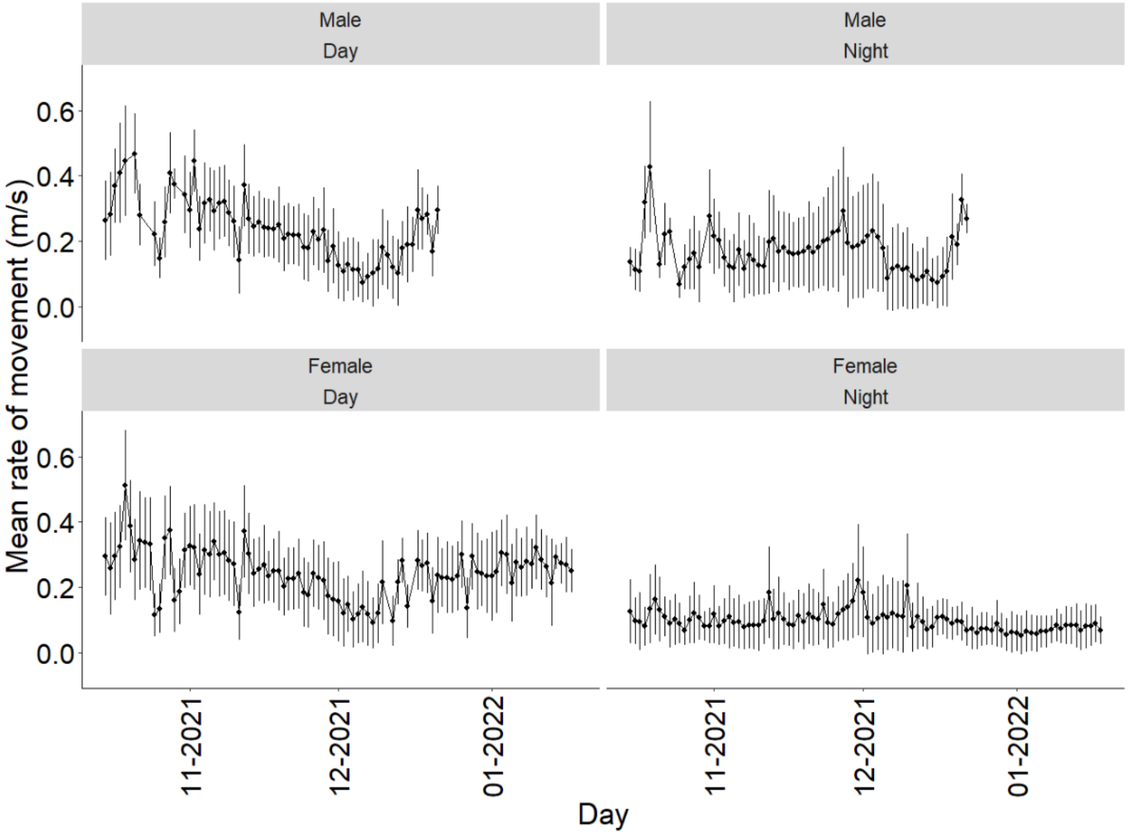

Figure 2.16. Mean rate of movement (m/s) per sex and diel period over the study period (15 October 2021 – 18 January 2022) based on 15 males and 8 females. Error bars represent the standard deviation.

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# APPENDIX A: SUPPORTING MATERIALS AND METHODOLOGY DETAILS

## A1 Fine-scale Bathymetry mapping

Data collection for fine-scale bathymetry mapping occurred on July 6, 13-15, 2021 using a Kongsberg M3 multibeam sonar unit and Hemisphere Vector VS330 for positional information (GPS, heading, pitch and roll). Prior to mapping, a patch test was conducted for calibration purposes which was applied during analysis. The patch test consisted of surveying a predetermined set of lines to later calculate calibration values to account for equipment imprecision. The multibeam was run using M3 software (in Profiling – Bathy mode) and data were recorded with Hypack + Hysweep. The multi-beam transducer was pole mounted on the port side of the vessel 0.77 m below the water surface. Transects were spaced based on water depth to ensure good coverage over priority areas: lines were spaced 15 m apart over the main LPE shoal, 30 m apart over other areas 2 to 30 m deep, and 90 m apart in areas 30 to 70 m deep. Because the multibeam sonar beam is a wide cone, lines can be spaced further apart in deep water than in shallow water. Transects ended once the multibeam recorded a depth of approximately 2-3 m (to avoid hitting rock). The vessel speed during data collection was approximately 6.1 km/h. Temperature profiles were collected daily in the survey area to use for speed of sound calculations. Multibeam data were processed using Hypack-Hysweep Editor (MBMAX64). Patch test offsets were calculated and applied in MBMAX64. Erroneous bottom readings were identified and removed from the data using automated filters and visual inspection; filter settings were applied iteratively until a reasonable result. Data were interpolated and smoothed using a TIN model and exported as 0.5 m contour lines.

## A2 Programming of Tags and Receivers

All V16 tags were programmed to transmit randomly every 60 – 180 s (nominal 120 s) at a frequency of 158 dB. V16 tags had an estimated battery life of 2487 days whereas V16P tags had an estimated battery life of 2239 days. All VR2AR receivers (69 kHz) were programmed to have internal sync tags on and emit at the 'very high' frequency of 160 dB, the closest option to the frequency of the V16 tags. VR2AR's automatically logged the tilt, noise, depth, and temperature once an hour.

## A3 Filtering by HPE

All analyses were conducted in R 3.6.3 (R Core Team 2022; https://www.r-project.org/). Along with calculating synctag and animal positions, Innovasea provides error estimates, calculated from algorithms used when calculating positions (Smith 2013), associated with each position, known as horizontal positioning error (HPE). HPE is provided for both sync and animal tags where it is a relative, unitless estimate of error sensitivity (Smith 2013). Additionally, a measured error estimate ($HPE_m$) is provided for sync tag positions only, as we know the actual position of where the sync tags are. $HPE_m$ is the horizontal distance between a calculated sync tag position and the known location of the sync tag (Smith 2013). To filter positions using HPE, we followed methods from Coates et al. (2013) and Tom Binder (personal communication). We binned HPE values (bin width = 1 up to 200) and calculated the 90th and 95th percentiles of $HPE_m$. Following discussions of project goals and future uses of the data (Meckley et al. 2014), we decided that having an error of ≤ 10 m for fish positions would be sufficient. To preserve as much data as possible and filter out positions with higher error scatter, we chose to use the 90th percentile of $HPE_m$ as the cut-off. We determined if there was a relationship between

HPE and $HPE_m$, a typical step when deciding to filter using HPE, using a linear model (Coates et al. 2013, Meckley et al. 2014). We found there was a significant relationship between HPE and $HPE_m$ ($p<0.0001$). For synctag positions, a 90th percentile of $HPE_m$ at 10 m corresponded to HPE 14. Therefore, we filtered the animal positions based on HPE of 14. Filtering with HPE 14 left us with a 79.4% retention of fish positions (113,879). Filtering by HPE 14 resulted in a loss of three fish in the VPS dataset (64622 female, number of positions = 1; 64619 female, number of positions = 1; 4282 female, number of positions = 24).

### A4 Water depth approximation

To approximate water depth for each fish position, we interpolated the contour lines of the bathymetry map in QGIS software (v. 3.20.1). The *TIN interpolation* tool was used to interpolate between contour lines at 1x1 pixel resolution. This accounted for approximately 1x1 m resolution in real measurements. TIN stands for 'Triangular Interpolation Network' and is a common interpolation technique that relies on constructing a triangular network based on each sampled spatial location and the nearest neighbour point information. This method was chosen over others, such as Inverse Distance Weighting (IDW), for a couple of reasons. The contour lines were taken relatively evenly, with little gaps, to make weighted distancing 'more' effective than the TIN method. To further corroborate this choice, both methods were tested, where, visually, the TIN model appeared smoother. After applying the TIN interpolation, the resulting raster was converted to a scalar PC Raster map using *PCRaster* tool for further analysis. To obtain the relative water depth from all VPS positions, positions were overlaid onto the bathymetry raster and the tool *Sample raster values* was used to provide a depth value to each positional value.

# APPENDIX B: SUPPORTING TABLES

Table B1. Details for individual lake whitefish fish (n = 50) tagged at the Little Port Elgin shoal, Lake Huron. Table includes the number of positions calculated by the VEMCO Positioning System pre- and post- horizontal positional error (HPE) filtering.

| Transmitter ID | Sex | Fork length (mm) | Weight (g) | Condition | Number of positions calculated by VPS | Number of positions post-HPE filtering |
|---|---|---|---|---|---|---|
| 4278 | 2 | 608 | - | good | - | - |
| 4279 | 1 | 611 | - | good | - | - |
| 4280 | 1 | 612 | 3500 | good | - | - |
| 4281 | 1 | 679 | 3800 | excellent | - | - |
| 4282 | 2 | 548 | 2400 | good | 24 | - |
| 4283 | 2 | 605 | 3000 | excellent | 2119 | 1883 |
| 4284 | 2 | 635 | 4200 | good | - | - |
| 4285 | 1 | 583 | 2850 | good | - | - |
| 4286 | 2 | 634 | 4050 | good | 2815 | 2137 |
| 4287 | 1 | 655 | 3600 | good | 1193 | 752 |
| 64588 | 2 | 628 | - | poor | - | - |
| 64589 | 2 | 626 | - | great | - | - |
| 64590 | 1 | 671 | - | excellent | 1896 | 1602 |
| 64591 | 1 | 637 | 3200 | good | - | - |
| 64592 | 1 | 560 | 2400 | poor | 3300 | 2843 |
| 64593 | 1 | 574 | 2500 | good | 4958 | 4115 |
| 64594 | 1 | 590 | 3200 | excellent | - | - |
| 64595 | 1 | 602 | 3050 | fair | 5852 | 4065 |
| 64596 | 1 | 668 | 3600 | excellent | 6345 | 5484 |
| 64597 | 2 | 611 | 3300 | excellent | - | - |
| 64598 | 2 | 570 | 3000 | excellent | - | - |
| 64599 | 1 | 581 | 2550 | good | 7160 | 5763 |
| 64600 | 2 | 583 | 2850 | excellent | 234 | 121 |
| 64601 | 2 | 601 | 3700 | excellent | 25762 | 19652 |
| 64602 | 1 | 540 | 1850 | fair | - | - |
| 64603 | 1 | 570 | 2750 | good | 5089 | 4284 |
| 64604 | 2 | 615 | 4300 | good | 1794 | 1505 |
| 64605 | 2 | 675 | 5350 | excellent | 27727 | 23805 |
| 64606 | 2 | 608 | 3950 | excellent | - | - |
| 64607 | 2 | 667 | 4000 | good | 2008 | 1663 |
| 64608 | 1 | 650 | 3450 | excellent | - | - |
| 64609 | 2 | 580 | 2350 | good | - | - |
| 64610 | 1 | 605 | 2900 | excellent | 3517 | 2383 |
| 64611 | 1 | 552 | 2550 | good | - | - |
| 64612 | 2 | 581 | 3450 | fair | - | - |
| 64613 | 1 | 571 | 2800 | good | - | - |
| 64614 | 1 | 609 | 3550 | very good | - | - |
| 64615 | 2 | 576 | 2850 | good | - | - |
| 64616 | 1 | 615 | 3200 | good | 2742 | 1351 |
| 64617 | 1 | 596 | 3000 | good | 6869 | 5149 |
| 64618 | 1 | 593 | 2950 | good | - | - |
| 64619 | 2 | 587 | 3100 | fair | 1 | - |
| 64620 | 2 | 590 | 3600 | excellent | - | - |
| 64621 | 2 | 598 | 3300 | good | 9165 | 6863 |
| 64622 | 2 | 616 | 3950 | good | 1 | - |
| 64623 | 1 | 665 | 4300 | good | 9651 | 7702 |
| 64624 | 1 | 692 | 4650 | okay | - | - |
| 64625 | 1 | 576 | 2500 | okay | 4830 | 4107 |
| 64626 | 1 | 608 | 2900 | excellent | 4935 | 4230 |
| 64627 | 1 | 671 | 4100 | excellent | 3331 | 2420 |

Table B2. Summary table of mean total distance (km) and mean rate of movement (ROM; m/s) for males and females during the day (MD and FD, respectively) and night (MN and FN, respectively) between 15 October 2021 and 22 December 2021 for each stage of activity.

| Stages of activity | Mean Total Distance (km) | Mean ROM (m/s) |
|---|---|---|
| 'Pre-activity' | MD – 3.09 (± 2.13)<br>FD – 6.12 (± 3.67)<br>MN – 3.76 (± 1.62)<br>FN – 3.58 (± 1.69) | MD – 0.301 (± 0.11)<br>FD – 0.201 (± 0.12)<br>MN – 0.190 (± 0.12)<br>FN – 0.12 (± 0.08) |
| 'Escalation' | MD – 4.70 (± 2.18)<br>FD – 5.61 (± 2.22)<br>MN – 5.53 (± 2.38)<br>FN – 4.14 (± 1.51) | MD – 0.239 (± 0.09)<br>FD – 0.248 (± 0.09)<br>MN – 0.178 (± 0.11)<br>FN – 0.114 (± 0.09) |
| 'Peak activity' | MD – 3.29 (± 1.48)<br>FD – 3.90 (± 1.87)<br>MN – 4.10 (± 3.20)<br>FN – 4.67 (± 1.67) | MD – 0.173 (± 0.09)<br>FD – 0.184 (± 0.09)<br>MN – 0.204 (± 0.13)<br>FN – 0.143 (± 0.10) |
| 'De-escalation' | MD – 2.62 (± 1.44)<br>FD – 2.84 (± 1.64)<br>MN – 3.31 (± 2.52)<br>FN – 3.87 (± 1.89) | MD – 0.129 (± 0.09)<br>FD – 0.142 (± 0.09)<br>MN – 0.137 (± 0.11)<br>FN – 0.115 (± 0.09) |
| 'Post-activity' | MD – 1.78 (± 2.20)<br>FD – 3.22 (± 2.03)<br>MN – 0.76 (± 0.51)<br>FN – 3.38 (± 0.87) | MD – 0.240 (± 0.08)<br>FD – 0.214 (± 0.07)<br>MN – 0.276 (± 0.08)<br>FN – 0.09 (± 0.04) |

# APPENDIX C: SUPPORTING FIGURES

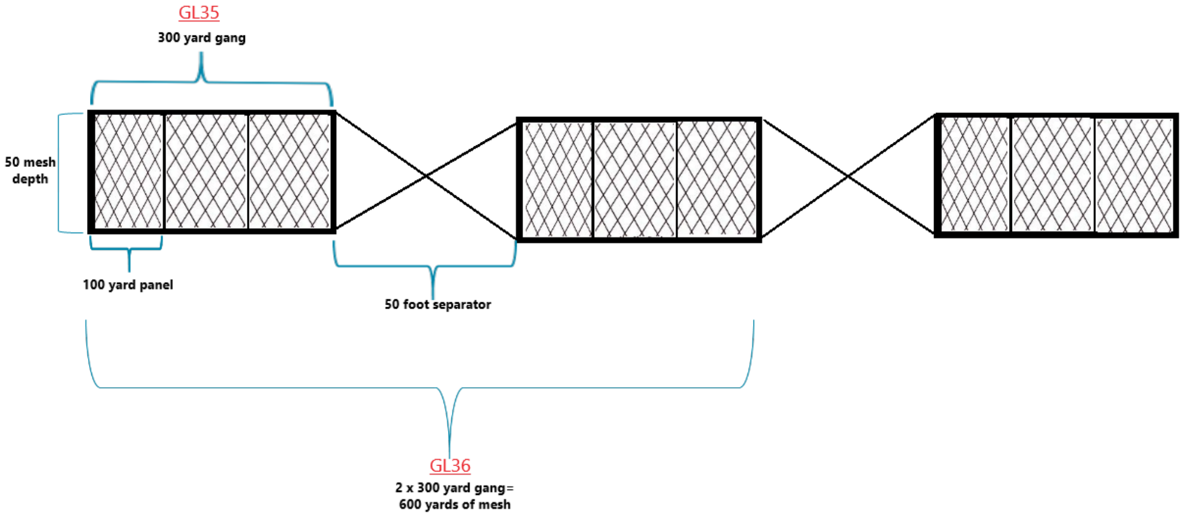

Figure C1. Graphic of the gear used to capture lake whitefish in November 2020 at the main Little Port Elgin shoal. GL35 and GL36 refer to different lengths of gill nets. Figure from Upper Great Lakes Management Unit, Ontario Ministry of Natural Resources and Forestry.

Figure C2. Surgery station within the mobile trailer used for tagging lake whitefish in 2020 and 2021 at Port Elgin Bay, Lake Huron.

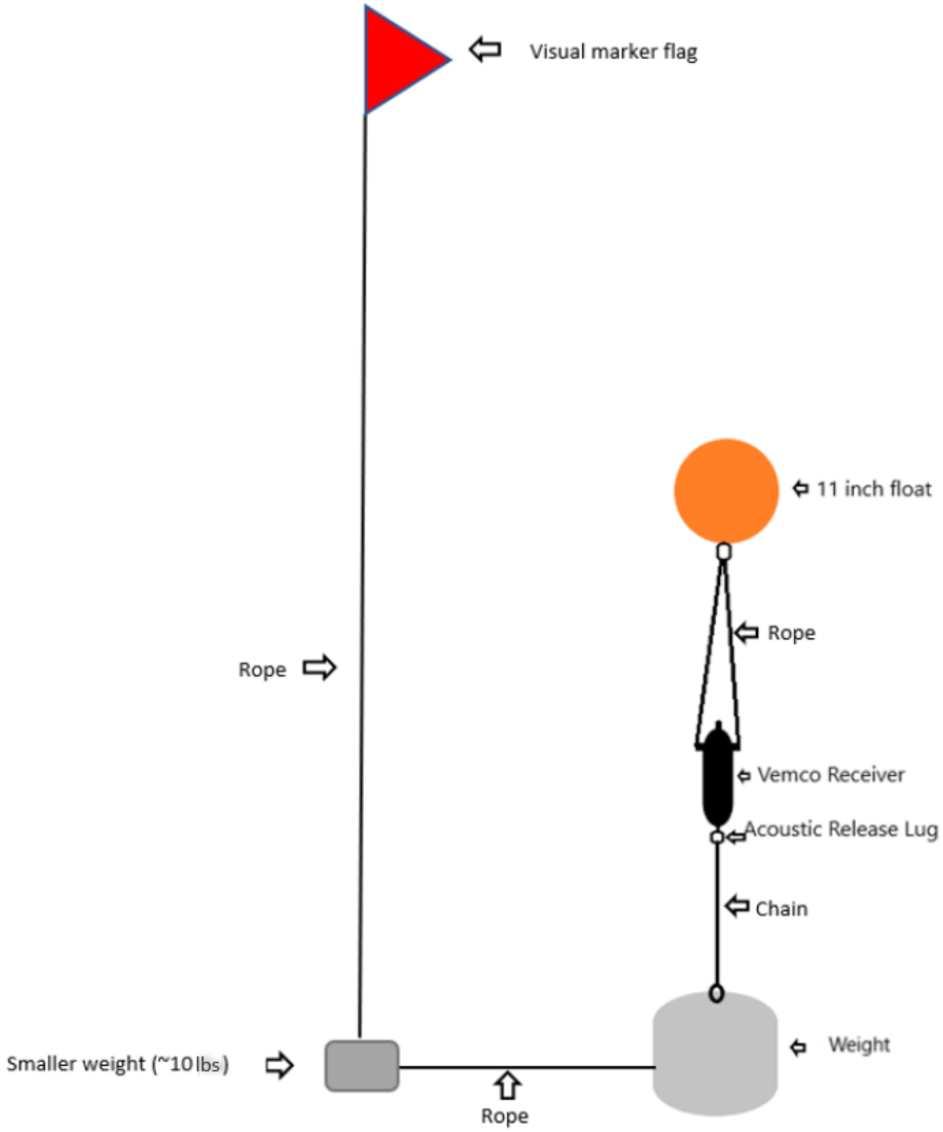

Figure C3. Mooring design for VR2AR receivers deployed in Port Elgin Bay, Lake Huron.

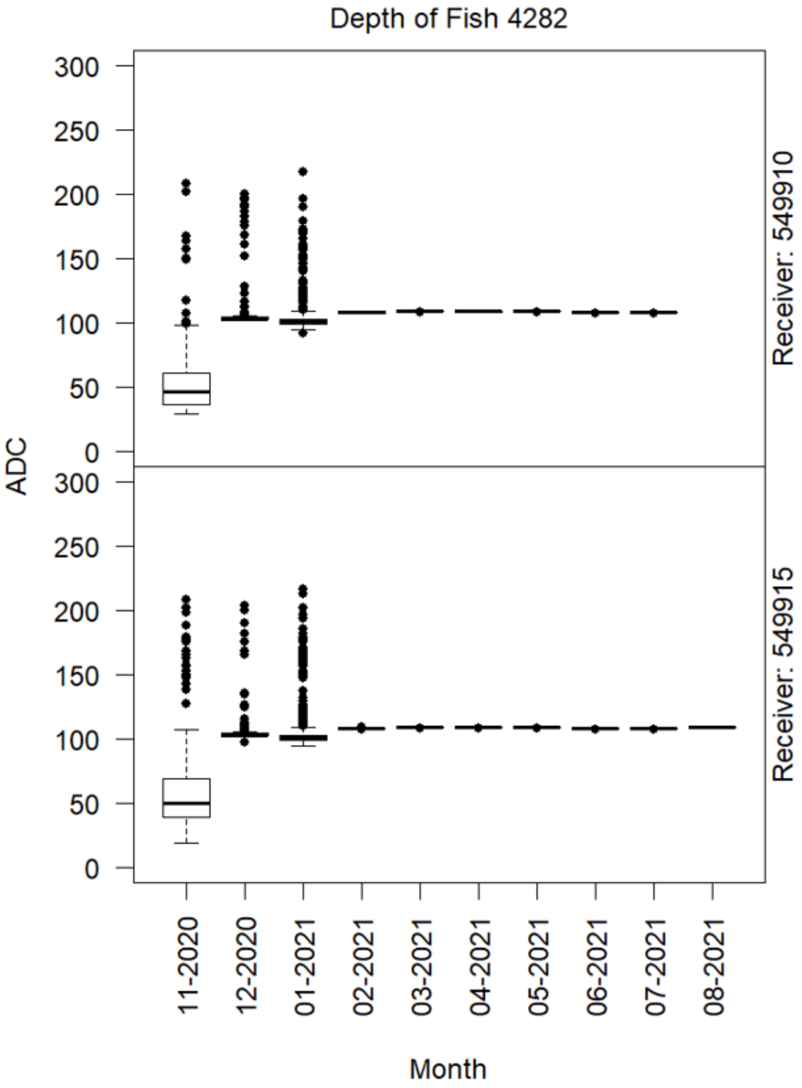

Figure C4. Box plots of depth tag recordings for fish 4282 (female) in Analog to Digital Converter (ADC) units (Innovasea Ltd.), prior to conversion to meters.

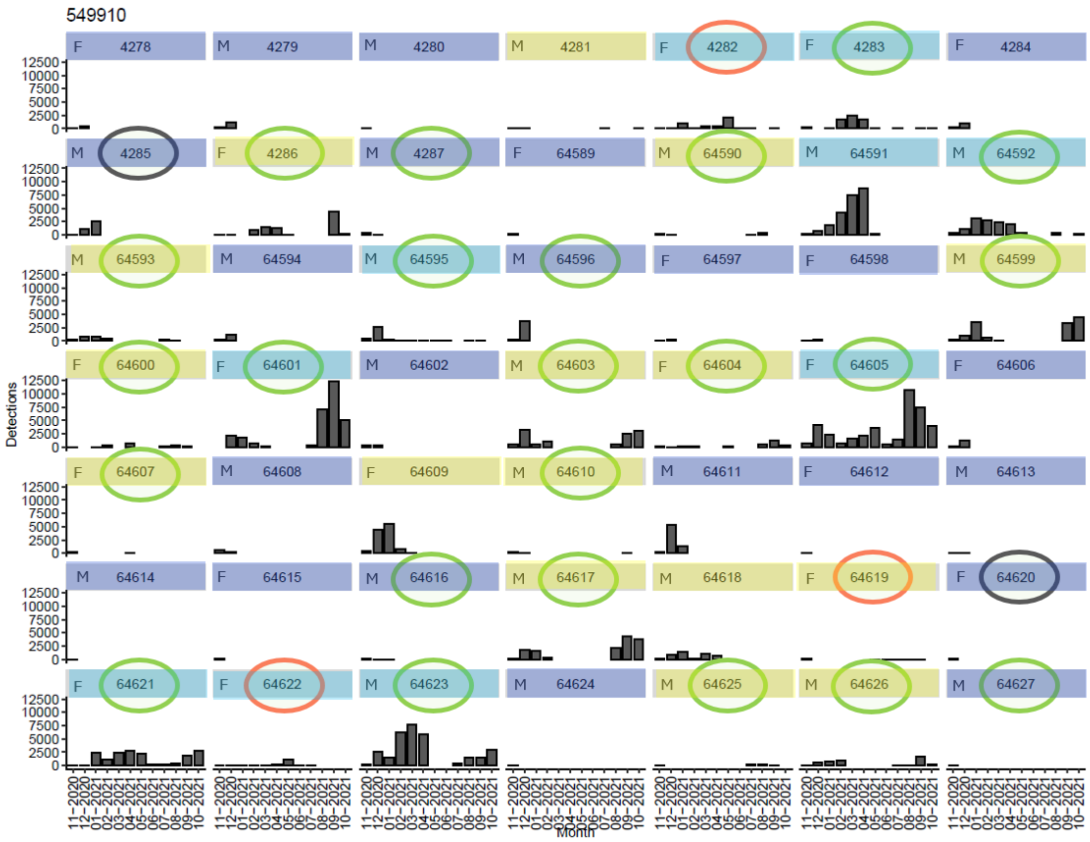

Figure C5. Total detections from the sentinel receiver ID 549910, located closest to the main Little Port Elgin shoal that was present during and post-tagging in the study area between 26 November 2020 – 15 October 2021. Dark blue labels represent fish that were present in the area 1-3 months post-tagging and then left (n = 23). Yellow labels represent fish that left the area but returned at various times throughout 2021 (n = 16). Light blue labels represent fish that could be classified as more resident in nature (n = 10). All circles represent fish detected during the VEMCO Positioning System (VPS) deployment (n = 28). Green circles indicate fish that were kept in the VPS analysis (n = 23). Grey circles indicate fish that the VPS was not able to calculate positions for (n = 2). Orange circles indicate fish that were removed post-HPE filtering. M denotes males and F denotes females.

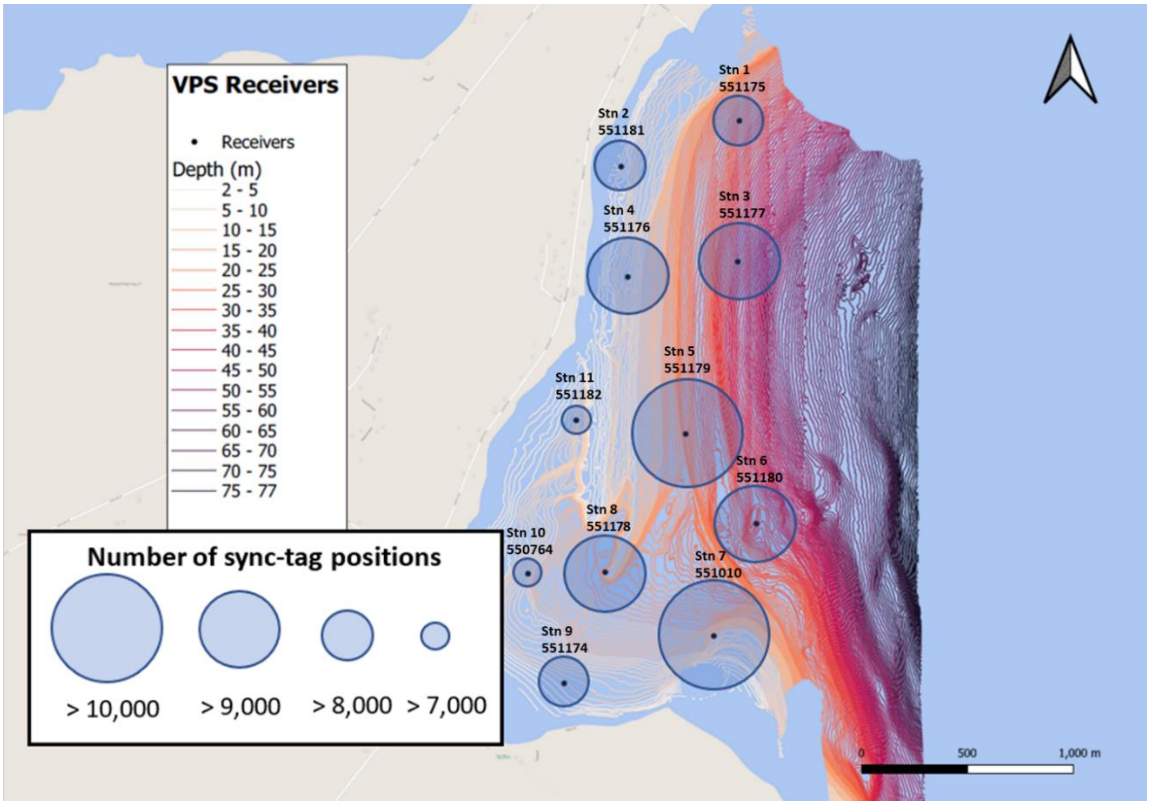

Figure C6. Map of the VEMCO Positioning System (VPS) showing the number of internal sync-tag positions that were calculated for each receiver in the VPS array deployed in Port Elgin Bay, Lake Huron.

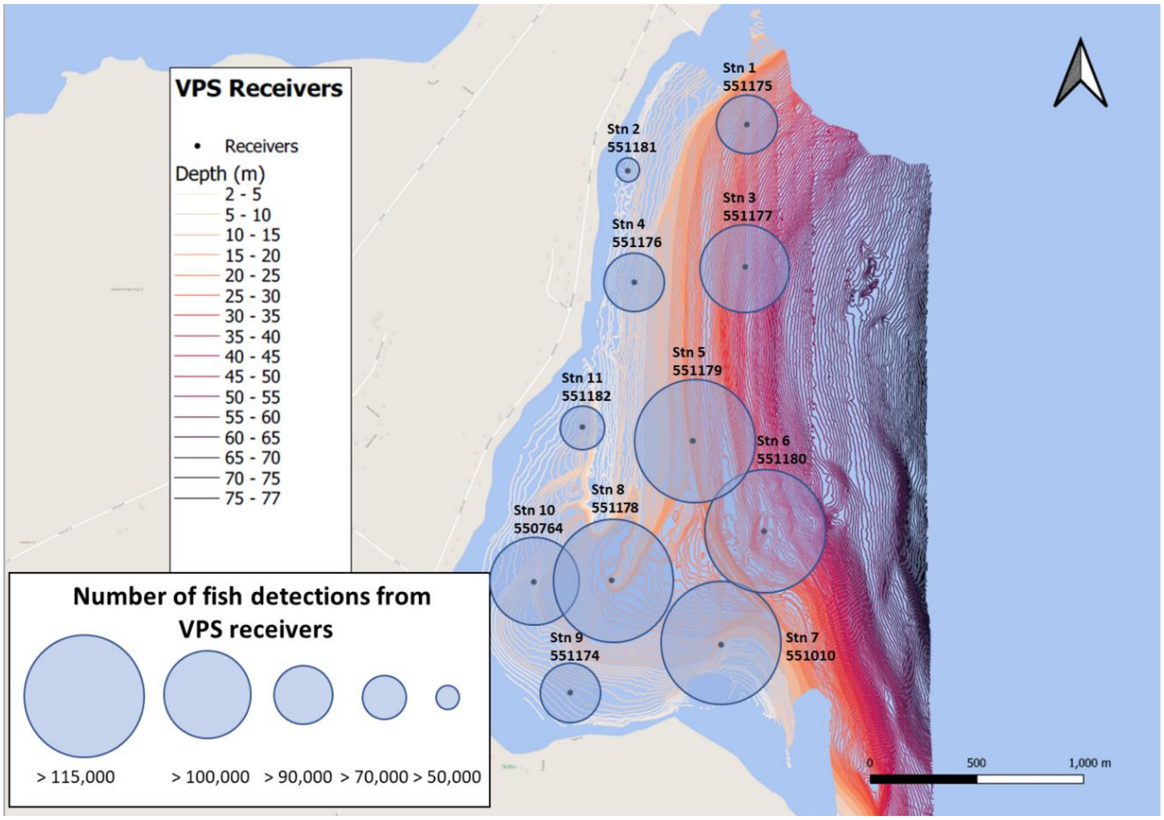

Figure C7. Map of the VEMCO Positioning System (VPS) showing the number of total fish detections at each receiver in the VPS array deployed in Port Elgin Bay, Lake Huron.

Figure C8. Synctag and animal detections over the VEMCO Positioning System deployment in Port Elgin Bay, Lake Huron.

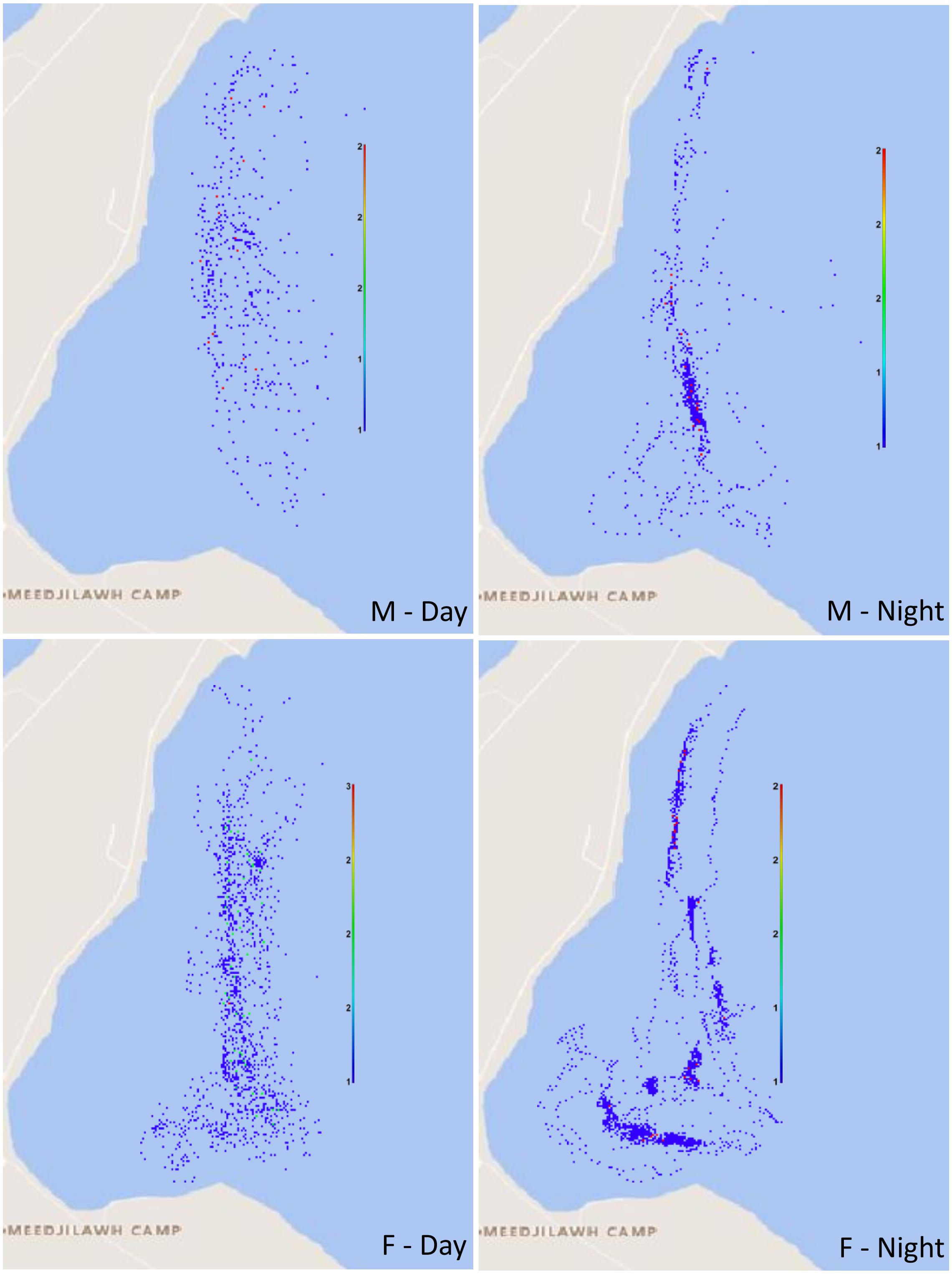

Figure C9. Sex- and diel-specific heatmaps depicting the number of individuals during 15 – 21 October 2021. Total number of positions = 5245 including 13 individuals (8 male, 5 female).

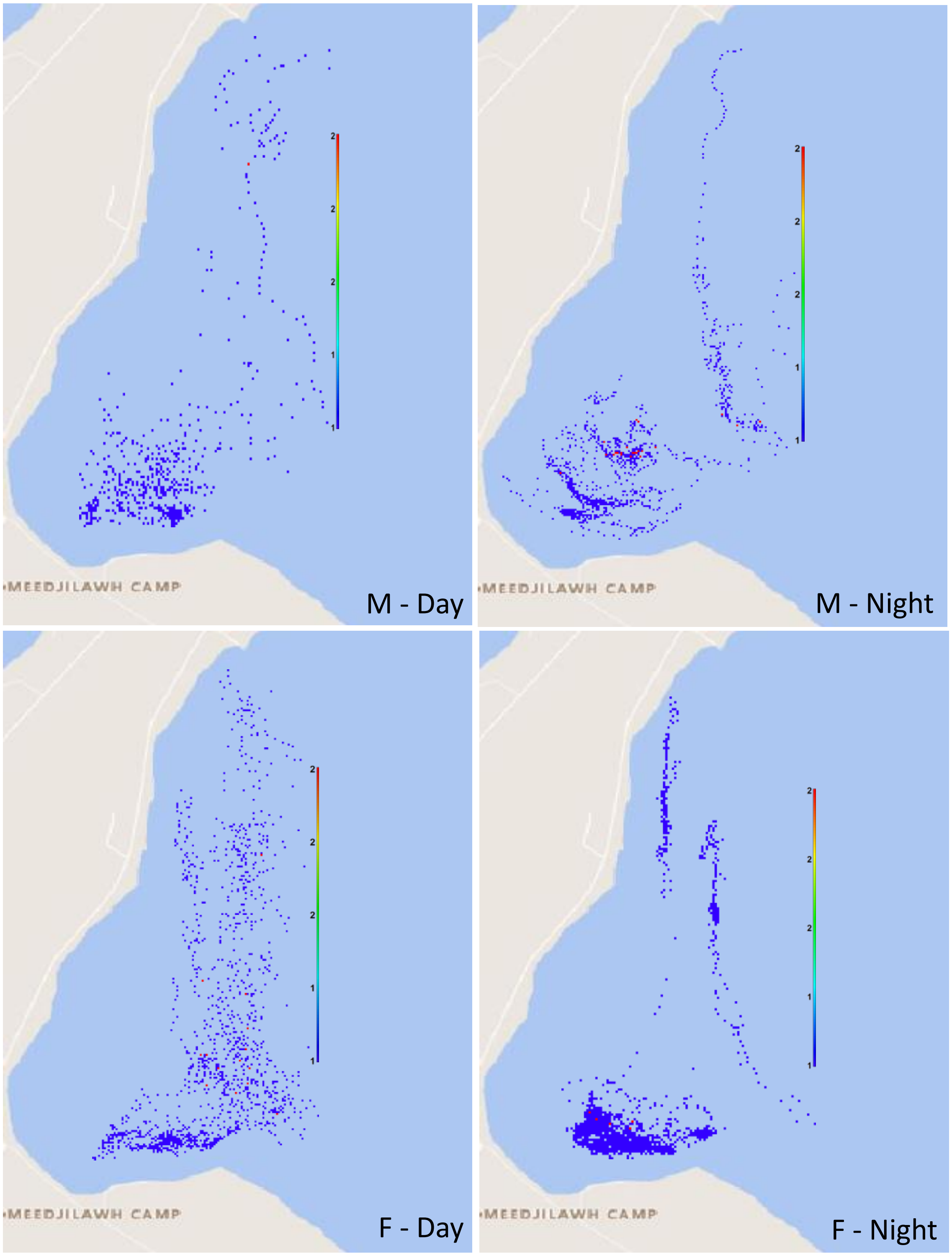

Figure C10. Sex- and diel-specific heatmaps depicting the number of individuals during 22 – 28 October 2021. Total number of positions = 5569 including 10 individuals (5 males, 5 females).

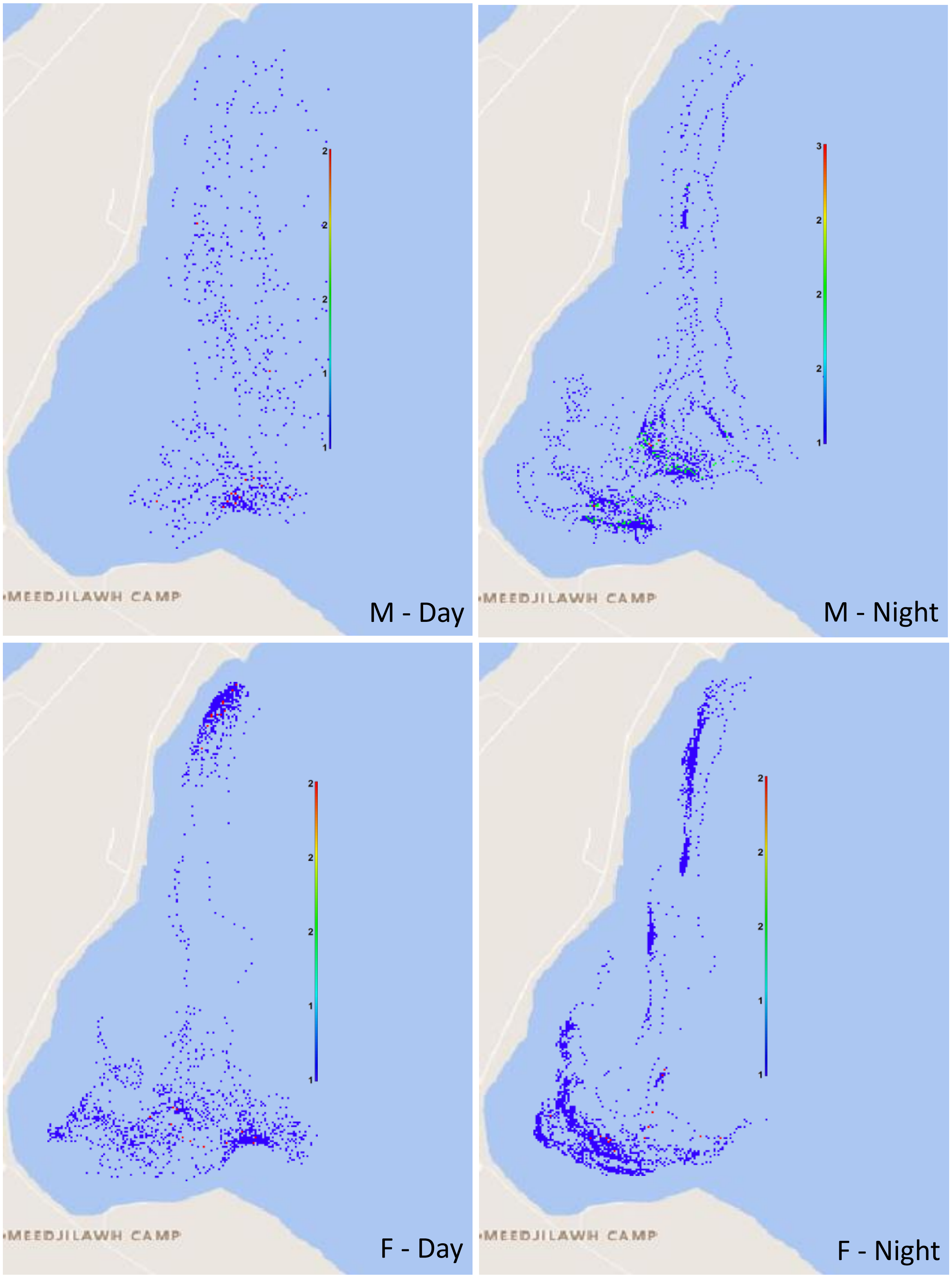

Figure C11. Sex- and diel-specific heatmaps depicting the number of individuals during 29 October – 4 November 2021. Total number of positions = 8407 including 11 individuals (7 males, 4 females).

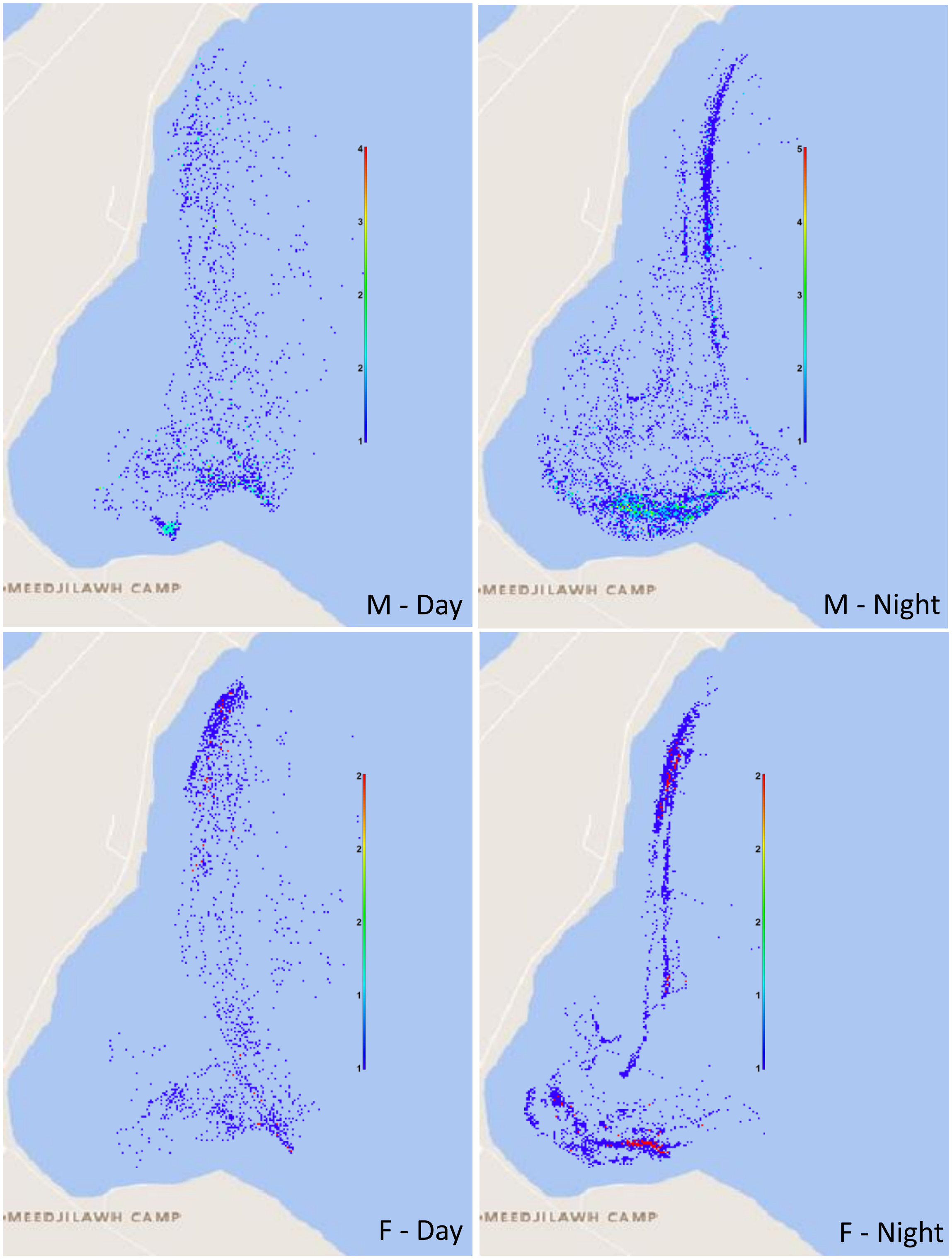

Figure C12. Sex- and diel-specific heatmaps depicting the number of individuals during 5 – 11 November 2021. Total number of positions = 13,193 including 12 individuals (9 males, 3 females).

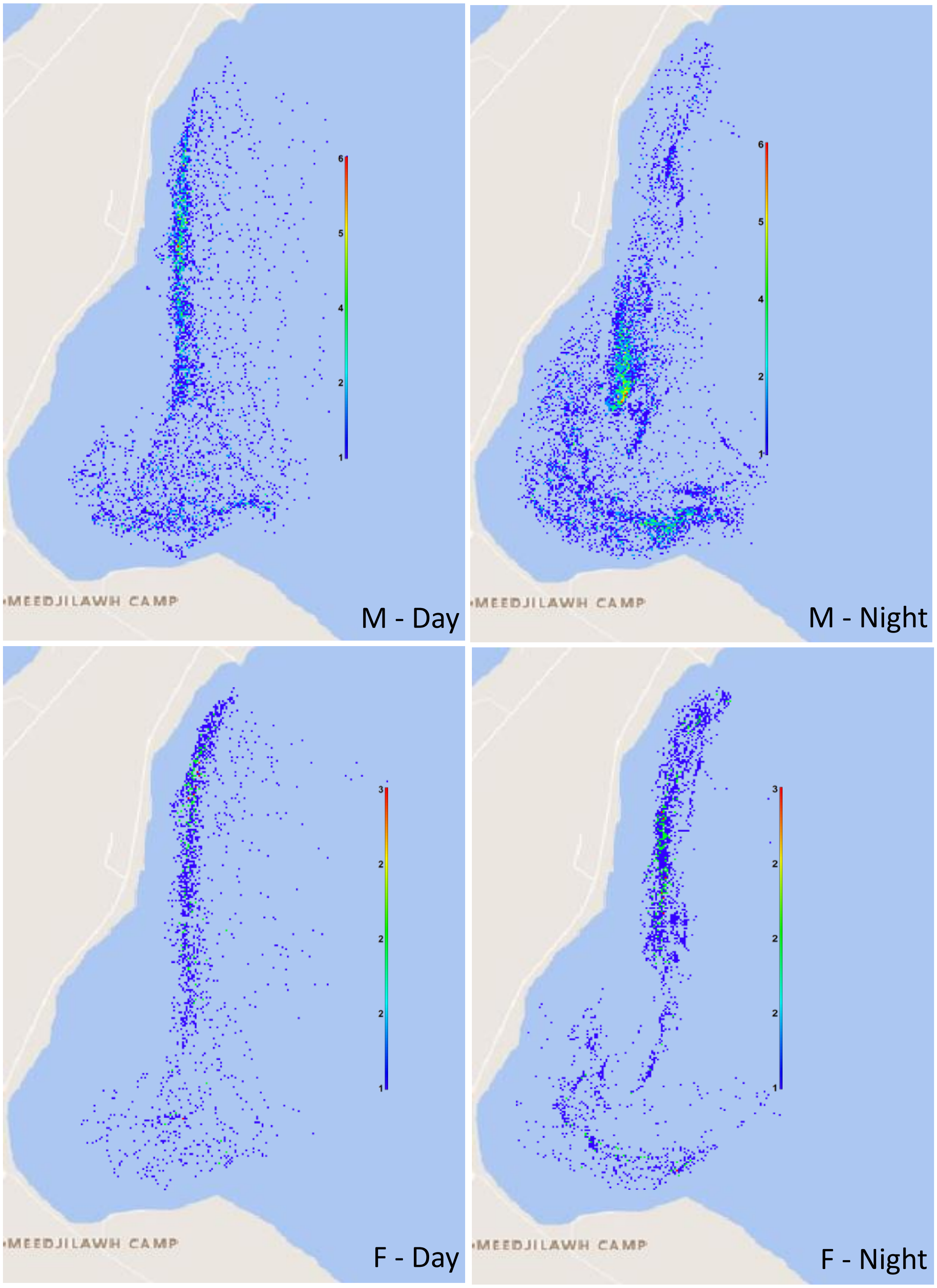

Figure C13. Sex- and diel-specific heatmaps depicting the number of individuals during 12 – 18 November 2021. Total number of positions = 16,257 including 20 individuals (15 males, 5 females).

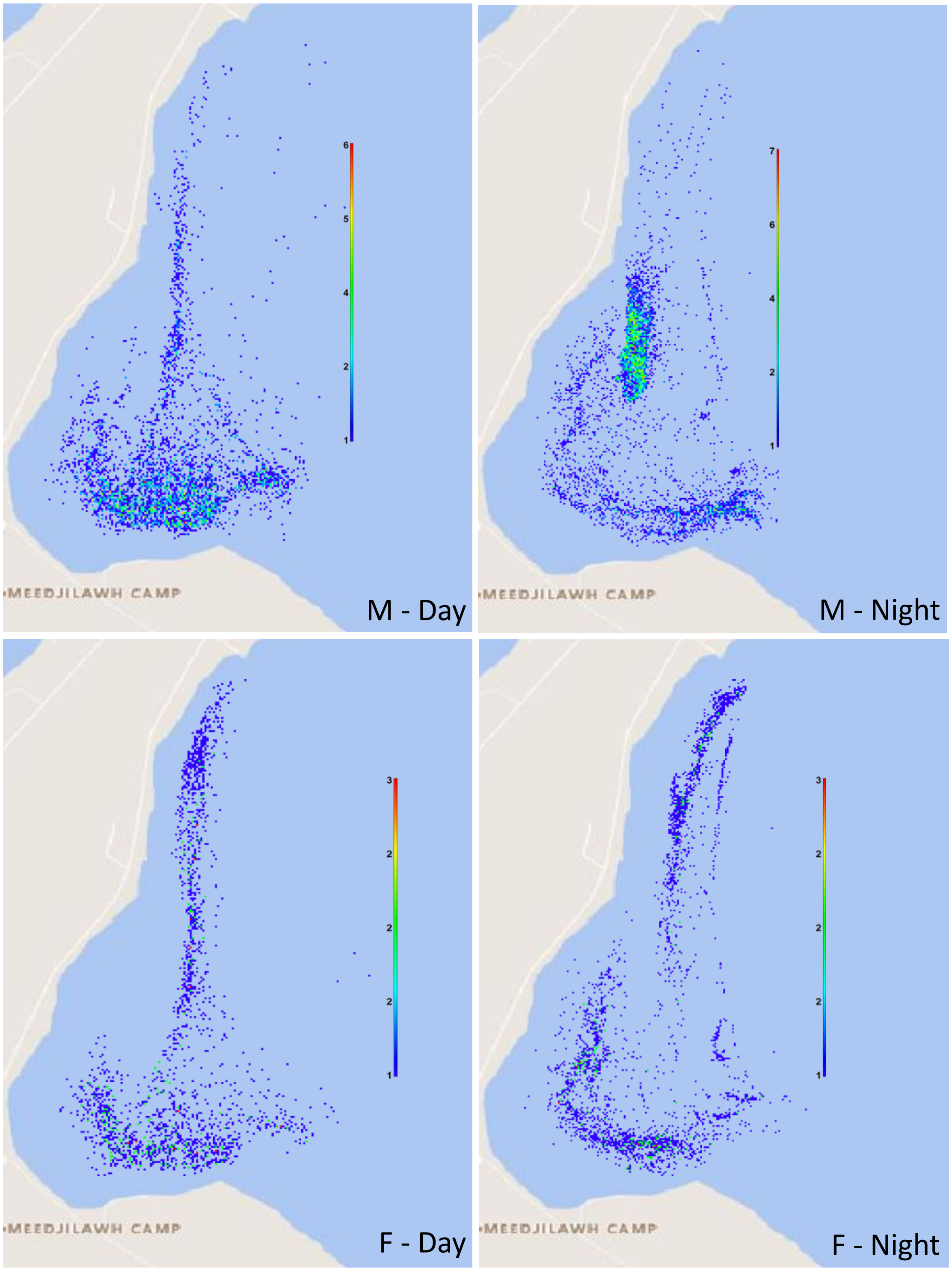

Figure C14. Sex- and diel-specific heatmaps depicting the number of individuals during 19 – 25 November 2021. Total number of positions = 15,191 including 22 individuals (15 males, 7 females).

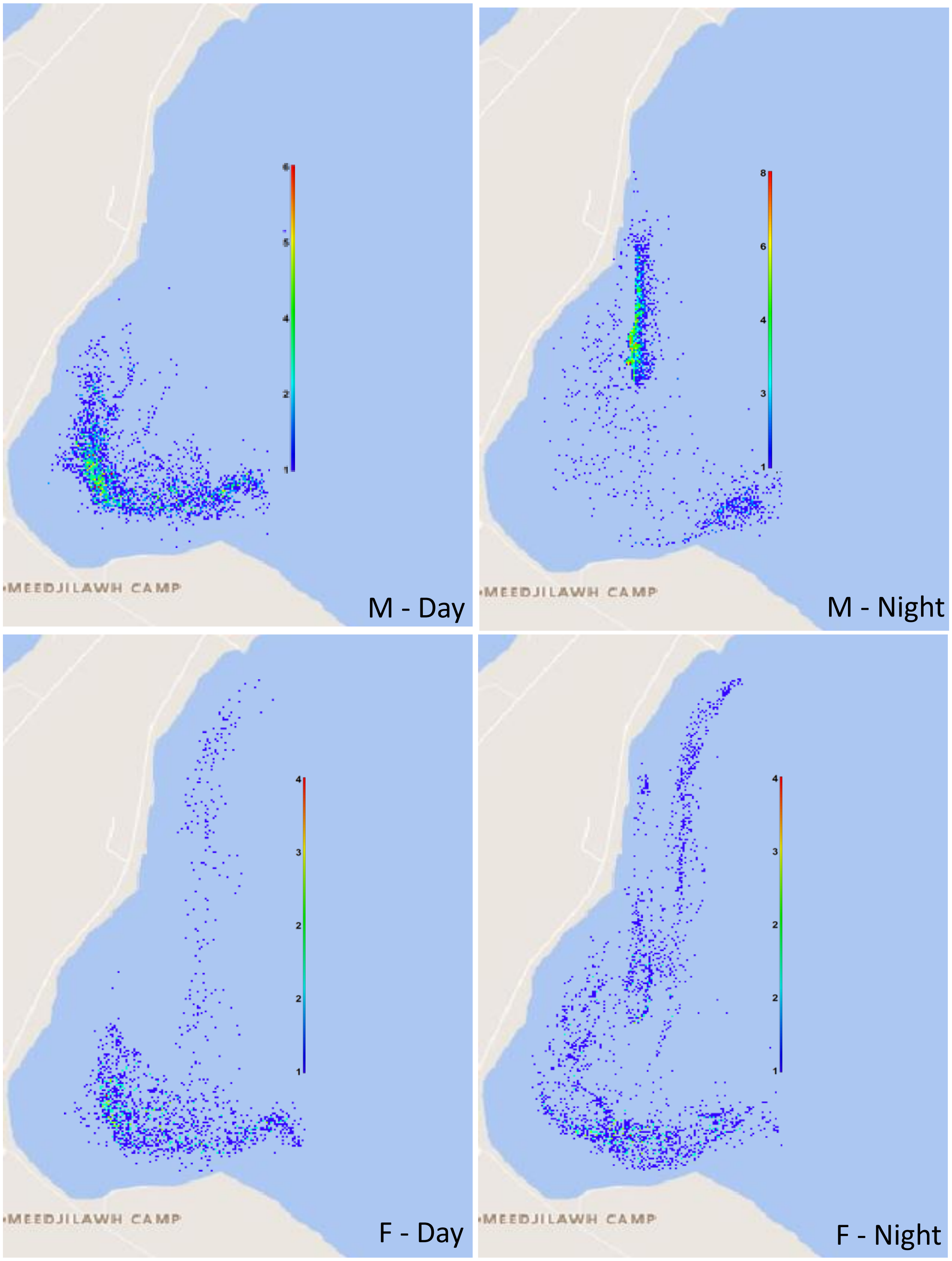

Figure C15. Sex- and diel-specific heatmaps depicting the number of individuals during 26 November - 2 December 2021. Total number of positions = 9697 including 22 individuals (15 males, 7 females).

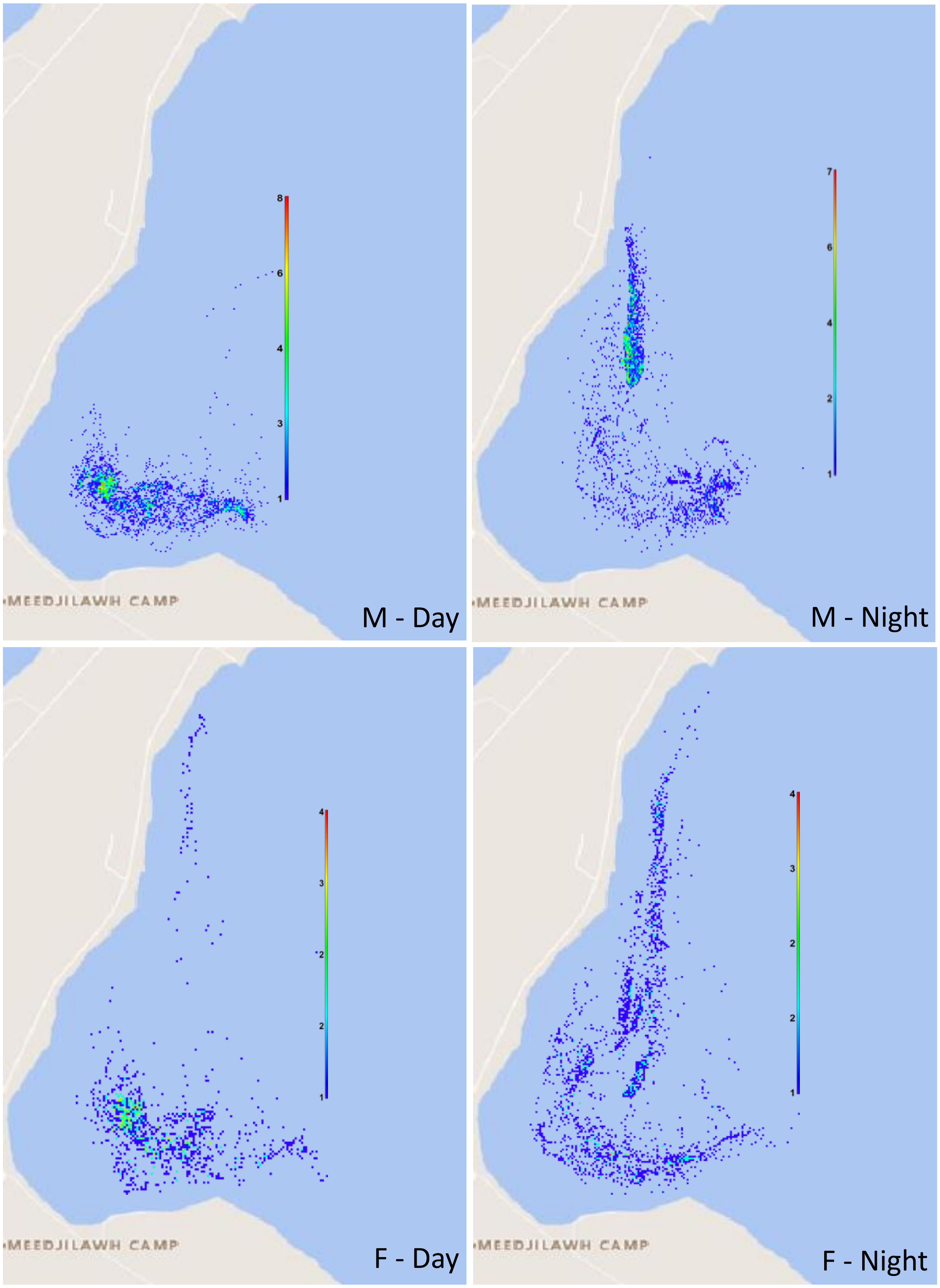

Figure C16. Sex- and diel-specific heatmaps depicting the number of individuals during 3 – 9 December 2021. Total number of positions = 11,249 including 20 individuals (14 males, 6 females).

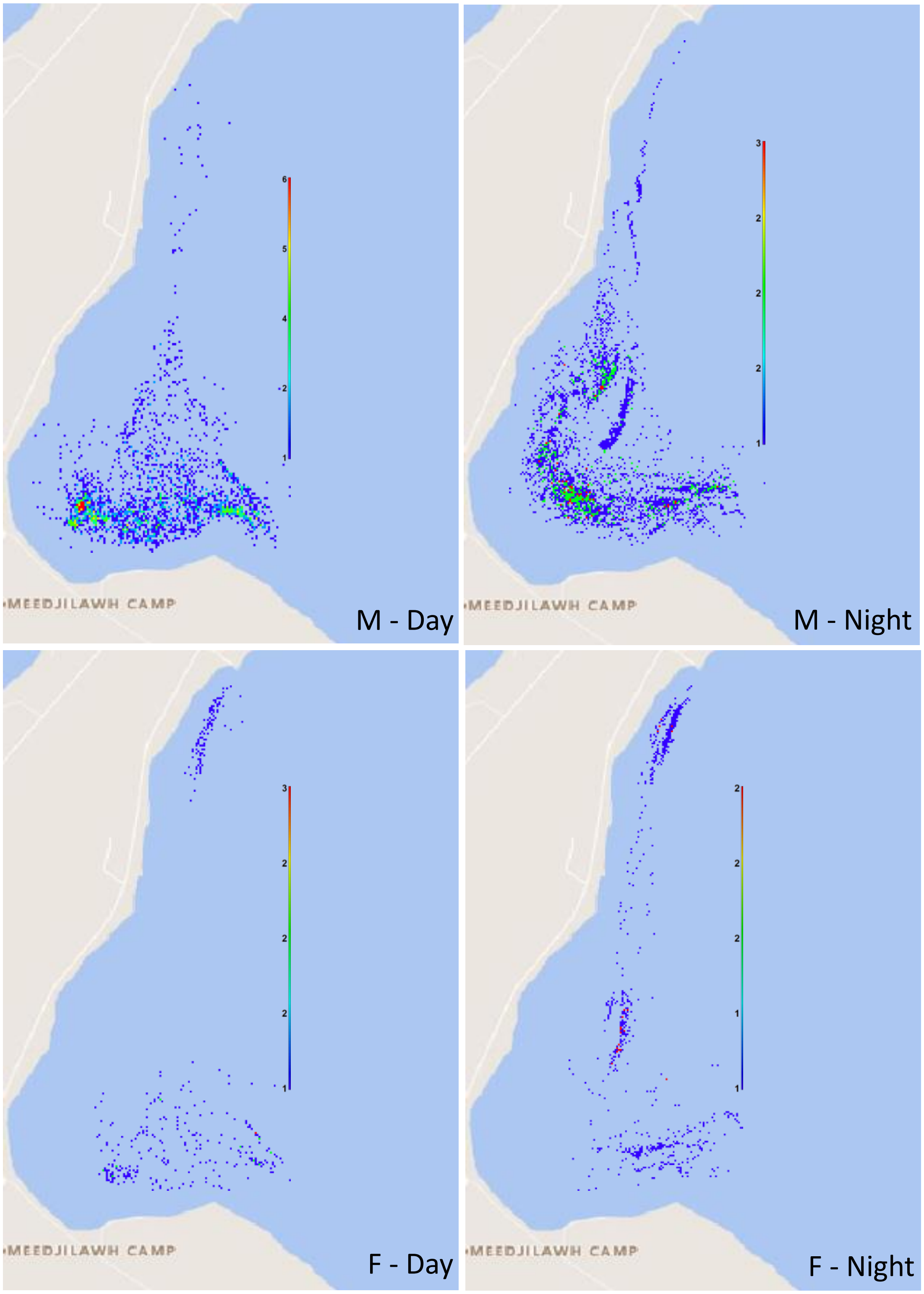

Figure C17. Sex- and diel-specific heatmaps depicting the number of individuals during 10 – 16 December 2021. Total number of positions = 9342 including 14 individuals (9 males, 5 females).

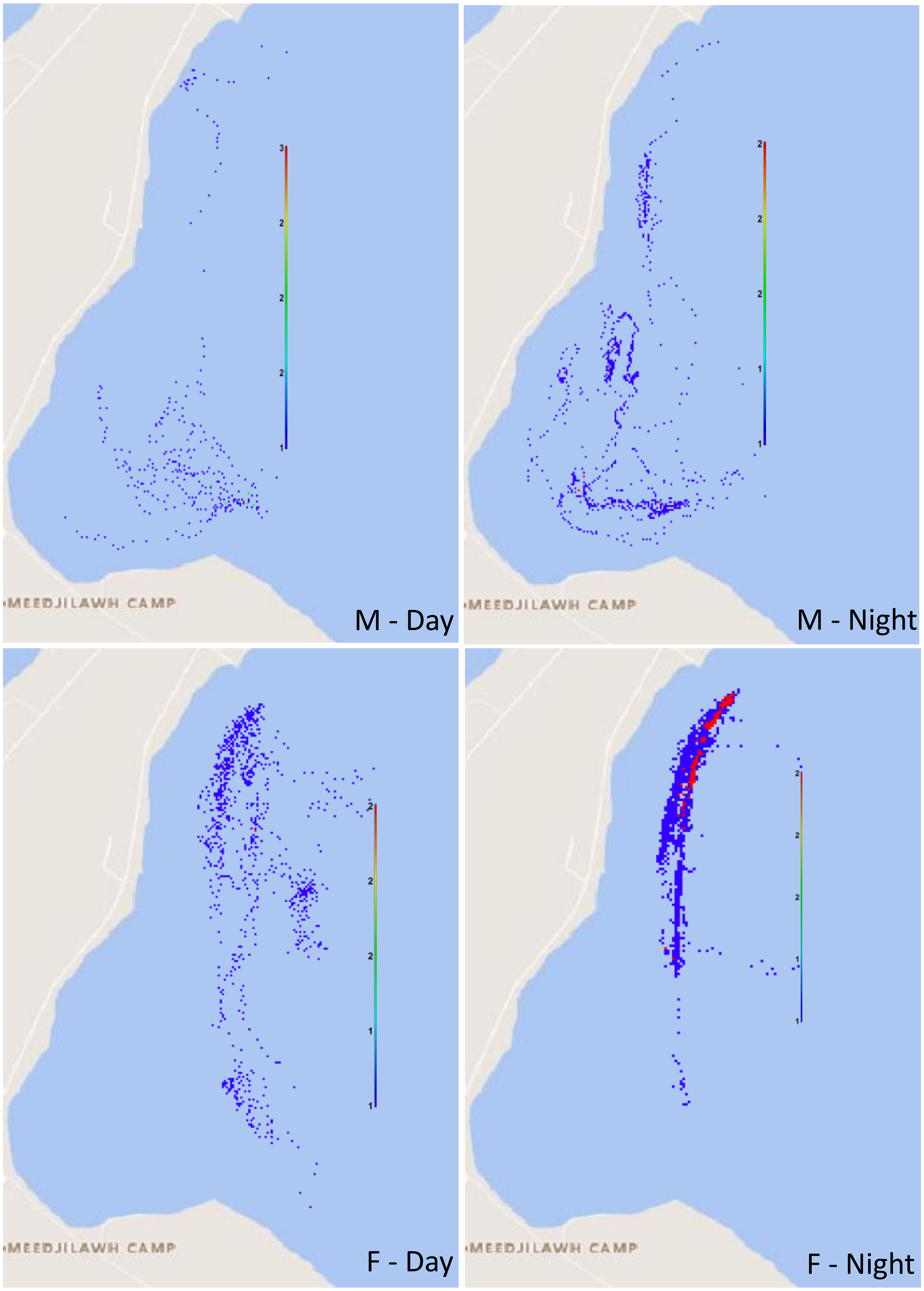

Figure C18. Sex- and diel-specific heatmaps depicting the number of individuals during 17 – 23 December 2021. Total number of positions = 4966 including 6 individuals (3 males, 3 females).

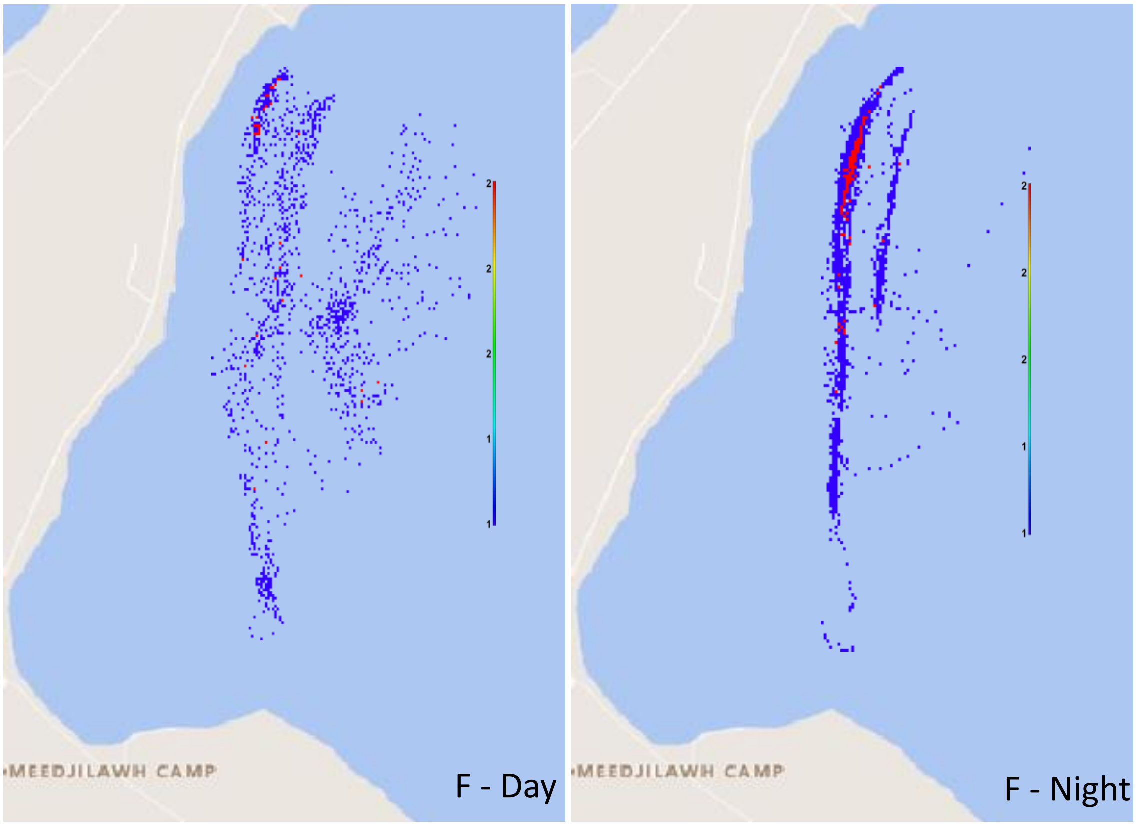

Figure C19. Sex- and diel-specific heatmaps depicting the number of individuals during 24 – 30 December 2021. Total number of positions = 5724 including 3 individuals (0 males, 3 females).

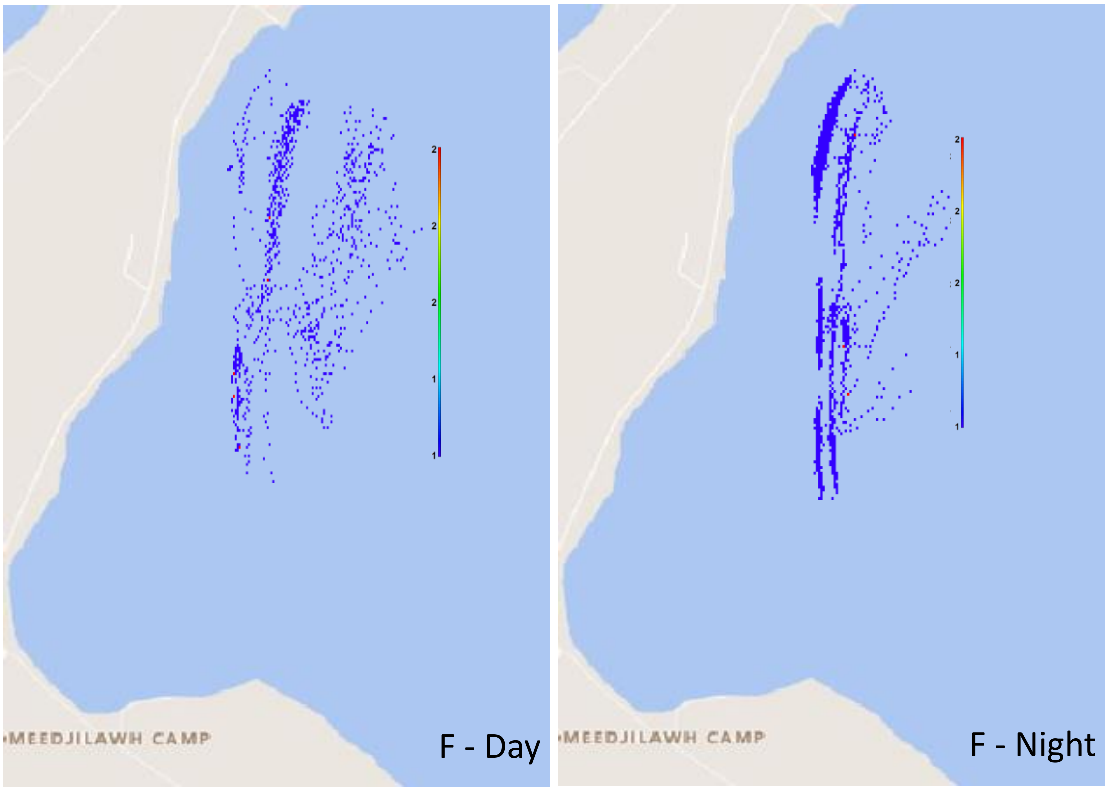

Figure C20. Sex- and diel-specific heatmaps depicting the number of individuals during 31 December 2021 – 6 January 2022. Total number of positions = 5143 including 3 individuals (0 males, 3 females).

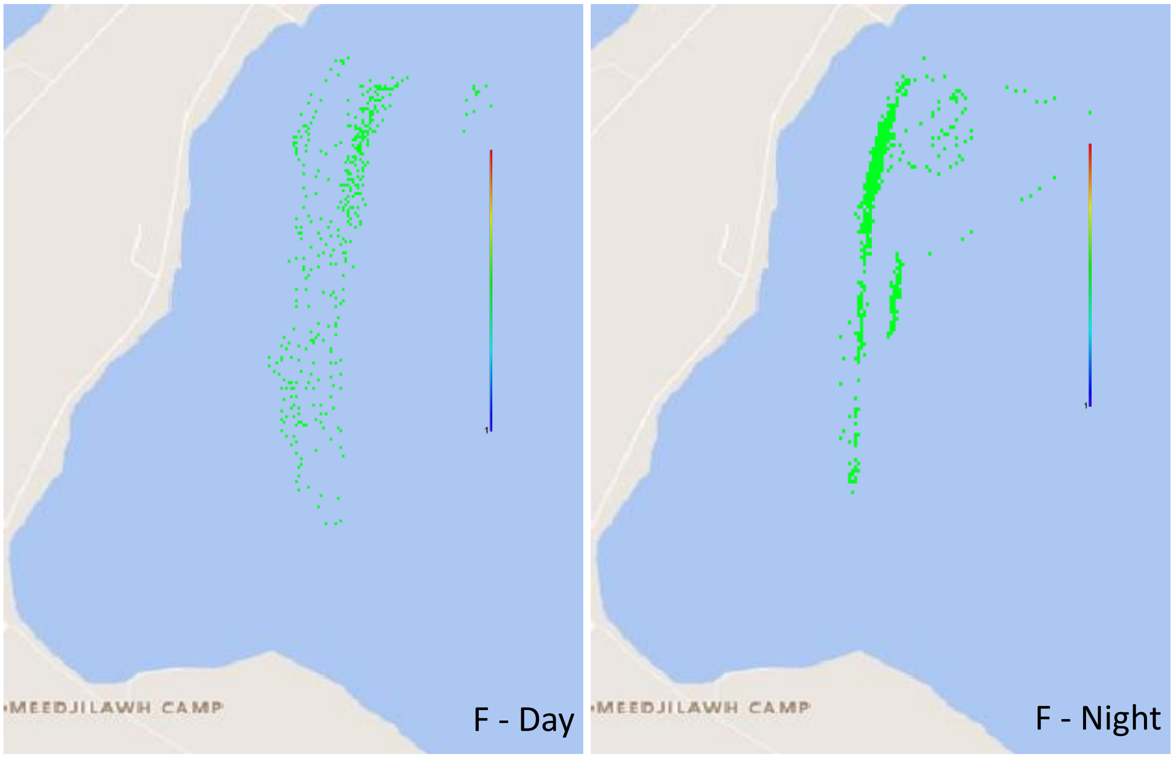

Figure C21. Sex- and diel-specific heatmaps depicting the number of individuals during 7 – 13 January 2022. Total number of positions = 2607 including 2 individuals (0 males, 2 females).

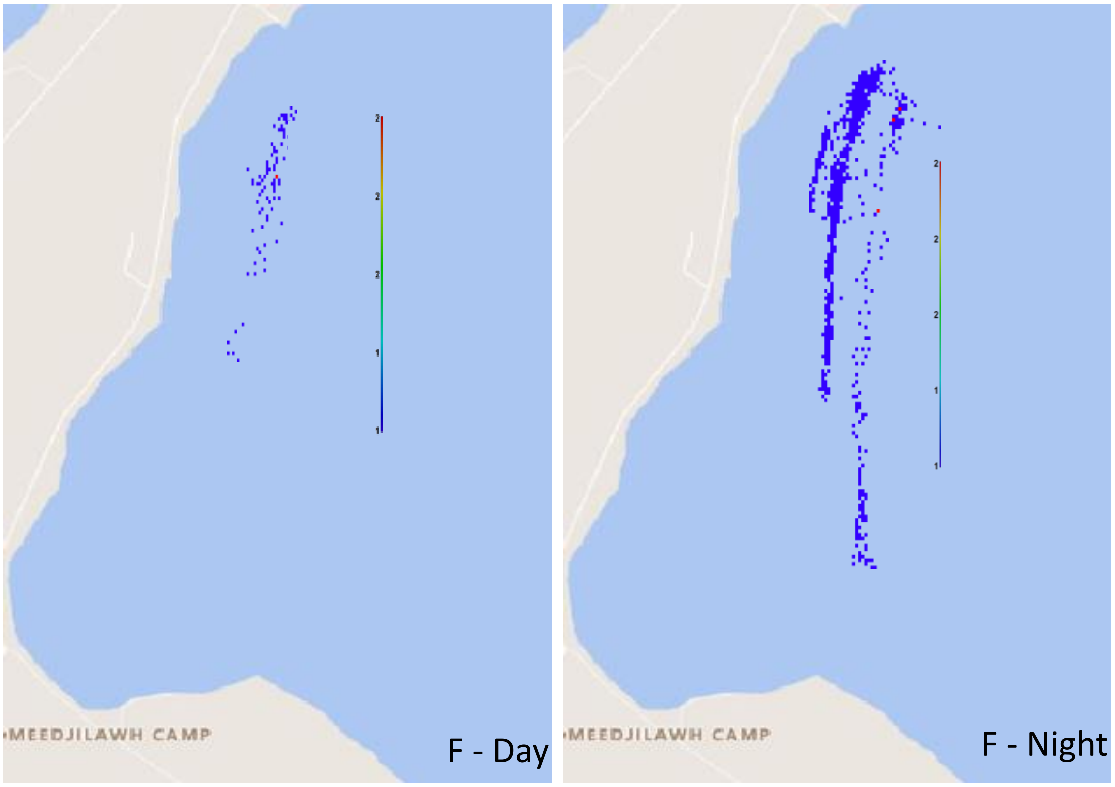

Figure C22. Sex- and diel-specific heatmaps depicting the number of individuals during 14 – 18 January 2022. Total number of positions = 1289 including 3 individuals (0 males, 3 females).

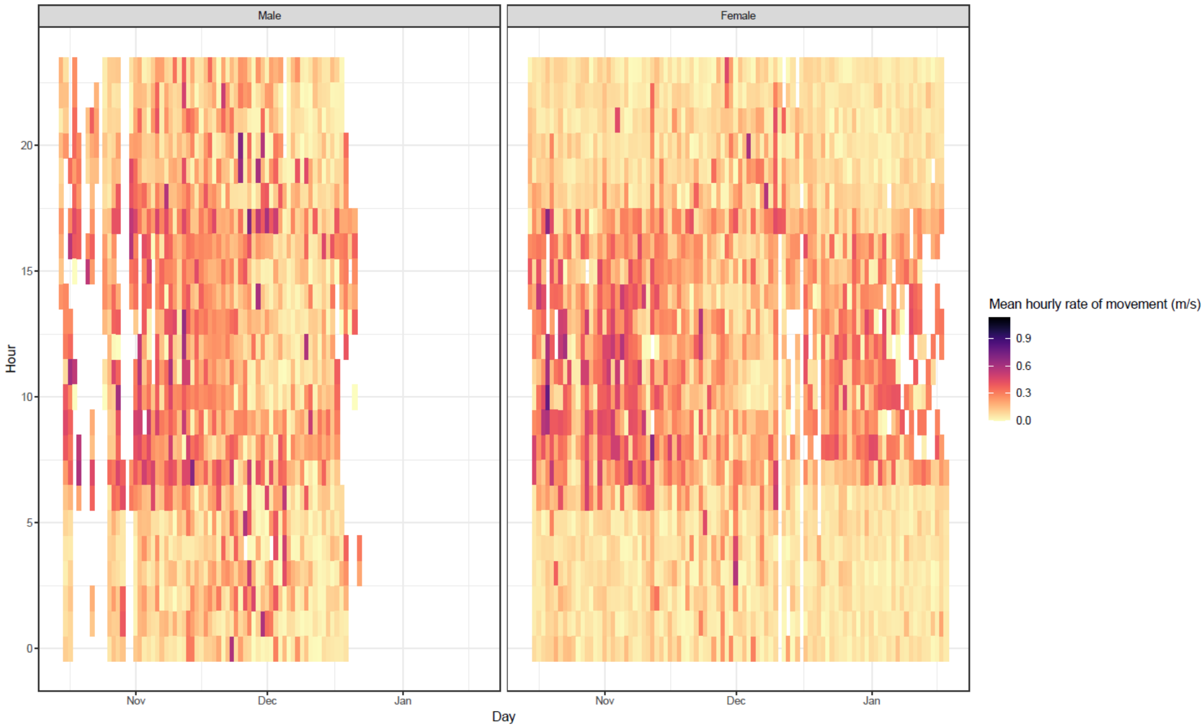

Figure C23. Mean rate of movement (m/s) per hour for each day over the study period (15 October 2021 – 18 January 2022) based on 15 males and 8 females.

# APPENDIX D: RANGE TESTING METHODOLOGY AND RESULTS

## D1 Range tests:

### Methodology

Range testing was conducted at the study site on August 25th and 26th 2021. Four range tests were completed where tags were placed at roughly 100 m increments (100 m up to 600 m then 200 m increments up to 1 km if space allowed) from a receiver that was slightly east of the main shoal (Fig. D2). This receiver was one of two sentinel receivers placed in the LPE shoal to detect fish year-round. Each test ran a different direction from the receiver (N, E, SW, W), as we tried to cover as much of the area as possible of the proposed array location. Transmitters were moored by rope and anchored by a small 5 lb weight, where the tag was attached roughly 1 m off bottom and connected to a flotation flag for visual identification. Each range test lasted 2 hours and tags were programmed to randomly transmit every 60 – 180 s (nominal 120 s). Range test results were plotted using the 'Range Test' software from Innovasea Ltd. (Bedford, Nova Scotia).

### Results

In general, there was a 60% detection probability rate during range testing at around 400-600 m, depending on the test location. However, after consultation with GLATOS experts, it was revealed that our range testing was compromised due to the testing design and collision rates. Having one receiver and multiple tags as we did, increases the chance for collisions. According to Binder et al. (2016), 8 tags pinging at once with a nominal delay of 120 seconds is estimated to have a ~45% collision rate. The low detection probabilities were likely driven by collisions, which includes the flat curves observed in Figures D3-4. Effectively, the number of tag collisions leads to counterintuitive results because the maximum detection probability at a given distance decreases when range increases (Chris Holbrook, personal communication). Based on consultation with GLATOS, it was established that tag range was likely >1 km (Chris Holbrook, personal communication). Based on this and consultation with SON harvesters, receivers within the VPS array were placed no more than 750 m apart.

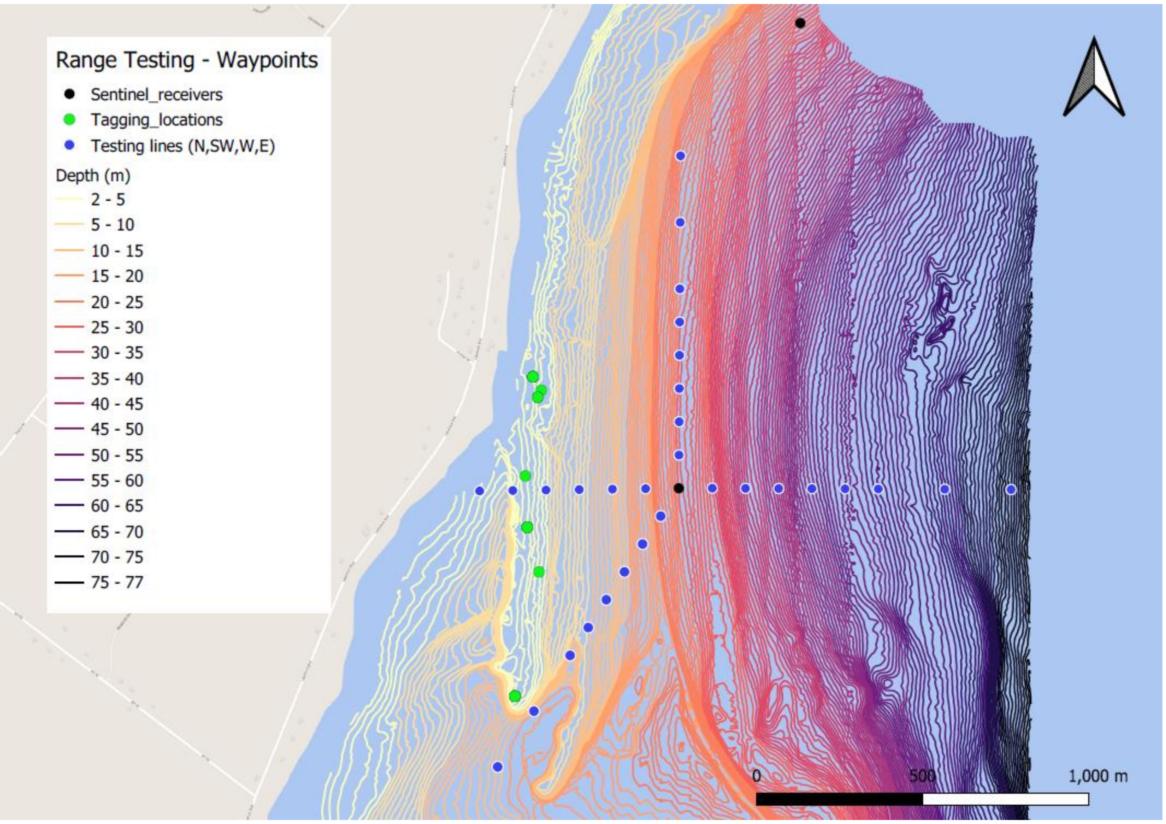

Figure D2. Range tests (N, SW, W, E) that occurred at Port Elgin Bay on 25 - 26 August 2021. Each line represents a separate range test. Green circles are depicting lake whitefish capture locations in November 2020.

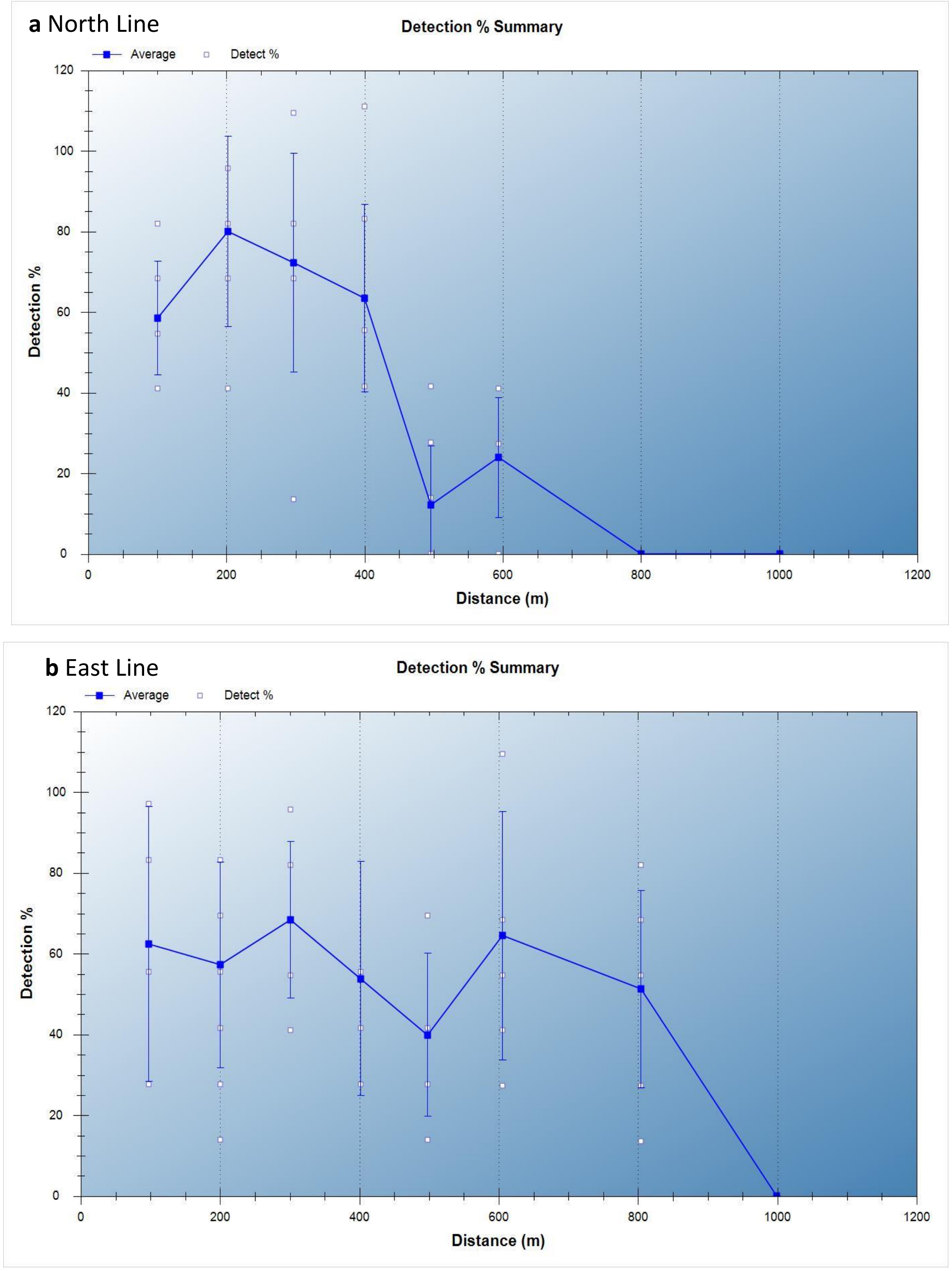

Figure D3. Range testing results from the North (a) and East (b) lines of ranges tests that were completed in the study area (see Figure D2 for reference on what the tests looked like).

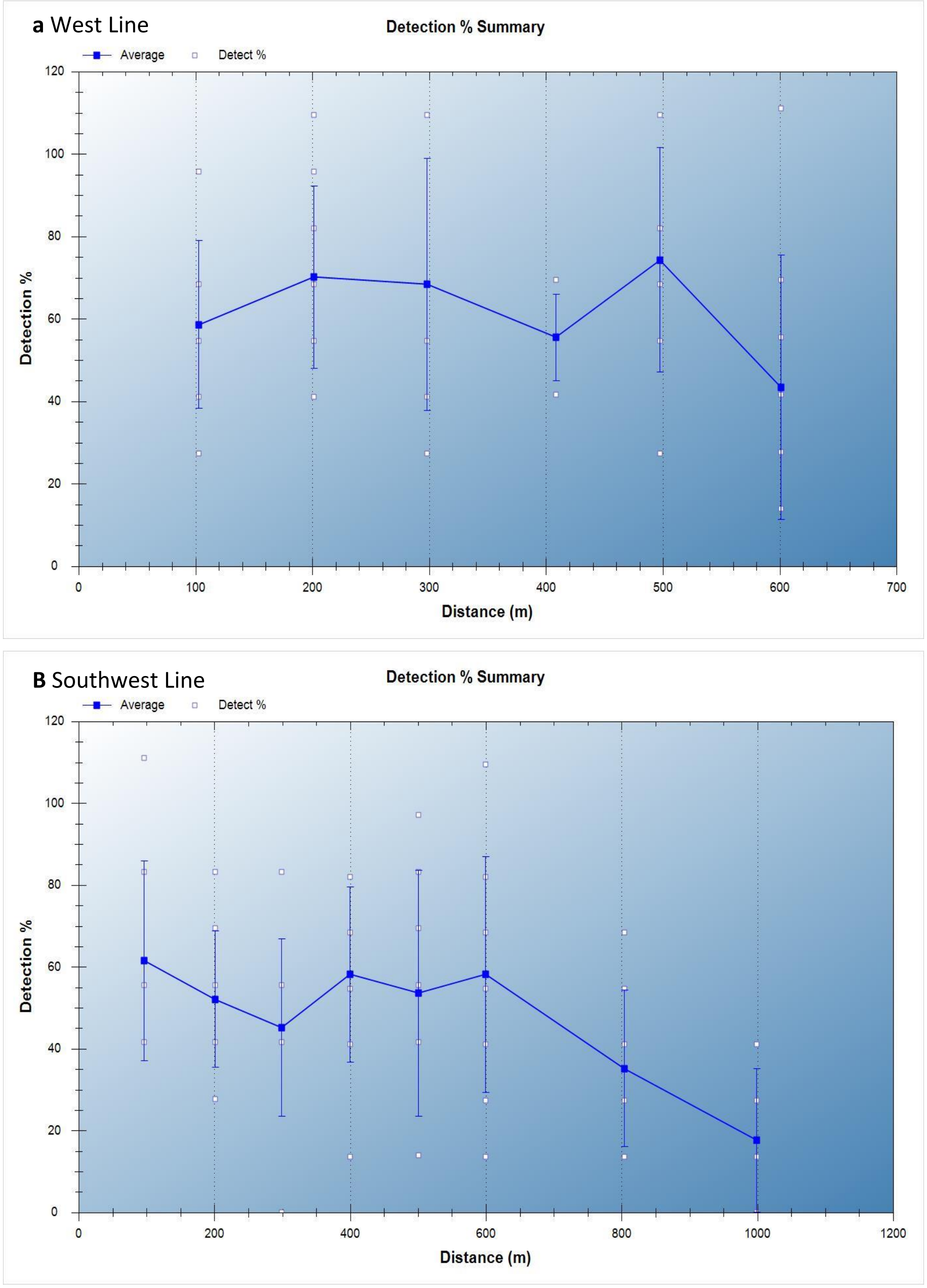

Figure D4. Range testing results from the West (a) and Southwest (b) lines of ranges tests that were completed in the study area (see Figure D2 for reference on what the tests looked like).

# APPENDIX E: SUPPORTING STATISTICAL TABLES AND TESTS

Table E1. Linear mixed model results for predicting variation in mean hourly lake depth displacement (n = 12,808). Sex (male or female) and diel period (night or day) were included as explanatory variables. ΔAIC is the difference between the model with the lowest AIC (the top-ranked model; i.e. ΔAIC = 0) and each subsequent alternative model. Hourly mean lake depth displacement is measured in meters per hour.

| Linear mixed models: Main and (random effects) | AIC | ΔAIC | Independent variables | Estimate (Direction of effect) | Std. Error | F-value | P-value |
|---|---|---|---|---|---|---|---|
| Mean hourly lake depth displacement ~ Diel + (1\|Hour) | 59610.21 | 0 | Intercept<br>Diel | -0.077 (-)<br>0.239 (+) | 0.276<br>0.110 | -<br>4.716 | -<br>**0.030** |
| Mean hourly lake depth displacement ~ Sex + Diel + (1\|Hour) | 59615.72 | 5.51 | Intercept<br>Sex<br>Diel | -0.019 (-)<br>-0.042 (-)<br>0.236 (+) | 0.283<br>0.045<br>0.110 | -<br>0.839<br>4.620 | -<br>0.360<br>**0.032** |
| Mean hourly lake depth displacement ~ Sex + (1\|Hour) | 59615.76 | 5.55 | Intercept<br>Sex | 0.129 (+)<br>-0.044 (-) | 0.274<br>0.045 | -<br>0.935 | -<br>0.334 |
| Mean hourly lake depth displacement ~ Sex + Diel + Sex:Diel + (1\|Hour) | 59619.71 | 9.50 | Intercept<br>Sex<br>Diel<br>Sex:Diel | -0.094 (-)<br>0.032 (+)<br>0.361 (+)<br>-0.089 (-) | 0.294<br>0.073<br>0.170<br>0.093 | -<br>0.456<br>4.491<br>0.916 | -<br>0.500<br>**0.034**<br>0.338 |

Table E2. Linear mixed model results for predicting variation in total horizontal distance (n = 1370). Sex (male or female), diel period (night or day), and the number of positions were included as explanatory variables. Day (each day of the study period) and Individual fish (unique IDs of the fish) were included as random variables. ΔAIC is the difference between the model with the lowest AIC (the top-ranked model; ΔAIC = 0) and each subsequent alternative model. Total distance is measured in meters.

| Linear mixed models: Main and (random effects) | AIC | ΔAIC | Variables / Parameters | Estimate (Direction of effect) | Std. Error | F-value | P-value |
|---|---|---|---|---|---|---|---|
| Total distance ~ Sex + Diel + Number of positions + Sex:Diel + (1\|Day) + (1\|Individual fish) | 24496.44 | 0 | Intercept | 2041.533 (+) | 246.503 | - | - |
| | | | Sex | 646.999 (+) | 328.788 | 0.947 | 0.341 |
| | | | Diel | 255.243 (+) | 119.283 | 40.277 | **<0.0001** |
| | | | Sex:Diel | -1902.521 (-) | 204.386 | 86.648 | **<0.0001** |
| | | | Number of Positions | 21.914 (+) | 1.169 | 351.461 | **<0.0001** |
| Total distance ~ Sex + Diel + Number of positions + (1\|Individual fish) + (1\|Day) | 24590.68 | 94.28 | Intercept | 2489.736 (+) | 244.233 | - | - |
| | | | Sex | -302.591 (-) | 320.741 | 0.893 | 0.356 |
| | | | Diel | -318.365 (-) | 105.354 | 9.142 | **0.003** |
| | | | Number of Positions | 20.070 | 1.187 | 288.330 | **<0.0001** |
| Total distance ~ Sex + Number of positions + (1\|Individual fish) + (1\|Day) | 24608.92 | 112.48 | Intercept | 2426.348 (+) | 244.192 | - | - |
| | | | Sex | -285.408 (-) | 325.206 | 0.773 | 0.390 |
| | | | Number of Positions | 18.750 (+) | 1.109 | 287.887 | **<0.0001** |
| Total distance ~ Diel + Number of positions + (1\|Individual fish) + (1\|Day) | 24602.95 | 106.51 | Intercept | 2392.237 (+) | 220.809 | - | - |
| | | | Diel | -316.613 (-) | 105.341 | 9.045 | **0.003** |
| | | | Number of Positions | 20.018 (+) | 1.186 | 287.649 | **<0.0001** |
| Total distance ~ Sex + Diel + Sex:Diel + (1\|Day) + (1\|Individual fish) | 24806.46 | 310.02 | Intercept | 3418.37 (+) | 300.46 | - | - |
| | | | Sex | 563.08 (+) | 465.66 | 0.029 | 0.866 |
| | | | Diel | 752.45 (+) | 130.63 | 0.983 | 0.322 |
| | | | Sex:Diel | -1280.30 (-) | 226.51 | 31.950 | **<0.0001** |
| Total distance ~ Sex + Diel + (1\|Individual fish) + (1\|Day) | 26584.96 | 2088.52 | Intercept | 3444.75 (+) | 289.03 | - | - |
| | | | Sex | -142.68 (-) | 438.62 | 0.106 | 0.748 |
| | | | Diel | 103.76 (+) | 103.76 | 6.720 | **0.010** |
| Total distance ~ Diel + (1\|Individual fish) + (1\|Day) | 26597.04 | 2100.6 | Intercept | 3399.89 (+) | 242.78 | - | - |
| | | | Diel | 269.10 (+) | 103.77 | 6.725 | **0.010** |
| Total distance ~ Sex + (1\|Individual fish) + (1\|Day) | 26600.79 | 2104.35 | Intercept | 3585.19 (+) | 284.47 | - | - |
| | | | Sex | -143.81 (-) | 439.66 | 0.107 | 0.747 |

Table E3. Linear mixed model results for predicting variation in the horizontal rate of movement (n = 13,107). Sex (male or female), diel period (night or day), and the number of positions were included as explanatory variables. Hour (hour of the day), Day (each day of the study period), and Individual fish (unique IDs of the fish) were included as random variables with Hour nested within Day. ΔAIC is the difference between the model with the lowest AIC (the top-ranked model; ΔAIC = 0) and each subsequent alternative model. Rate of movement is measured in meters per second.

| Linear mixed models: Main and (random effects) | AIC | ΔAIC | Variables / Parameters | Estimate (Direction of effect) | Std. Error | F-value | P-value |
|---|---|---|---|---|---|---|---|
| Rate of movement ~ Sex + Diel + Sex:Diel + Number of positions + (1\|Day/Hour) + (1\|Individual fish) | -25069.5 | 0 | Intercept | 0.214 (+) | 0.007 | - | - |
| | | | Sex | 0.006(+) | 0.007 | 12.303 | **0.002** |
| | | | Diel | -0.028 (-) | 0.003 | 498.644 | **<0.0001** |
| | | | Sex:Diel | -0.063 (-) | 0.003 | 363.200 | **<0.0001** |
| | | | Number of Positions | -0.009 (-) | 0.0002 | 16.788 | **<0.0001** |
| Rate of movement ~ Sex + Diel + Sex:Diel + (1\|Day/Hour) + (1\|Individual fish) | -25070.27 | 0.77 | Intercept | 0.205 (+) | 0.007 | - | - |
| | | | Sex | 0.006 (+) | 0.007 | 12.716 | **0.002** |
| | | | Diel | -0.027 (-) | 0.003 | 497.099 | **<0.0001** |
| | | | Sex:Diel | -0.006 (-) | 0.003 | 374.442 | **<0.0001** |
| Rate of movement ~ Sex + Diel + Number of positions + (1\|Day/Hour) + (1\|Individual fish) | -24722.6 | 346.9 | Intercept | 0.232 (+) | 0.008 | - | - |
| | | | Sex | -0.032 (-) | 0.007 | 18.344 | **0.0004** |
| | | | Diel | -0.053 (-) | 0.003 | 391.545 | **<0.0001** |
| | | | Number of Positions | -0.001 (-) | 0.0001 | 28.225 | **<0.0001** |
| Rate of movement ~ Diel + Number of positions + (1\|Day/Hour) + (1\|Individual fish) | -24719.43 | 350.01 | Intercept | 0.221 (+) | 0.008 | - | - |
| | | | Diel | -0.053 (-) | 0.003 | 392.680 | **<0.0001** |
| | | | Number of Positions | -0.001 (-) | 0.0002 | 28.525 | **<0.0001** |
| Rate of movement ~ Sex + Diel + (1\|Day/Hour) + (1\|Individual fish) | -24712.79 | 356.71 | Intercept | 0.220 (+) | 0.007 | - | |
| | | | Sex | -0.032 (-) | 0.007 | 19.094 | **0.0003** |
| | | | Diel | -0.053 (-) | 0.003 | 387.974 | **<0.0001** |
| Rate of movement ~ Diel + (1\|Day/Hour) + (1\| Individual fish) | -24709.33 | 360.17 | Intercept | 0.210 (+) | 0.007 | - | - |
| | | | Light | -0.053 (-) | 0.004 | 389.1 | **<0.0001** |
| Rate of movement ~ Sex + Number of positions + (1\|Day/Hour) + (1\|Individual fish) | -24388.37 | 681.13 | Intercept | 0. 199 (+) | 0.007 | - | - |
| | | | Sex | -0.033 (-) | 0.007 | 20.231 | **0.0002** |
| | | | Number of Positions | -0.001 (-) | 0.0002 | 22.895 | **<0.0001** |
| Rate of movement ~ Sex + (1\|Day/Hour) + (1\| Individual fish) | -24383.70 | 685.80 | Intercept | 0.188 (+) | 0.007 | - | - |
| | | | Sex | -0.033 (-) | 0.007 | 20.954 | **0.0002** |

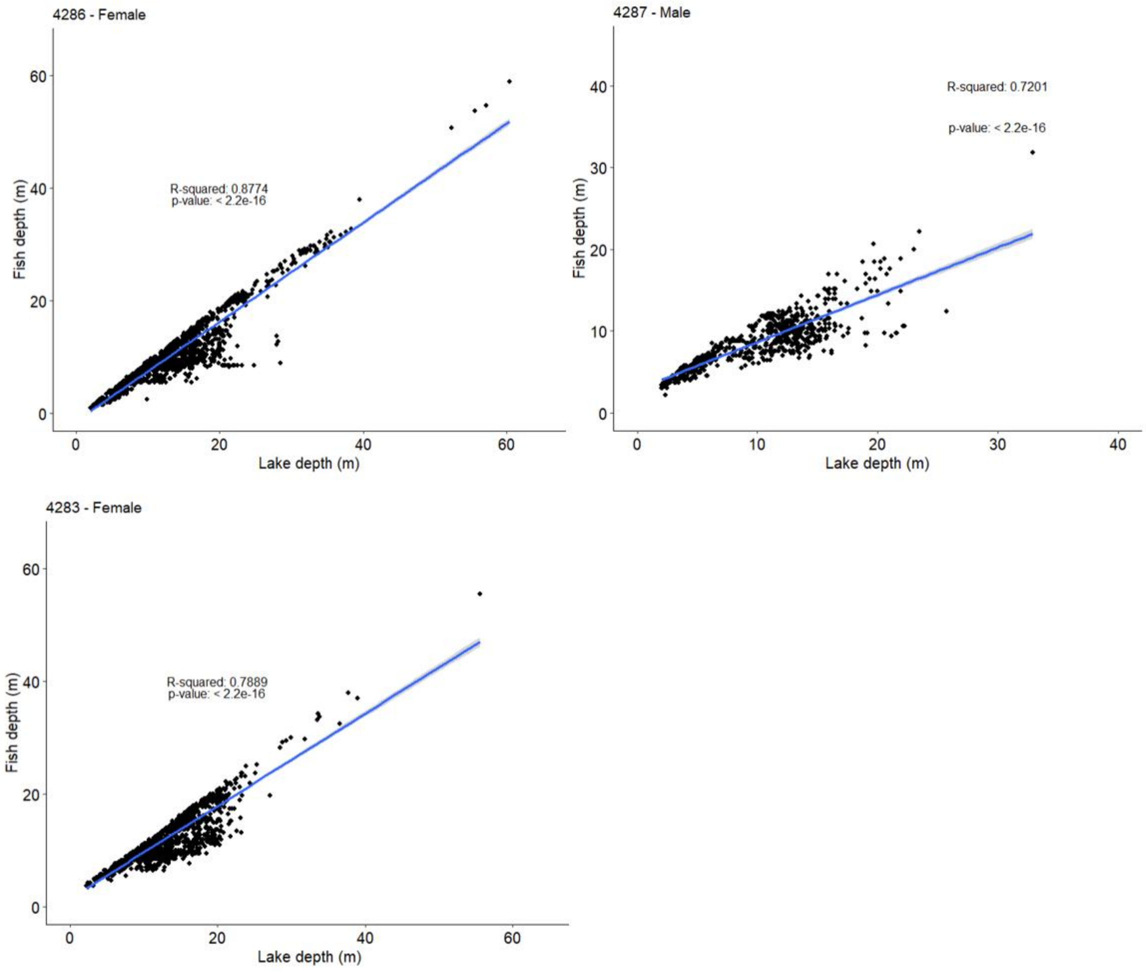

Figure E1. Linear regressions comparing the relationship between lake depth and tag depth for three fish implanted with pressure tags (females 4283 and 4286 and male 4287). $R^2$ and p-values are provided in each plot.