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Effects from environmental factors and individual characters on activity and depth use in a Northern pike (*Esox lucius)* population subjected to recreational fishing: an acoustic telemetry study

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Preface

This study is the last part of my education at the Norwegian University of Life sciences. The study was done to increase the knowledge about what affected the pikes' spatial distribution in Lake Aremarksjøen, and has been a collaboration between NMBU, Utmarksavdelingen for Akershus and Østfold, Ara-Aspern fiskelag, Havass fiskelag, Regionalpark Haldenkanalen, and Haldenvassdragets Brukseierforening among others.

I would like to thank my supervisor Thrond Oddvar Haugen for all the guidance during the field work, statistics and the thesis, and for teaching me as much as he did about pikes. Thanks to Øystein Toverud for help and lending his cabin and boat to us during field work. Lastly, thanks to Axel and Clara for proof reading and support throughout the thesis period.

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Abstract

Northern pike (*Esox lucius*) is a common top- predator in freshwater systems all over the Northern Hemisphere. For centuries it has been a popular target for recreational anglers. In many freshwater ecosystems, recreational fishing has even replaced commercial fisheries, and this fishing pressure can have negative impacts on a pike population. To impose proper management, detailed knowledge about the targeted pike population's ecology, including individual behavior ecology, is important. Recent studies indicate that pike angling vulnerability is positively associated with the pike individual's activity level (e.g., swimming distance and home range). Therefore, knowledge on what factors affect individual pike activity level may constitute key factors for sustainable regulations of pike angling systems. Motivated by this, an acoustic telemetry study was set up to explore what factors and how they affected pikes' spatial distribution in a population subjected to recreational fishing. In addition were temporal factors (day of year, time of day), environmental factors such as water temperature, air pressure, moon phase, precipitation along with physical properties of the individuals, such as sex, length, and back-calculated growth included in the analyses.

The study location was the lake Aremarksjøen in Østfold county in Norway, which is a middle sized, deep and humic lake. The study lasted from May 2017 to December 2017. For the acoustic telemetry study, 37 pike individuals were caught in gillnets during the spawning period and they got implanted with a transmitter. In total, 30 receivers were placed throughout the lake, and 20 of these were placed in a spatial pattern that allowed for triangulation in the study area. The remaining 10 were placed in arrays and narrow areas for detection of coarse-scale lake use and migration pattern. Data from the receivers were used in statistical analyses to estimate the pikes' depth use, 50% utilization distribution (UD50), swimming distance (D) and "turboness" (i.e., D/UD50).

The results showed that depth use increased with day of year, individual length and at sunrise and sunset. UD50 increased with precipitation intensity, full and waning moon and length but decreased with increasing air pressure. Water temperature was involved in complex interactions and lead to diverse UD50 results. Small and medium female pikes increased the UD50 at low and high temperatures, but at medium temperature the UD50 decreased. On contrary, large females decreased the UD50 at low and high water temperatures and increased the UD at medium temperature. The UD50 of male pikes increased continusly with increasing temperatures. Turboness increased with day of year, air pressure, precipitation, waxing, - full- and waning moon and length, especially male pikes, and decreased with water temperature. Lastly, swimming distance increased

with length, precipitation, increasing air pressure, decreasing water temperature and varied slightly with moon phase.

Based on recent findings, active pikes are easier for anglers to catch. My results indicate that the most valued large individuals are most vulnerable for angling at sunrise or sunset when it is full moon, precipitation, cold water temperature and high air pressure.

Anglers can affect the pike population in a multitude of negative ways. Large individuals are the most active and utilize a larger part of the lake, while smaller pike spend more time in the vegetation. Active fish are easier to catch, which makes large, active pike individuals attractive targets. However, if active and large individuals are removed from the population, there may be an unintended selection for timid and small individuals that mature early. A good management strategy that counteract these non-wanted effects is therefore important. Recent studies have shown that harvest size-slots (minimum size and maximum-size-limits) may contribute to a sustainable pike stock when combined with bag limits. For the Aremarksjøen system, future studies need to settle whether the hooking vulnerability can be linked to individual activity level in this system. However, based on the principle of precaution, regulations of recreational pike fishing in the lake should be formulated under the assumption that individual activity is positively correlated with hooking vulnerability.

Sammendrag

Gjedde er en toppredator i ferskvann og finnes over hele den nordlige halvkule. I århundrer har gjedda vært en populær fisk for fritidsfiskere. I flere ferskvannssystemer har fritidsfiske tatt over for kommersielt fiske, og dette fiskepresset kan ha negative konsekvenser for en gjeddepopulasjon. Detaljerte kunnskaper om gjeddebestandens økologi, inkludert økologien på individnivå, er viktig for å kunne fremme den beste fiskeforvaltningen. Nyere studier viser at gjeddas sårbarhet for å bli kroket er positivt korrelert med gjeddas individuelle aktivitetsnivå (f. eks. svømmedistanse og hjemmeområde). Kunnskap om hvilke faktorer som påvirker gjeddas individuelle aktivitetsnivå kan derfor utgjøre nøkkelfaktorer som er viktige for utforming av bærekraftig regulering av systemer med gjeddefiske. En akustisk telemetristudie ble derfor satt opp for å undersøke hvilke faktorer og hvordan disse påvirket den romlige distribusjonen av en gjeddepopulasjon som er påvirket av fritidsfiske. I tillegg ble tidsmessige faktorer (dag i året, tidspunkt på dagen), miljøfaktorer slik som vanntemperatur, lufttrykk, månefase, nedbør, og fysiske egenskaper til individene som kjønn, lengde, og tilbakeregnet vekst inkludert i analysene.

Lokasjonen for studiet var Aremarksjøen i Østfold, som er en mellomstor, dyp og humusholdig innsjø. Studiet varte fra mai 2017 og fram til desember 2017. For studiet ble 37 gjedder fanget med garn under gyteperioden, og hver av disse fikk operert inn en sender. Totalt 30 mottakere ble plassert i innsjøen, hvorav 20 av disse ble triangulert i studieområdet. De 10 resterende mottakerne ble plassert på smale steder i innsjøen for å få en grov oversikt over bruken av resten av innsjøen og migrasjonsmønsteret. Dataene fra mottakerne ble brukt i statistiske analyser for å estimere gjeddas dybdebruk, 50 % hjemmeområde (UD50), svømmedistanse (D) og turboness (dvs. D/UD50).

Resultatene viste at dybdebruken økte med dag på året, individlengde, og ved soloppgang og solnedgang. 50% hjemmeområde utvidet seg med økt nedbør, full- og avtagende måne, lengde, og ble redusert ved høyt lufttrykk. Vanntemperatur var involvert i komplekse interaksjoner og førte til varierte resultater av UD50. Små og medium hunngjedder økte UD50 ved lave og høye vanntemperaturer, men reduserte UD50 ved medium vanntemperatur. I motsetning ble store hunngjedders UD50 redusert ved lave og høye vanntemperaturer og økte ved medium vanntemperatur. UD50 til hanngjedder økte med økende vanntemperatur. Turboness økte med dag på året, lufttrykk, nedbør, alle månefasene bortsett fra nymåne, lengde, spesielt hos hanngjeddene, og reduserte med økende vanntemperatur. Til slutt, svømmedistanse økte med lengde, nedbør, lufttrykk, lav vanntemperatur, og varierte noe ved de ulike månefasene.

I og med at nylige funn i andre studiesystemer har vist at er det lettere for sportsfiskere å kroke aktive gjedder enn mindre aktive gjedder indikerer resultatene fra min studie at de store gjeddene,

som er mest verdsatte blant fiskerne, er mest sårbare for fisking ved soloppgang, solnedgang, ved mye nedbør, kalde vanntemperaturer og høyt lufttrykk.

Fiskere kan påvirke gjeddepopulasjonen negativt på flere måter. Store individer er mer aktive og bruker en større del av innsjøen enn små gjedder som bruker mer tid i vegetasjonen. Aktive gjedder er sannsynligvis enklere å fange, noe som gjør at store, aktive individer er attraktive mål. Dersom store og aktive individer blir tatt ut av populasjonen kan det skje en utilsiktet seleksjon i favør av små og lite aktive individer som kjønnsmodnes fortere. Det er derfor viktig med en forvaltningsstrategi som motvirker disse uønskede virkningene. Nylige studier har vist at døgnkvoter i kombinasjon med minstemål og størstemål på fisken som blir tatt opp kan bidra til en bærekraftig gjeddebestand. I fremtidige studier av systemet i Aremarksjøen er det viktig å se om fangstsannsynligheten kan knyttes opp mot aktivitetsnivået til gjeddeindividene, men basert på føre-var-prinsippet bør reguleringer av fritidsfiske i innsjøen formuleres med forutsetning om at individaktiviteten er positivt korrelert med fangbarheten.

Contents

2 Introduction

In 1653, Sir Izaak Walton, the author who first wrote about recreational fishing, described the Northern pike (*Esox lucius*, L., hereafter referred to as pike*)* as “the tyrant of the rivers, or the fresh-water wolf, by reason of his bold, greedy, devouring disposition” (Walton and Cotton, 1847). The pike is a ferocious, freshwater, apex predator that eats almost anything that moves, even other members of its species. It is easy to understand why this “tyrant” has for centuries been, and continues to be, one of the most popular species for recreational fishing (Lewin et al., 2006).

Over the past few decades, inland commercial fishing has decreased in industrialized countries and no longer holds much economic or social importance (Lewin et al., 2006). Recreational fishing, however, is a popular activity for an estimated 225 million people worldwide (World Bank, 2012), providing social and economic benefits at the local and national levels (Lewin et al., 2006). Australia, North-America and Europe are hot spots for recreational fishing, with Norway featuring as an especially popular destination for anglers (Arlinghaus and Cooke, 2009). In 2009 alone, Norway’s total revenue from the inland fishing industries was estimated at 1,360 million NOK. Despite the large sum, the potential total revenue is much higher. By increasing the cost of fishing licenses, promoting organized angling packages (accommodation, boat rentals, guides, food, transportation, etc.), and doubling the number of foreign fishing tourists, the prospective turnover is 2.095 million NOK in 2020 (Norges Skogeierforbund, 2010).

Despite the benefits, recreational fishing can impose negative consequences such as population declines and evolutionary changes in a fish population through factors like high and selective exploitation, reduced size and age structure, harvest and “trophy fishing” (Arlinghaus and Cooke, 2009, Lewin et al., 2006). Since many pike anglers in particular prefer trophy fishing (Schroeder and Fulton, 2013), size-selectivity poses a particular threat to pike populations (Kuparinen et al., 2018). When removing large, cannibalistic individuals from a pike population, medium-sized fish will become more abundant, due to reduced cannibalism and increased survival of young fish (Haugen and Vøllestad, 2018a). Removal of large fish improve the opportunities of reproduction for small fish, which in turn favors selection of small-sized and slow-growing fish (Matsumura et al., 2011).

Pike has an increasing potential as a magnet for inland fishing tourism (Aas and Dervo, 2010). For instance, in the lake Aremarksjøen alone, angling tourists have increased from about zero anglers in 2006 to approximately 2000 angling days a year (one angler a day is one angling day) in 2017 (Øystein Toverud pers. Comm.). Regulations to protect pike resources are therefore crucial (Aas and

Dervo, 2010). Harvesting- slot length limits (Arlinghaus et al., 2010), strict bag limitations, gear restrictions, organization of licensees, and a functioning operating plan are examples of some steps needed to maintain a stable and sustainable harvesting of fish (Aas and Dervo, 2010). The regulations applied in Aremarksjøen are maximum length-limit, bag-limitation of 2 pikes per day and catch-and-release of the pikes that are not used as food (Øystein Toverud pers. Comm.). Particularly, catch-and-release are a common harvest regulation for pike fishing (Klefoth et al., 2008). While Arlinghaus et al. (2009) demonstrated that catch-and-release caused some physical homeostasis disruptions and behavioral changes in pike specimens, their recovery was rapid and their resilience against air exposure was high. However, in a long-term study done on catch-and-release behavior in pike by Klefoth et al. (2011), pike exhibited reduced swimming activity, decreased growth, and increased time in refuge locations, such as reed growths. Another issue affecting catch-and-release fishing is the conservation of old, large fish. Since large pike are not taken out of the population, these large cannibalistic fish will increasingly prey on medium sized pikes. A reduction of medium sized pike will lead to decreased predation on planktivorous and omnivorous fish, such as roach (*Rutilus rutilus*). The presence of larger numbers of roach will in turn decrease zooplankton populations and increase plankton populations, which in turn can lead to algal blooms (Sharma et al., 2011). Hence, in lakes where eutrophication is ongoing or a potential threat, the amount of large pike individuals should be balanced to secure sufficient amounts of mid-sized individuals to control densities of zooplanktivorous and omnivorous fish species like roach.

In addition to physical variation, animal populations contain different behavior types that are unrelated to size, sex or age. These are commonly known as “personalities” and are heritable traits (Krebs and Davies, 1987). Three different personality types have been observed in pike (Kobler et al., 2009) and different fishing methods favors different personalities. Angling, which is one of the most common category of recreational fishing, constitute a passive harvesting type. Passive gears generally select for bold and active fish personalities (Arlinghaus et al., 2017b) called “habitat opportunists”. Habitat opportunists are the most active of the behavioral categories; they use the entire lake, including the pelagic area (Kobler et al., 2009). The selection of active fish can cause increased timidity in a pike population, potentially creating a “timid” population that consists mostly of shy behavioral types (Arlinghaus et al., 2017b). The shy personality category comprises “reed selectors” and “submerged macrophyte selectors”. Though both prefer the littoral zone, they have different vegetation preferences, and submerged macrophyte selectors also tend to be more active than reed selectors (Kobler et al., 2009).

With the goal of attaining novel knowledge about environmental drivers of pike activity level pertinent to construction of sustainable pike recreation fishing regulations, this study used acoustic telemetry to map individual pike spatial-temporal behavior over a course of 9 months (Skov et al., 2017). Acoustic telemetry was first used in marine environments but is now frequently used in freshwater systems. Using acoustic telemetry with fixed triangulated stations makes it possible to generate three-dimensional tracks of fish movement (Cooke et al., 2013, Lagardere et al., 2012, Alós et al., 2016). The detailed data can be used to study fish behavior and to map the activity of the specific personality types (Bøe, 2013). Increased knowledge about the behavioral composition of the pike populations in the lakes and rivers of the Østfold region can improve management strategies in these and similar areas.

The purpose with this thesis was to investigate 1) which environmental factors and individual characters affect the pikes' activity behavior, 2) what conditions will increase the anglers' probability to catch pike, and finally I will discuss what consequences recreational anglers may have on the pike population and which measures are needed to maintain a sustainable pike stock.

3 Materials and method

3.1 Area description

The study location is the lake Aremarksjøen in Østfold county Norway (Figure 1). It is a 7.46 km^2 middle sized lake, which is approximately 10 km long and between 0.7 to 2 km wide (Bjar et al., 2013) with a maximum depth of 39.5 meters. The water is humic and lime deficient and located 105 meters above sea level (Vann-nett, 2017). Measurements in September 2017 showed a thermocline the depth of 11 m. The ecological status is classified as "poor" according to the Norwegian classifying system of freshwater lakes (Vanndirektivet, 2013) due to crayfish plague and few eutrophication sensitive macrophytes (trofiindex). Farmland and scattered settlements located close to the lake contribute to water pollution to some extent (Vann-nett, 2017). The lake is part of the 132 km long Halden water course, which is a lowland water course containing seven large and shallow lakes. These are closely linked to each other by short rivers. The lake Øymarksjøen runs through a sluice that empties into Aremarksjøen (NVE, 2009). Agriculture and forestry is what dominate the catchment area. The ground consists of high-nutrient marine- and moraine deposits, which make the soil valuable especially for agriculture (Bjar et al., 2013, Løddesøl and Smith, 1938). Coniferous trees like Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), including some deciduous trees such as Downey birch (*Betula pubescens*), are tree species dominating the forest around the lake.

Figure 1. View over Lake Aremarksjøen. (Photo: Amalie Haugen)

In 2012, Fylkesmannen i Østfold registered 25 different types of water plants in Aremarksjøen. The most common water plants in the lake which got the cover score "3" are hairgrass (*Eleocharis acicularis),* shoreweed (*Littorella uniflora),* creeping spearwort (*Ranunculus reptans),* alternate-flowered water-milfoil (*Myriophyllum alterniflorum),* water smartweed (*Persicaria amphibia),* yellow water-lily *(Nuphar lutea)* and floating pondweed *(Potamogeton natans)* (Bjar et al., 2013).

A diversity of fish species have been documented in the lake, such as Northern pike (*Esox lucius*), perch (*Perca fluviatilis*), white bream (*Blicca bjoerkna*), crucian carp (*Carassius carassius*), alpine bullhead (*Cottus poecilopus*), European bullhead (*Cottus gobio*), European river lamprey (*Lampetra fluviatilis*), eel (*Anguilla anguilla*), brown trout (*Salmo trutta*), burbot (*Lota lota*), zander (*Sander lucioperca*), bream (*Abramis brama*), bleak (*Alburnus alburnus*), common roach, common rudd (*Scardinius erythrophthalmus*), common minnow (*Phoxinus phoxinus*), European smelt (*Osmerus eperlanus*), and vendace (*Coregonus albula*) (Øystein Toverud pers. comm). Other species like European crayfish (*Astacus astacus*) is observed in the lake as well, including the non-native species signal crayfish (*Pacifastacus leniusculus*) from North America which have brought crayfish plague to the lake (Vøllestad, 1988).

3.2 Study species

Northern pike is a freshwater predator found in lakes, rivers and low-salinity coastal waters (Arlinghaus et al., 2017a) and is distributed throughout the Northern Hemisphere. However, humans have contributed the spreading of pike beyond its natural range (Crossmann, 1996).

The pikes' body is long with unpaired fins (dorsal, caudal and anal) located at the rear end, as an adaption to sprint predation (Crossmann, 1996). Due to its olive green and camouflage colored skin, pikes blend in with the vegetation (Kjøsnes and Rustadbakken, 2010). The head is composed by a long, flattened snout with a large mouth and a noteworthy number of teeth on jaws, vomer, palatines and tongue (Crossmann, 1996).

Pike is a top-predator with a broad diet, including invertebrates, fish, amphibians, birds and small mammals (Persson et al., 2017). The consumption of prey varies frequently and depend on prey abundance, physical condition, predator opportunities and vulnerabilities (Diana, 1996). Density, species composition and size structure of the prey fish community of a lake can be strongly affected due to the presence of pike. Pike also affect its own population through cannibalism (Persson et al., 2017). In systems with relatively dense populations and depleted prey quantities, small to intermediate sized pike are at risk of being cannibalized by larger pike (Nilsson and Brönmark, 1999).

Size, rather than age, determines when the pike reaches maturity. This depends on various factors such as temperature, food availability and growth rate at juvenile stage. Spawning takes place during spring between February and June, depending on the geographical distribution. The spawning grounds are close to the water edge within a maximum depth of 50 cm (Billard, 1996).

Vegetation plays an important role during spawning. Pikes are open substratum spawners belonging to the phytophile group (Bry, 1996). Plants work as substratum for eggs, hiding places and provide food for the juveniles. Males mature earlier and arrive first to the spawning grounds and stay longer than the females (Billard, 1996). Because of long mating acts, both females and males cover a large area during reproduction and scatter eggs over large areas of the spawning grounds (Bry, 1996). After hatching, the juveniles grow approximately 10 mm per week until mid- or late summer, depending on the temperature. The juveniles' diet after the yolk sac is digested, is for a short period of time zooplankton, before it goes over to eat other small aquatic organisms, such as insect larvae and crustaceans (Harvey, 2009). Due to the change of diet to bigger prey at the age of approximately 3 years, pike can grow between 1 and 1.5 kg annually for 8 to 10 years (Casselman, 1996).

3.3 Methods

3.3.1 Fish capture

Two methods were used to sample pike. The first was based on scaring the pike into the gillnets, while the second method the gillnet was based on keeping the nets in the water for an up to eight hours period before lifting them. The fishing lasted over four days from the end of April to the beginning of May. Gillnet with the mesh diameter of 40-80 mm was placed parallel and close to the belt of common reed. Two to three people with paddle oars and branches walked in water along the shore while beating and splashing the water to scare the pike into the gillnets. The gillnets were lifted into the boat and the pike was cut out of the meshes and placed in a 50 L black plastic tray with fresh water from the lake. A wet towel was put on top of the tray to prevent the water from being heated too quickly by the sun and to calm down the fish. The water was frequently changed to prevent oxygen depletion. The procedure for the second method was similar, but instead of scaring the fish into the net, the gillnets were left in the water for a few hours to allow the fish to swim into it before being picked up. This latter method captured more fish than the first method but is potentially more harmful to the fish because it is captured in the net for several hours. However, the low water temperatures (<5 ^{0}C) and the highly mobilized immune system during spawning mode justify the use of this particular method (Thrond Oddvar Haugen pers. comm.). The method of using cold water conditions when gillnetting pike for tagging has been used in long time series-study in the U.K (Carlson et al., 2007), as well as in Norwegian studies (Aasrum, 2014). These fishing methods were used on four different locations. In total, 38 live pikes were caught and inspected for potential net-induced wounds before tagging and all were suitable.

3.3.2 Implanting the transmitter

The fish were tagged with 13x31 mm D-LP13 transmitters (weight in air 9.7 g) with transmitter power 150 dB re 1 µPa at 1m from Thelma Biotel (www.biothelma.com). The weight of the transmitters was far below 2 percent of the fishes' weigh, which is the recommended limit. The transmitters in this study were coded to transmit an acoustic signal with the information of ID and depth at random time intervals between every 30 and 90 sec. The signals were transmitted at a randomly selected time to avoid code collisions with other transmitters and estimated battery life is minimum 25 months.

For implanting the transmitter in the fish, a small operation was needed. To do this, an approval from Norwegian Food Safety Authorities is mandatory and must be done by a qualified scientist (jf. Forskrift om bruk av dyr i forsøk, 2015, §§ 5 og 6: the permit ID in this project was 12085). The pike was first placed in a deep tray with water from the lake blended with the anesthetic benzocaine 200 mg/ml (Figure 2). When the fish was unconscious (assessed by pressing the caudal peduncle), it was placed in a tube filled with water from the lake including approximately 20% of full anesthetic to stay sedated (Figure 3) with the abdomen facing upwards.

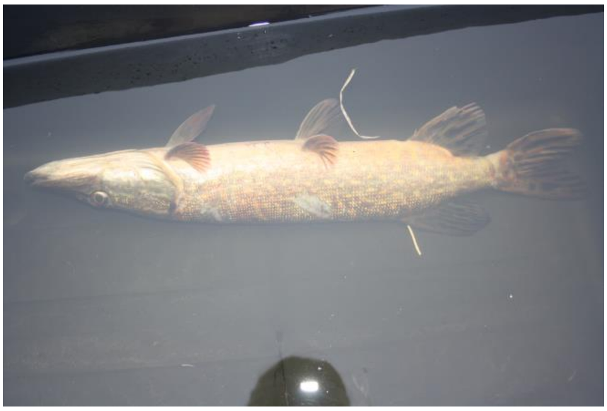


Figure 2. Sedated pike ready for operation. (Photo: Amalie Haugen).

Figure 3. Tube used for operation on pike. (Photo: Amalie Haugen).

A 1.5 cm incision was made with a scalpel on the abdomen and a small ethanol-disinfected transmitter was placed inside of it (Figure 4). The incision was then sewn together with two stiches by using RESOLON® Suture 4/0 45cm DS-24 Blue 0.20 mm monofilament suture kit (Figure 5). While the fish was unconscious, approximately five scales were sampled for age- and individual growth history determination. Scales from the pike was taken from the side of the body, between the dorsal fin and the caudal fin, and put into a paper. A Floy T-bar anchor tag was used to mark the fish with an externally visible individual number, and this was placed at the basis of the dorsal fin. Sex, length, GPS waypoint number, ID (Floy tag number) and transmitter number were noted, and a small piece of the dorsal fin was collected and stored in Ependorph vials on 96% ethanol for genetic testing.

Figure 4. Disinfected transmitter ready to be placed inside the pike. (Photo: Amalie Haugen)

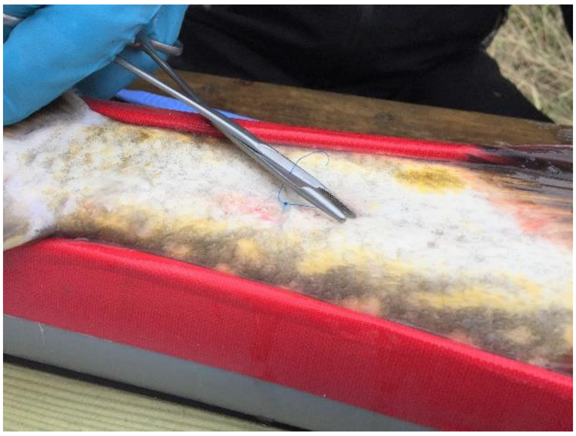


Figure 5. Pike sewn together by using a suture kit. (Photo: Amalie Haugen)

The unconscious fish were then carried over to another 50 L wake-up tray with fresh lake water. When the fish was conscious (i.e. balance was regained and reacting to caudal peduncle pressing), it was released into the lake again close to the same spot as being caught. The same procedure was done on re-captured individuals from 2016 floy-tagged individuals, but instead of giving the fish a new Floy tag, the number of the old tag was noted.

3.3.3 Receiver

To pick up and log detections from the transmitters, 30 THELMABIOTEL TBR-700 receivers were used. These are acoustic receivers with the size of 75 mm in diameter, 230 mm long, 1140 g in air and 260 g in freshwater, and were set up to record at 69 kHz frequencies. In addition to the transmitted information (ID, depth, and signal entrance time to milli sec), the receivers also log water temperature (at deployment depth), strength of received signals and background noise. 20 of these receivers were placed in a bay west of the lake in a triangulated formation (Figure 6) allowing for detailed positioning. This triangulation bay is located close to where all individuals were captured and tagged. The rest of the receivers were placed into arrays or narrow lake areas allowing for detection of coarse-scale lake use and migration patterns (Figure 7).

From September 19th 5 synchronization tags (ART-13-MP) were placed at strategic locations within the triangulation network. These synchronization tags were used for synchronizing the receiver clocks and thus allowing for triangulation of single transmitter signals rather than the position averaging that was used for the pre-synchronization tag deployment period. The synchronization tags transmitted on average every 5 minutes, with an output of 153 dB re 1 µPa at 1m and at the same frequency as the fish tags.

Figure 6. Map over the locations and ID-numbers of the triangulated receivers in the study area.

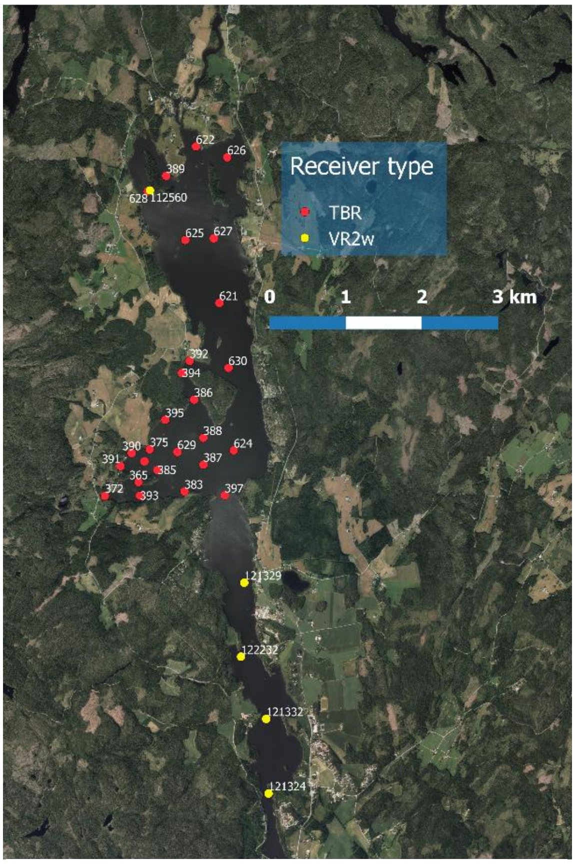


Figure 7. Aremarksjøen with all the receiver locations and ID-numbers.

3.3.4 Water temperature

To measure the water temperature and the changing stratification of the water throughout the study period, HOBO temperature loggers were mounted at 1, 3, 5, and 20 m depth within the triangulation network area. The temperature loggers were attached to a string and fastened to one of the receivers. They were set up to record temperature every four hour.

3.3.5 Range test

A range test was done to map the reception of the receivers and the blind zones. A tag was attached 1 meter from the bottom of a string in which a small anchor was fastened. For every 150 meters in the triangulated area a grapnel was dropped to anchor the boat, then the tag was lowered down in the water until its anchor hit the bottom. Since the tag sends out the same signals as the transmitters in the fish, the signals can collide or get jammed if there is another transmitter nearby. A manual VR100 receiver (www.vemco.com) was therefor used to listen to the tag until it sent an undisturbed signal the receivers could detect if they were in the range of the tag. After retrieving data from the TBRs within the triangulation network, the number of TBRs that received signals at every drop-point was counted and a detection coverage map was constructed, showing that just two of the drop-points had no TBR-detections (Figure 8). The reason for not having detections is likely due to these locations to be very deep (>50 m), but also one of the closest TBRs (TBR 397) were astray at the time of range testing. The longest detection range recorded was 1067 m. Hence, the acoustic conditions seem very good in the study area.

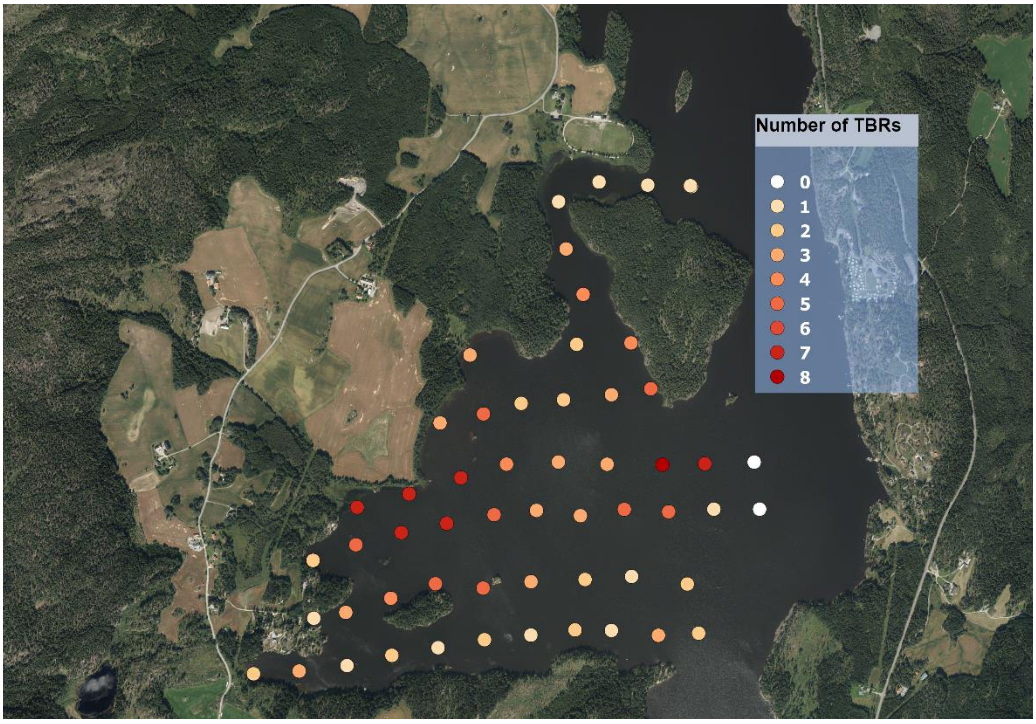


Figure 8. A detection coverage map over the number of TBRs that received signals from the test tag at every drop-point.

3.3.6 Scale readings

Pike scales were used to determine age, back-calculate the length and growth rate of the fish. Fish scales consist of ridges on the surface called circuli, or growth rings (Lagler, 1947). In slow growing seasons, the distances between the circuli are narrower. This is called an annuli, and marks a year (Williams, 1955). Though calcified structures like otoliths, cleithrum and opercular are more accurate for age determination (Kipling and Frost, 1970, Casselman, 1996), scales were used in this study because they are easy to acquire, can be used to back-calculate the length, and the removal of the scales is non-lethal to the fish (Khan and Khan, 2009, Haraldstad, 2011). There are three recurrent challenges related to scalimetry: The first annulus can be difficult to detect on slow-growing pikes (Casselman, 1996); due to stop in scale growth or too few circulus deposited to separate the annulus from each other, especially in fish over 8 years (Sikveland, 2013), hence underestimation of age is common when the growth stagnates; and lastly, regenerated scales cannot be used due to lack of previous circulus (Figure 9) (Borgstrøm, 2000).

The scales were first cleaned with soap water in a Petri dish while rubbing the scales clean between two fingers. When the scales were dry, images were obtained by using a stereoscopic microscope attached to a digital camera. The program Image pro express 6.3 (Copyright© 1993-2008) were used to estimate radius of the scale and to locate the annulus and the distances between (Figure 10) (Haraldstad, 2011). The estimated lengths between the annulus were used to back-calculate the length of the fish from previous years (Haraldstad, 2011) by using the Dahl-Lea equation: $L_c = L_i\left(\frac{S_i}{S_c}\right)$ (Aasrum, 2014). The pikes' maximum length (L_∞) and coefficient of growth (K) for both female and male pike were estimated by using the von Bertalanffy model: $l_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$ (Aasrum, 2014).

Figure 9. Replacement pike scale. (Photo: Amalie Haugen)

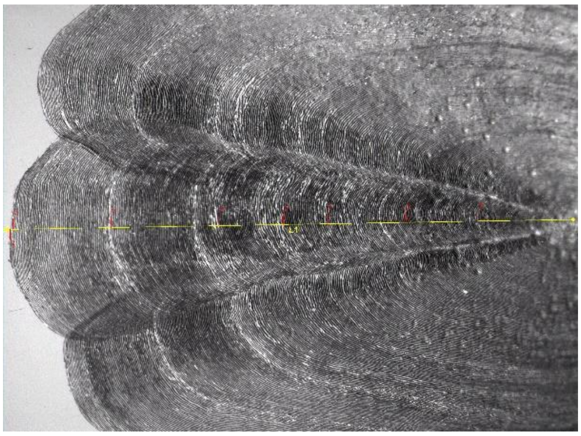


Figure 10. Image of a pike scale with markings on the annulus. (Photo: Amalie Haugen)

3.3.7 Weather data

Precipitation data was retrieved from eklima.no, while air temperature and air pressure data were retrieved from Met.no. Strømfoss sluice was the closest weather station, but the only available information was precipitation. The closest working weather stations with complete air temperature and air pressure data were Arebekken and Aurskog, respectively (Figure 11).

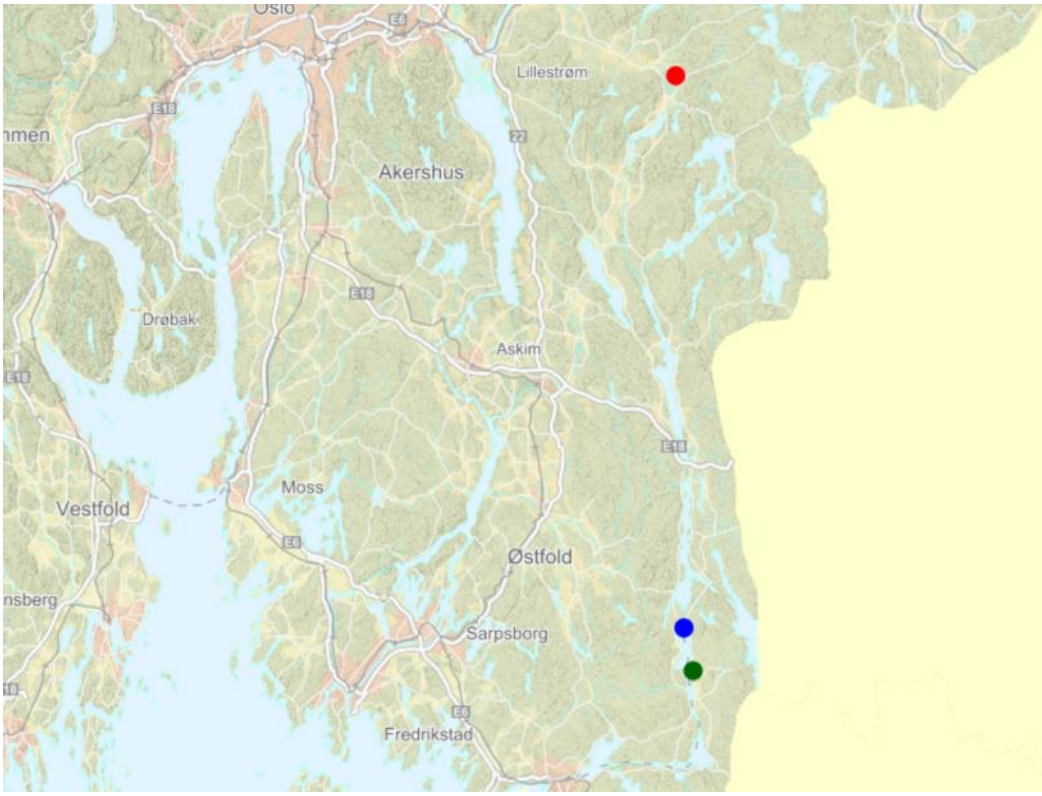


Figure 11. Locations of the weather stations used to perceive air temperature, air pressure and precipitation. Red= Aurskog, blue= Strømfoss sluice, and green= Arebekken. (Map from norgeskart.no)

3.3.8 Quantitative analyses of activity data

All statistical analyses and plots were performed in programs R version 3.2.5 (R Development Core Team, 2012, Team, 2016) using the support program R Studio.

In order to utilize all detection data (the synchronization tags were deployed WHEN), the mean-position-algorithm (Simpfendorfer et al., 2002) was used for estimation of individual positions at 10 minute intervals. Assemblages of the TBRs have overlapping listening areas (Figure 8), meaning that the same transmitter signal can be detected by multiple TBRs, but as the fish moves new TBRs may be recruited and others lost for a given fish during a given 10 min time slot. By calculating the weighted mean X and Y position, i.e. mean adjusted for number of detection per TBR, an average position per time slot results (Hedger et al., 2008). Hence, if one TBR receive more signals than the neighboring and overlapping TBR, the fish can be assumed to be closer to this receiver

(Simpfendorfer et al., 2002). This method does not give the exact position of the fish, but it provides an approximate position during the chosen time slot often referred to as PAVs from the position averaging (PAV, Simpfendorfer et al., 2002) A minimum of three TBRs had to be included per timeslot per individual in order to estimate a given PAV.

The individual PAVs were used to estimate individual utilization distributions (UDs), the estimated PAVs were used by only including the area in which the individual spent most time (Rogers and White, 2007). The UD was estimated using the smoothing parameter h = 22.1 for all individuals. This h-value is the median value after running least squared cross validation fittings individual-wise across all individuals where h was allowed to be estimated under no constraints. Using the median among-individual h allowed for direct comparison of UDs among individuals. Daily individual UDs were estimated using the kernelUD function from the R-package adehabitatHR. To focus on the pike's core area, only 50% UDs were estimated (UD50). Daily swimming distances, or lateral displacement, at individual level were estimated using the R package adehabitatLS using the PAVs as input data. Finally, so-called delta displacement, or "turboness", was estimated from the ratio between swimming distance and UD50 (unit: m/hectare/day). The purpose for estimating the turboness trait was to explore just how intensively the pike use its most favorable areas.

In order to explore and quantify effects of potential environmental and individual-specific variables and their potential interactions on each of the four activity response variables (i.e., UD50, swimming distance, turboness and depth use) candidate models where fitted and subjected to model selection. Model selection was performed using a corrected version of Akaike's Information Criterion (AICc) (Akaike, 1974) where models having ΔAICc>2 where assumed to have little support in the data than those below 2 (Anderson, 2007). The candidate models where fitted as linear mixed effects (LME) models where fish ID was included as random intercepts to account for within-individual dependency in the data, leaving residuals more independent than what would otherwise be the case (Nakagawa and Schielzeth, 2010). The fixed effect model structure was based on combining different models of interest exploring effects of weather variables, individual size and time (season and time of day). The LMEs where fitted using the lmer-function in the R package lme4 (Bates et al., 2014). Testing statistical effects of the various model terms in the most supported models were performed using anova for LME by using the car-package in R (Fox, 2008, Fox, 2015).

4 Results

4.1 Back-calculated length and growth rate

Of the total 37 pikes caught, 15 were females and 22 were males. The age distribution of females varied from 1 to 11 years, though no females were 9 years. Males varied between 1 and 9 years, but no males were 3 years. Females were more evenly distributed than males, but males had a higher total number of individuals (Figure 12).

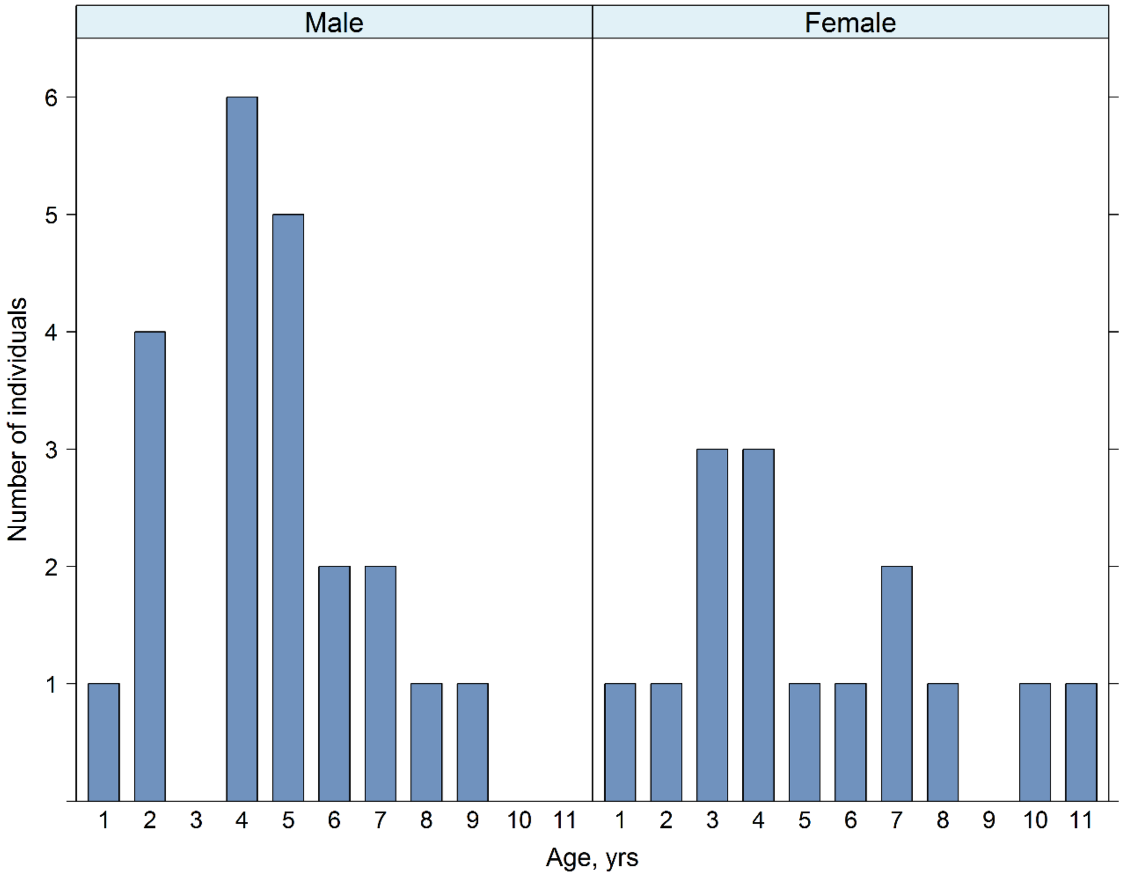


Figure 12. The distribution of ages from scale readings of female and male pikes, and the number of individuals per year group.

Up to the age of 4, the back-calculated growth pattern of both female and male were similar. However, females had a higher growth rate after the age of 4 and stagnated later than males (Figure 13)

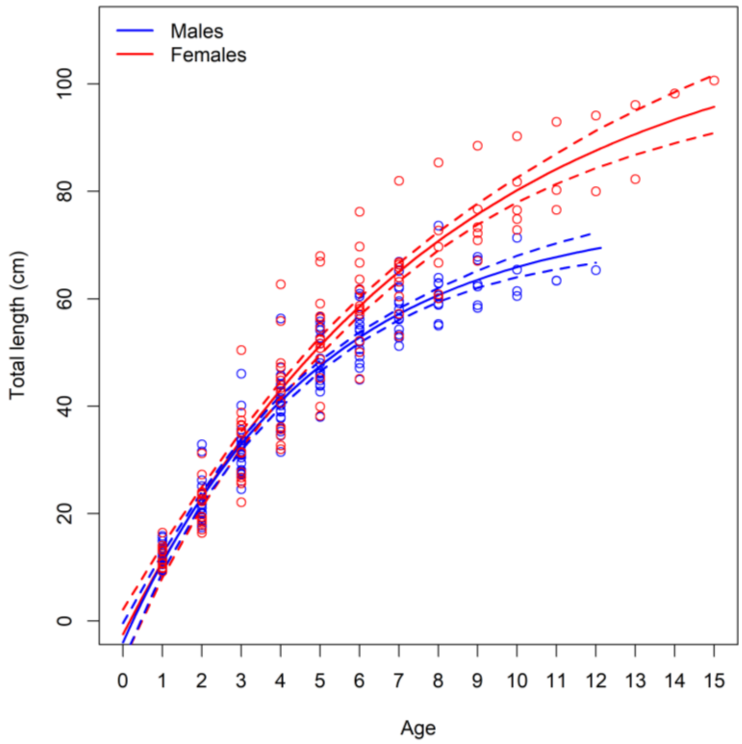


Figure 13. Estimated von Bertalanffy growth trajectories with corresponding confidence intervals (dashed lines) in both female and male pike from Aremarksjøen 2017. The trajectories were based on back- calculated lengths and model parameters provided in Table 1.

According to , the estimated coefficient of growth for male and female was 0.21 and 0.12, respectively. The maximum length of females was estimated to be almost 40 cm longer than males.

Table 1. Parameter estimates from the von Bertalanffy model for both male and female pike in Aremarksjøen 2017 with corresponding lower and upper 95 % confidence interval (LCL and UCL).

	MALES			**FEMALES**		
PARAMETER	Estimates	LCL	UCL	Estimates	LCL	UCL
L_∞	76.12	70.96	82.98	113.87	100.54	135.08
K	0.21	0.17	0.24	0.12	0.09	0.16
T_0	0.25	0.03	0.43	0.17	-0.19	0.46

4.2 50% Utilization distribution (UD50)

Parameter estimates of the most supported 50% horizontal utilization distribution area (UD50) model indicated that the variables length, sex, water temperature², moon distance, moon phases, air pressure and precipitation were important predictors of the UD50 and resulted in a complex 21 parameter model (Table 2). Of these variables, the combined effect of moon distance and moon phase, air pressure and precipitation were additive effects, whereas waxing moon, water temperature and air pressure decreased the UD50, and precipitation, full- and waning moon increased the UD50. The most complex interaction effects included in the model were water temperature*length*sex, and the moon phase*moon distance effects (Table 3Table 3).

Table 2. The top models fitted to estimate effects on 50% utilization distribution ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	K	AICc	ΔAICc
Water temperature² * length * sex + moon distance * moon phase + air pressure + precipitation	23	11005.88	0.00
Water temperature * length * sex + moon phase + precipitation	18	11007.05	1.17
Water temperature * length * sex + moon phase + air pressure + precipitation	19	11007.30	1.42
Water temperature * length * sex + moon distance * moon phase + precipitation	22	11007.40	1.52

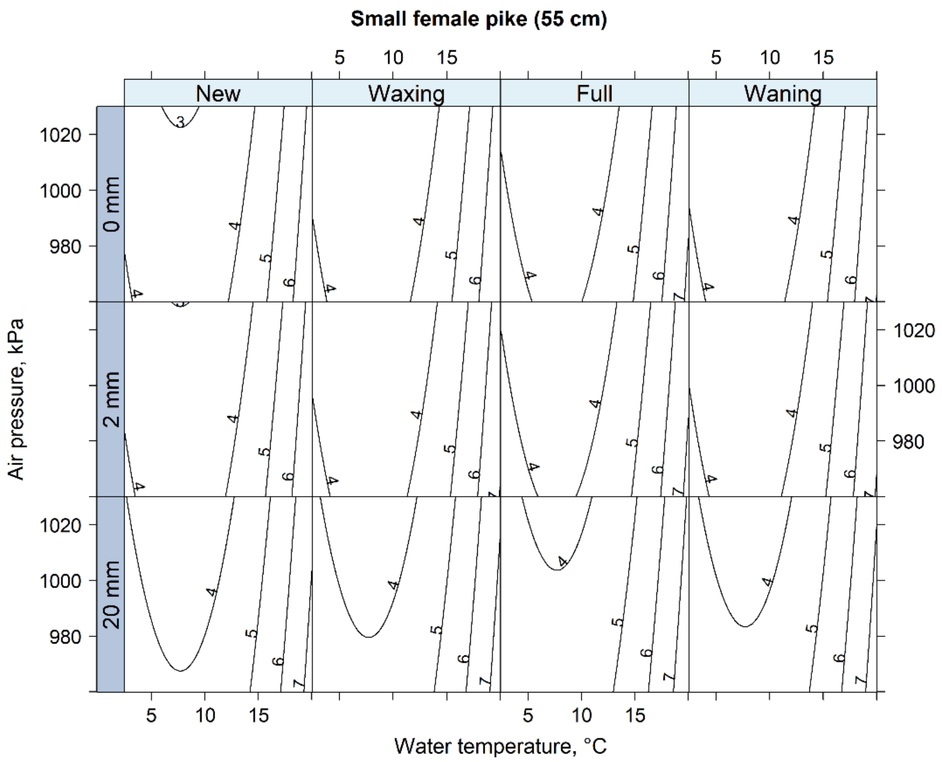
Table 3. Parameter estimates and effect test (Anova) of the most supported 50% utilization distribution model (Table 2). S= sex ([Fe]= female), L= length, AP= air pressure, T= water temperature, MD= moon distance, MP= moon phase ([Wx]= waxing, [F]= full and [Wa]= waning), P= precipitation.

Parameter estimates			Effect test			
Term	Estimate	SE	**Term**	F- value	Df	P-value
Intercept	1.383e+01	8.021e+00	**T**	78.3340	2	< 0.0001
T1	-3.349e-02	8.729e-01	**L**	0.1131	1	0.7366
T2	-4.290e-03	3.854e-02	**S**	0.6212	1	0.4306
L	-9.324e-02	9.698e-02	**MD**	0.4871	1	0.4852
S[F]	-4.810e+00	7.320e+00	**MP**	7.8646	3	0.0489
MD	6.340e-02	4.408e-02	**AP**	3.5555	1	0.0593
MP[Wx]	-2.993e+00	5.220e+00	**P**	11.1697	1	0.0008
MP[F]	8.716e+00	3.669e+00	**T*L**	11.3530	2	0.0034
MP[Wa]	6.167e+00	4.307e+00	**T*S**	12.6434	2	0.0018
AP	-8.916e-03	4.728e-03	**L*S**	0.8699	1	0.351
P	2.544e-02	7.611e-03	**MD*MP**	9.0837	3	0.0282
T1*L	2.394e-03	1.353e-02	**T*L*S**	10.3588	2	0.0056
T2*L	5.017e-05	5.986e-04				

T1*S[F]	-9.550e-01	1.029e+00	
T2*S[F]	6.791e-02	4.508e-02	
L*S[F]	1.041e-01	1.117e-01	
MD*MP[Wx]	4.745e-02	8.423e-02	
MD*MP[F]	-1.394e-01	6.071e-02	
MD*MP[Wa]	-1.009e-01	7.221e-02	
T1*L*S[F]	9.412e-03	1.560e-02	
T2*L*S[F]	-8.070e-04	6.850e-04	

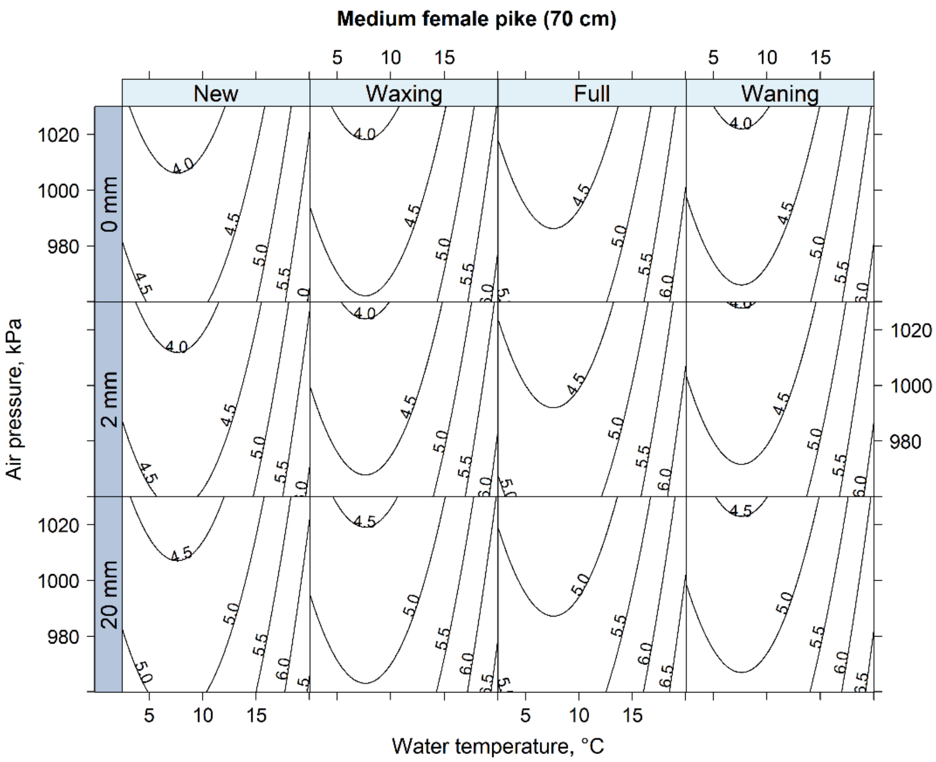
Predictive plots of the most supported UD50 model visualize how the UD50 for small, medium and large female pikes and small and medium male pikes were affected by various factors (Figure 14). Three variables affected all of the pikes similarly. Firstly, UD50 size correlated with the different moon phases. The UD increased with the increased appearance of the moon, thus at new moon the UD was smaller than at full moon. Secondly, UD increased with the precipitation intencity. Thirdly, the UD increased the most at low air pressure and least at high air pressure. Despite the similarities, there were rather great differences between the various length groups and sexes. Small and medium female pikes increased their UD50 at low (<5˚C) and high (>15˚C) water temperatures, but at medium (ca. 10˚C) water temperature the UD50 decreased. On contrary, large females decreased the UD50 at low and high water temperatures and increased the UD at medium water temperature. Also, female pikes' UD increased with increasing length. On the other hand, male pikes' UD50 affected differently to temperature and length groups than female pikes did. The UD50 increased continusly with increasing water temperatures and medium males had a slightly smaller UD than small males.

A)



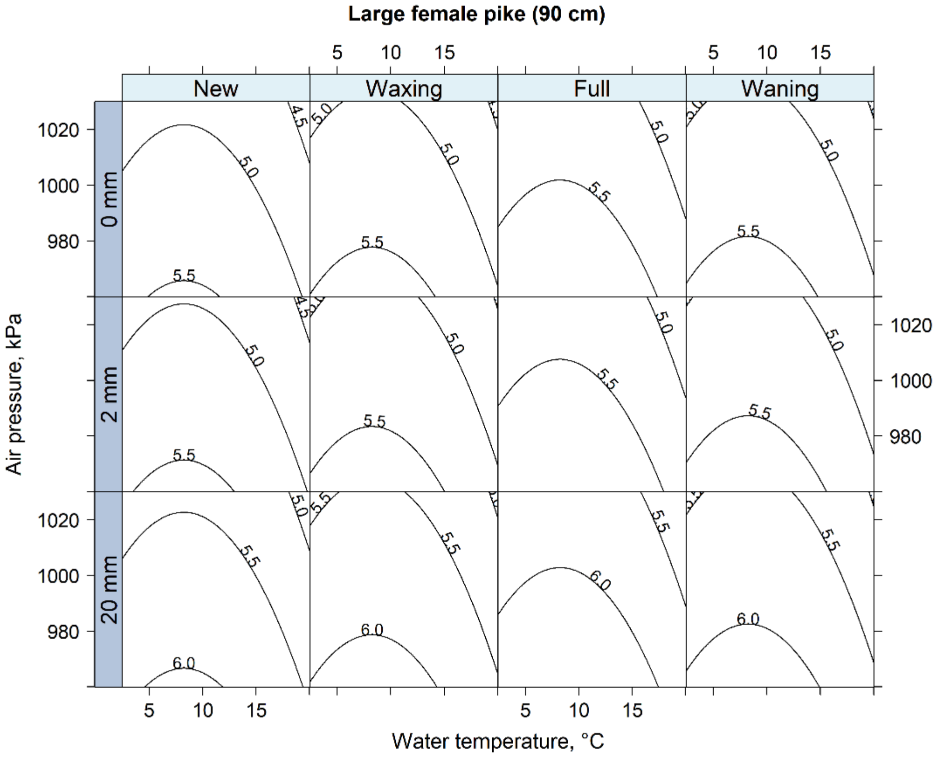
Small female pike (55 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Air pressure, kPa
Water temperature, °C

B)

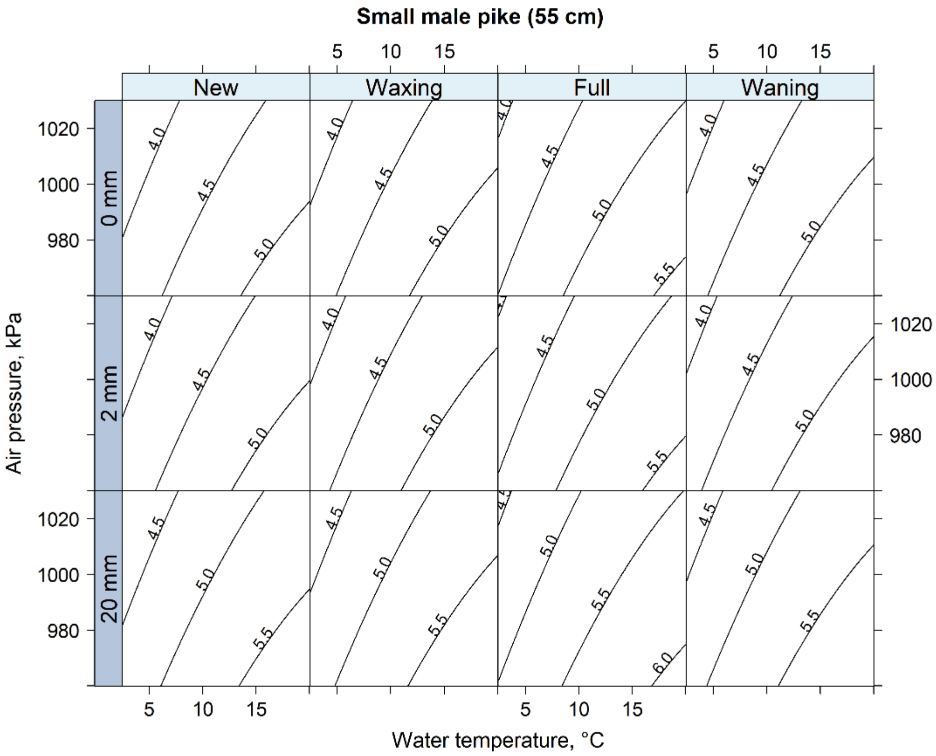


Medium female pike (70 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Air pressure, kPa
Water temperature, °C

C)


Large female pike (90 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Air pressure, kPa
Water temperature, °C
1020
1000
980
5
10
15
4.5
5.0
5.5
6.0

D)


Small male pike (55 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Air pressure, kPa
Water temperature, °C
1020
1000
980
5
10
15
4.0
4.5
5.0
5.5
6.0

E)

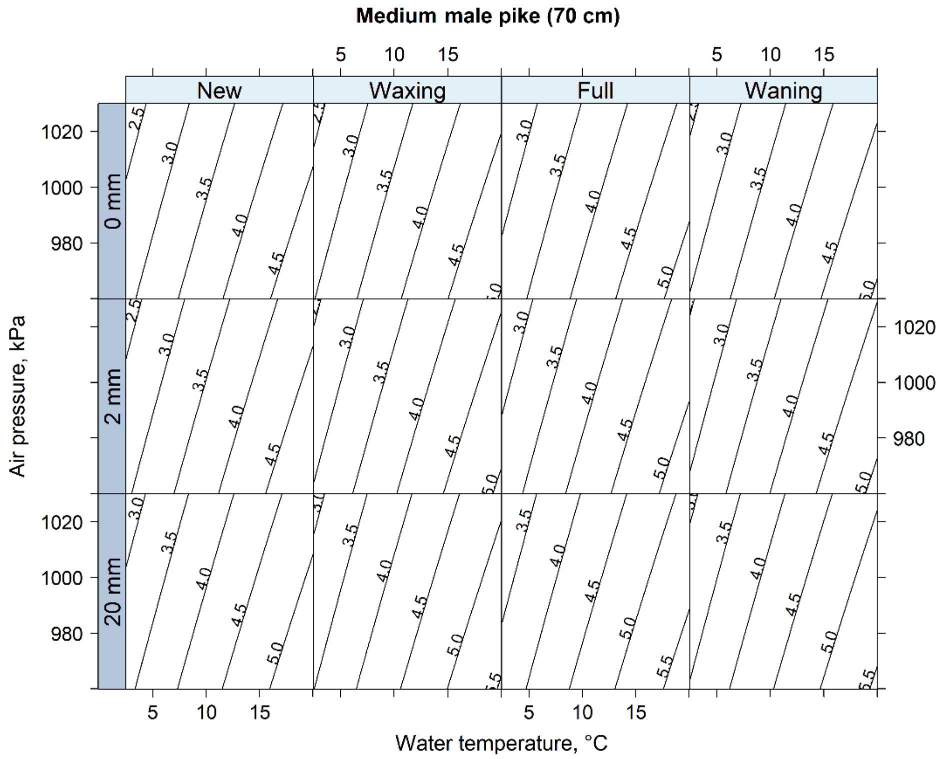


Figure 14. Prediction plots of the most supported 50% utilization distribution model shown in Table 3 and show how air pressure, precipitation, water temperature, moon phase, length and sex affected the pikes' utilization distribution 50. A) Small female pikes, B) medium female pikes, C) large female pikes, D) small male pikes and E) medium male pikes

4.3 Depth use

Parameter estimates of the most supported depth use model showed the factorial factors length, day of year and time of day (Table 4) to be important predictors of depth use. Time of day*day of year, length*day of year, and time of day*length*day of year were the most complex interaction effects included in the model (Table 5).

Table 4. The top models fitted to estimate effects on depth use ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	K	AICc	ΔAICc
Time of Day * length * day of year	10	2640410	0.00
Sunrise and sundown * length * day of year	18	2640451	41.33

Table 5. Parameter estimates and effect test (Anova) of the most supported depth use model (Table 4). L= length, D= day of year and Cos(ToD)= time of day.

Parameter estimates			**Effect test**			
Term	Estimate	SE	**Term**	F- value	Df	P- value
Intercept	1.228e+01	9.041e+00	**Cos(ToD)**	47.2904	1	<0.0001
Cos(ToD)	4.656e-01	2.229e-01	**L**	0.8653	1	0.3522472
L	-2.222e-01	1.358e-01	**D**	38208.7986	1	< 0.0001
D	-4.537e-02	8.136e-04	**Cos(ToD)*L**	10.8655	1	0.001
Cos(ToD)*L	-5.832e-03	3.366e-03	**Cos(ToD)*D**	20.8228	1	<0.0001
Cos(ToD)*D	-2.904e-03	9.283e-04	**L*D**	1228.7602	1	<0.0001
L*D	4.346e-04	1.242e-05	**Cos(ToD)*L*D**	6.7446	1	0.0094
Cos(ToD)*L*D	3.658e-05	1.409e-05				

An estimation of depth use indicated a correlation between seasons and mean swimming depth. Figure 15 shows as winter approach, pikes move toward deeper waters, especially smaller pikes. The variation of depth use during day and night are not substantial, although large pikes show a slight tendency to swim deeper at day- and nighttime.

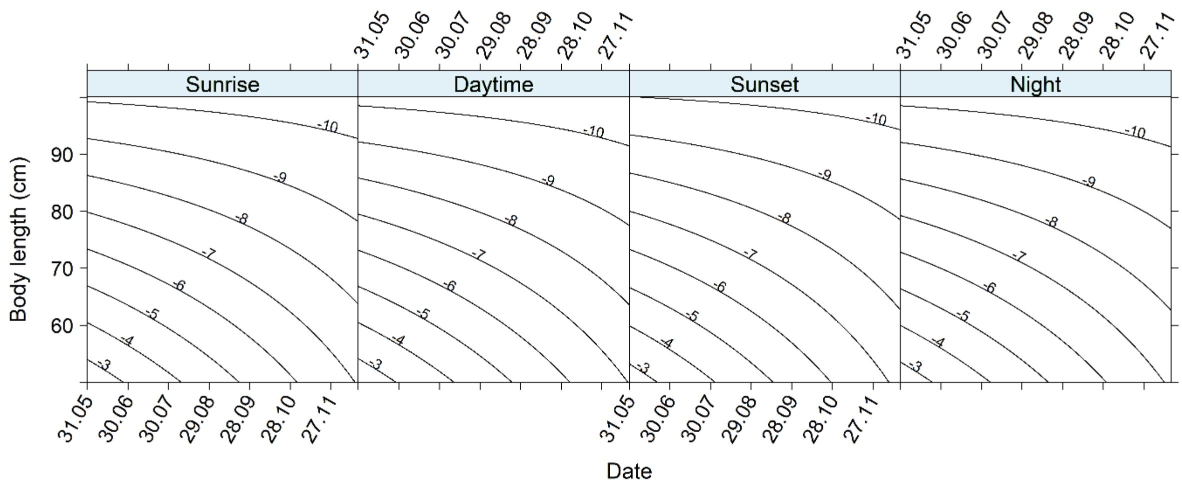


Figure 5. Prediction plot of the most supported depth use model provided in Table 5 and show how time of day, length and day of year affect the depth use of the pikes.

4.4 Turboness

Parameter estimates for the most supported turboness model revealed several important predictors resulting in a rather complex model. The factors were mainly additive, except from length and sex, which were factorial. All four top models had only few differences and very similar support (Table 6).

The additive factors day of year, air pressure, moon distance, moon phases and precipitation showed an increasing turboness, while temperature showed the opposite. Length*sex and moon phase*moon distance were the most complex interaction effects in the model (Table 7).

Table 6. The top models fitted to estimate effects on turboness ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc

Models	K	AICc	ΔAICc
Length *sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year	17	645176.6	0.00
Length + temperature + air pressure + precipitation + moon distance * moon phase+ day of year + length year 1	16	645176.7	0.08
Length + temperature + air pressure + precipitation + moon distance * moon phase + day of year	15	645176.9	0.32
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 1	18	645177.1	0.42

Table 7. Parameter estimates and effect test (Anova) of the most supported turboness model (Table 6). S= sex ([Fe]= female), L= length, AP= air pressure, T= temperature, MD= moon distance, MP= moon phase ([Wx]= waxing, [F]= full and [Wa]= waning), P= precipitation and D= day of year.

Parameter estimates			Effect test			
Term	Estimate	SE	**Term**	F- value	Df	P- value
Intercept	-1.576e+03	2.434e+02	**L**	2.0845	1	0.1488
L	8.364e+00	3.584e+00	**S**	1.0929	1	0.2958
S[Fe]	4.599e+02	2.640e+02	**T**	1089.1501	1	< 0.0001
T	-1.147e+01	3.475e-01	**AP**	176.6817	1	< 0.0001
AP	1.092e+00	8.219e-02	**P**	63.7747	1	< 0.0001
P	1.073e+00	1.343e-01	**MD**	10.83	1	0.0014
MD	5.323e+00	7.853e-01	**MP**	358.4230	3	< 0.0001
MP[Wx]	4.775e+01	9.117e+01	**D**	208.2253	1	< 0.0001
MP[F]	4.442e+02	6.787e+01	**L*S**	3.57	1	0.0604
MP[Wa]	5.054e+02	7.864e+01	**MD*MP**	57.3870	3	<0.0001
D	4.989e-01	3.457e-02				
L*S[Fe]	-7.603e+00	4.049e+00				
MD*MP[Wx]	-6.811e-01	1.472e+00				
MD*MP[F]	-6.727e+00	1.125e+00				
MD*MP[Wa]	-8.100e+00	1.319e+00				

The most supported turboness model is presented in a predictive plot and shows how various factors affected the pikes' turboness (Figure 15). The factor "day of year" affected the turboness of both males and females similarly. As the year approached winter, the turboness increased, though at the beginning of August, the turboness did not show an increasing trend. The factor length had a different affect on the turboness of female- and male pikes. Small males had a rather low turboness than female pikes of the same size. However, as the males' length increased, the turboness increased rapidly. On contrary, the turboness of female pikes increased only slightly with increased length and much less than the male pikes.

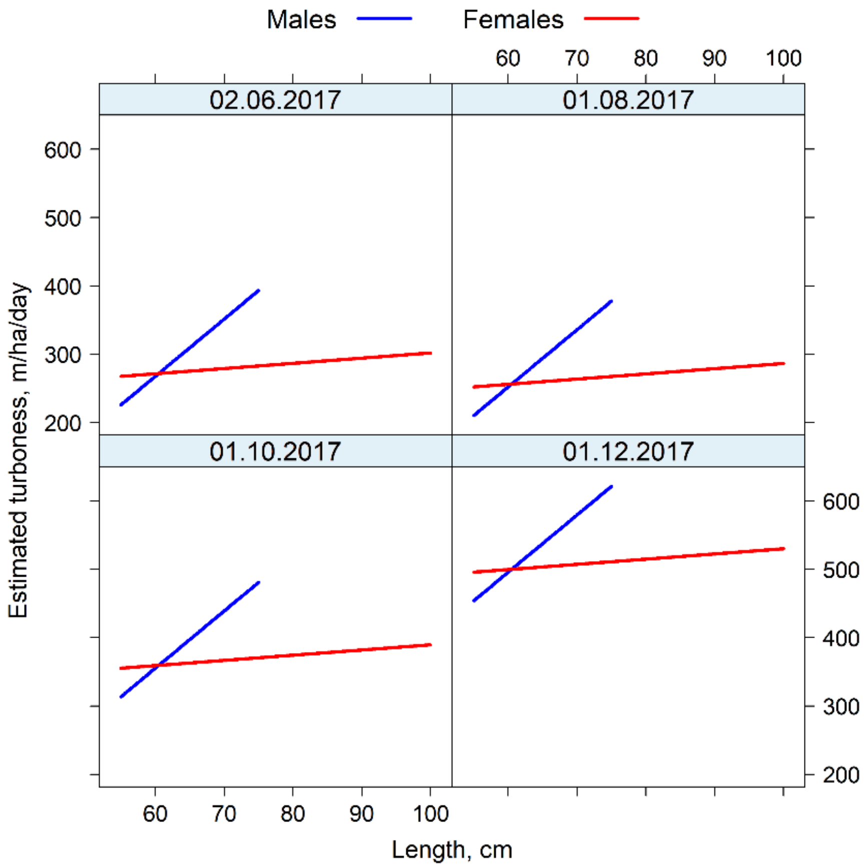


Figure 6. Prediction plot of the most supported turboness model provided in Table 6 and show how the turboness is affected by length, sex and day of year.

4.5 Swimming distance

The most supported swimming distance model is complex and include many variables. Length, air pressure and water temperature are additive effects which all increased the swimming distance. The factorial factors in the model are moon distance, moon phase and precipitation (Table 8). Precipitation, full- and waning moon increased the swimming distance, while waxing moon decreased it. Other variables included in the less supported models are sex and length year 1. The most complex interaction effects in the model were air pressure*water temperature*moon distance, air pressure*water temperature*moon phase, air pressure*moon distance*moon phase, water temperature*moon distance*moon phase, and air pressure*water temperature*moon distance*moon phase (Table 9).

Table 8. The top models fitted to estimate effects on swimming distance ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	**K**	**AICc**	**ΔAICc**
Length + air pressure * water temperature * moon distance * moon phase + precipitation	36	1303624.619	0
Length + sex + air pressure * water temperature * moon distance * moon phase + precipitation	37	1303626.527	1.9077
length + sex + air pressure * water temperature * moon distance * moon phase + precipitation	37	1303626.527	1.9077
length + air pressure * water temperature * moon distance * moon phase + length year 1 + precipitation	37	1303626.604	1.9844

Table 9. Parameter estimates and effect test (Anova) of the most supported swimming distance model (Table 8). L= length, AP= air pressure, T= water temperature, MD= moon distance, MP= moon phase ([Wx]= waxing, [F]= full and [Wa]= waning), P= precipitation.

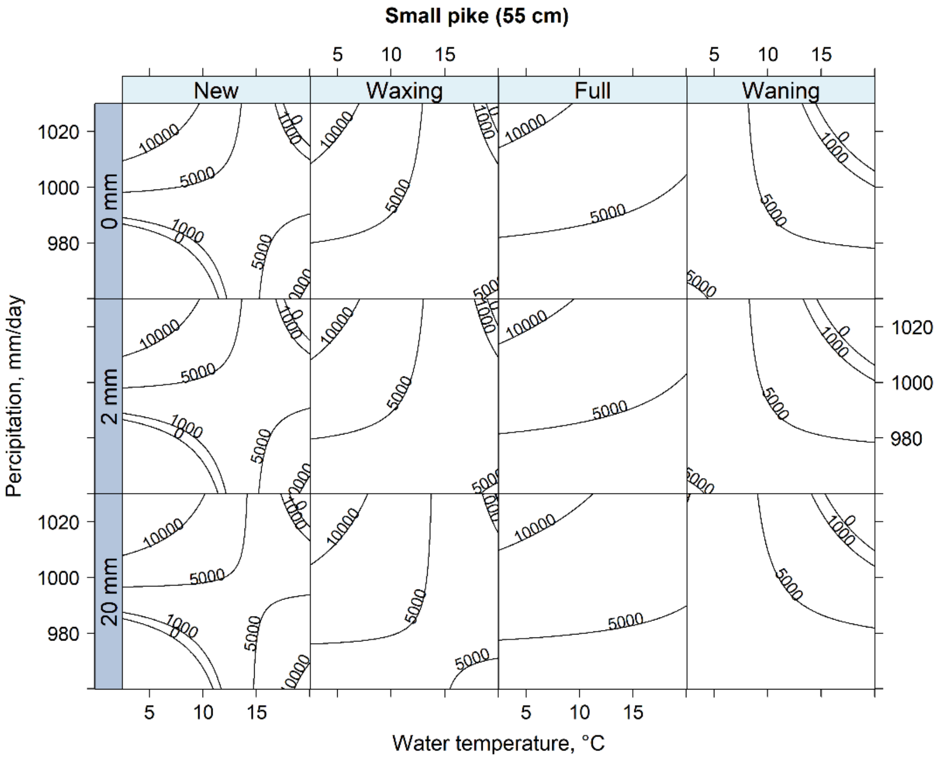
Parameter estimates			**Effect test**			
Term	Estimate	SE	**Term**	F-value	Df	P-value
Intercept	-8,38E+06	1,20E+06	**L**	3,1148	1	0,07758
L	8,63E+01	4,89E+01	**AP**	650,0063	4	<0.0001
AP	8,38E+03	1,21E+03	**T**	2171,7011	8	<0.0001
T	4,14E+05	6,50E+04	**MD**	1095,0381	4	<0.0001
MD	1,31E+05	1,90E+04	**MP**	2448,3066	15	<0.0001
MP[Wx]	-2,47E+06	1,75E+06	**P**	113,3195	1	<0.0001
MP[F]	1,04E+07	1,31E+06	**AP*T**	524,3185	1	<0.0001
MP[Wa]	7,37E+06	1,25E+06	**AP*MD**	254,9154	1	<0.0001
P	3,44E+01	3,23E+00	**T*MD**	384,298	4	<0.0001
AP*T	-4,16E+02	6,52E+01	**AP*MP**	601,8225	3	<0.0001
AP*MD	-1,31E+02	1,91E+01	**T*MP**	806,0574	6	<0.0001
T*MD	-6,28E+03	1,02E+03	**MD*MP**	1796,758	6	<0.0001

AP*MP[Wx]	2,65E+03	1,76E+03	**AP*T*MD**	18,4711	1	<0.0001
AP*MP[F]	-1,04E+04	1,32E+03	**AP*T*MP**	162,9382	3	<0.0001
AP*MP[Wa]	-7,31E+03	1,26E+03	**AP*MD*MP**	43,6513	3	<0.0001
T*MP[Wx]	4,33E+05	1,24E+05	**T*MD*MP**	290,329	3	<0.0001
T*MP[F]	-7,18E+05	7,23E+04	**AP*T*MD*MP**	183,4829	3	<0.0001
T*MP[Wa]	-4,86E+05	7,07E+04				
MD*MP[Wx]	4,01E+04	2,76E+04				
MD*MP[F]	-1,67E+05	2,11E+04				
MD*MP[Wa]	-1,15E+05	1,99E+04				
AP*T*MD	6,32E+00	1,03E+00				
AP*T*MP[Wx]	-4,45E+02	1,25E+02				
AP*T*MP[F]	7,25E+02	7,26E+01				
AP*T*MP[Wa]	4,87E+02	7,10E+01				
AP*MD*MP[Wx]	-4,29E+01	2,79E+01				
AP*MD*MP[F]	1,68E+02	2,12E+01				
AP*MD*MP[Wa]	1,14E+02	2,00E+01				
T*MD*MP[Wx]	-7,08E+03	1,96E+03				
T*MD*MP[F]	1,14E+04	1,16E+03				
T*MD*MP[Wa]	7,74E+03	1,13E+03				
AP*T*MD*MP[Wx]	7,26E+00	1,97E+00				
AP*T*MD*MP[F]	-1,15E+01	1,16E+00				
AP*T*MD*MP[Wa]	-7,76E+00	1,13E+00				

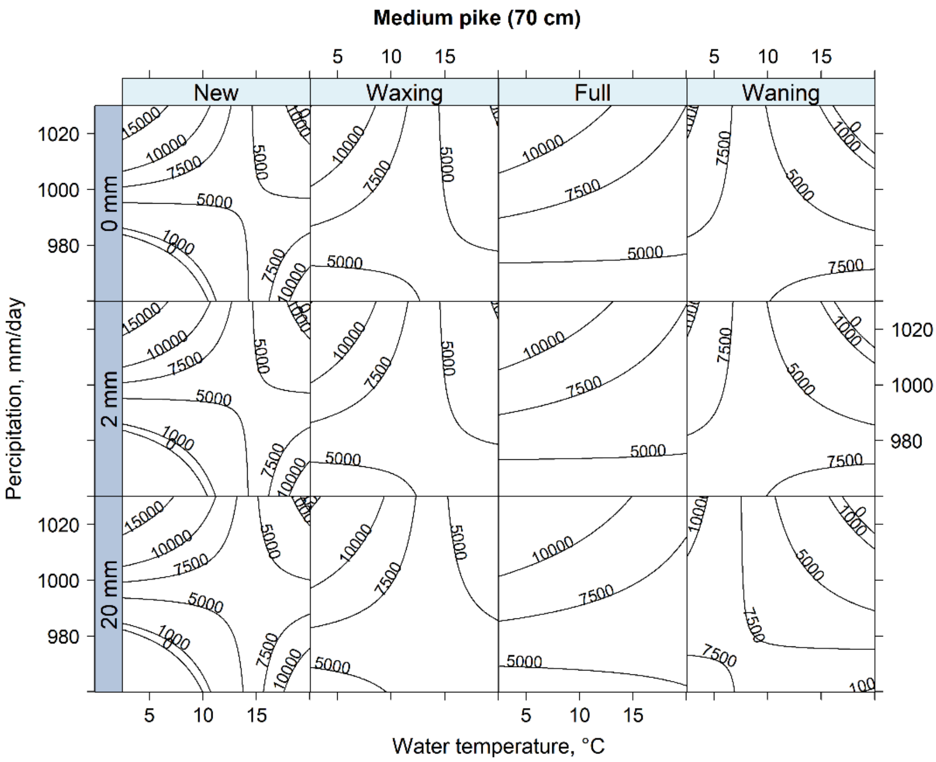
The most supported swimming distance model is presented in three prediction plots representing small, medium and large pike and visualize how the different factors affected the swimming distance (Figure 7). Three patterns are frequently repeated throughout the plots. Firstly, the swimming distance increased with increasing length and intensity of precipitation. Secondly, the predictive plots indicated a pattern in swimming distance where small, medium and large pike moved most at high air pressure and cold water temperatures, but reduced the level of activity as the water temperature increased and air pressure decreased. Thirdly, the degree of reduction of activity vary with air pressure. The activity level increased rapid at high air pressure and increasing water temperatures, but decreased less at low air pressure and increasing water temperature.

Although the patterns are repeating throughout the moon phases, there are slight differences within them. For instance, at new moon when the air pressure is low, the activity level increase with rising water temperature. Another difference is when the moon is full or waning, the decrease of swimming distance at high air pressure and increasing water temperature is smaller than at new and waxing moon.

A)


Small pike (55 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Percipitation, mm/day
Water temperature, °C

B)


Medium pike (70 cm)
New
Waxing
Full
Waning
0 mm
2 mm
20 mm
Percipitation, mm/day
Water temperature, °C

C)

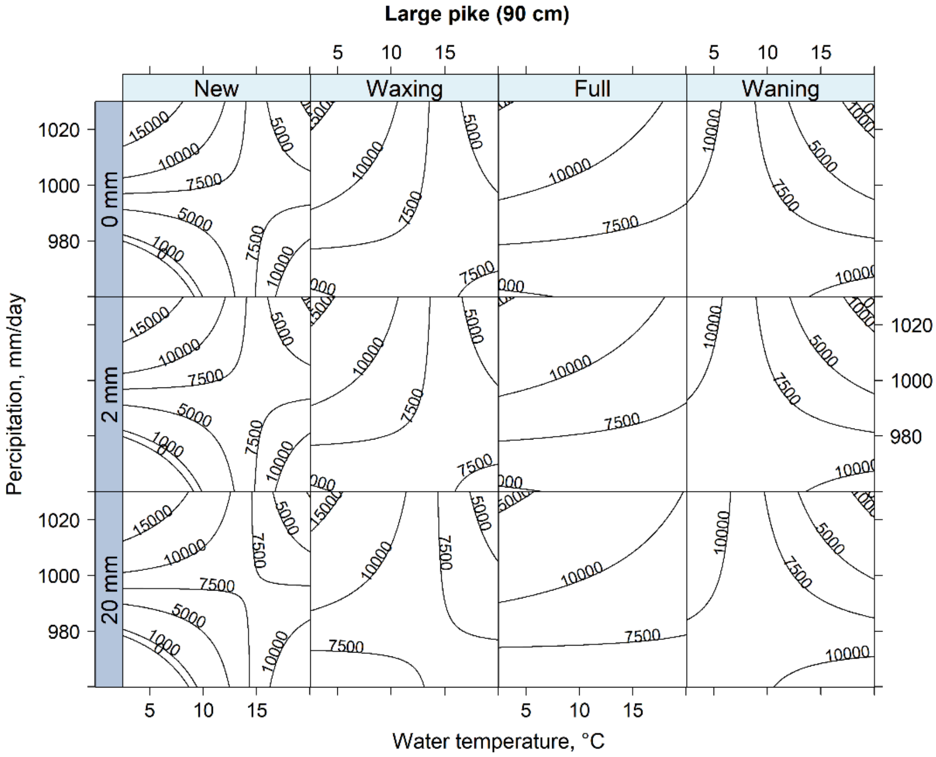


Figure 7. Prediction plot of the most supported swimming distance model provided in Table 8 and show how air pressure, precipitation, water temperature, length, and moon phase affect the pikes swimming distance. A) Small pikes, B) medium pikes and C) large pikes.

5 Discussion

5.1 Spatial distribution and behavior

The daily movement behavior and spatial distribution of the tagged Aremarksjøen pike was affected by several abiotic and physical features, such as precipitation, day of year, time of day, air pressure, lunar cycle, individual length, sex, and water temperature. Very often in complex interaction effects, but not always so.

Precipitation, especially high-intensity precipitation, increased pike turboness, utilization distribution and swimming distance. Heavy rainfall and wind can disturb the water and therefore increase turbidity and reduce transparency (Gray et al., 2011, Kuparinen et al., 2010). Pikes are visual predators, and reduced sight range might explain the changing activity behavior (Kuparinen et al., 2010). With reduced sight, the pike's possibility of spotting a prey is reduced (Lehtiniemi et al., 2005). A shift from a stationary, ambush technique to an active foraging strategy may therefore be more profitable (Vøllestad et al., 1986, Nilsson, 2006). In contrast, Jepsen et al. (2001) found no correlation between turbidity and the use of non-vegetated area. However, the study lake Jepsen et al. (2001) used was a small reservoir with a mean depth of 1.7 meters. The lakes Vøllestad et al.

(1986) used in their study was in the same water course as Aremarksjøen and they closely resemble each other. The geographic location, lake size and lake morphology difference may therefore have an influence on the behavioral outcomes.

Day of year was found to increase both turboness and depth use. However, the prediction plot of the turboness shows a halt in August. Because several environmental factors interact to influence turboness these interaction effects under the prevailing conditions may explain why August deviates from the overall temporal trend predicted by the day-of-year effect. The depth use increased as the year approached winter, especially in small pikes. Similar results were found in a catch-and-release study where the number of pike caught at the depth of three meters increased from June to September (Roach, 1993). As winter arrive, the vegetation habitat near the shore will alter as submerged macrophytes collapse and, if cold enough, an ice-sheet cover can impose oxygen depletion. Due to an alteration of the inshore habit, moving further out to a deeper habitat may therefore be favorable (Casselman and Lewis, 1996) and might be related to the pikes in Aremarksjøen.

The factor time-of-day only affected depth use. At sunrise and sunset, large pike slightly decreased their depth use. Shallower fish are easier for anglers to target than fish close to the bottom because bringing lures and bait to deeper waters requires more sophisticated tackle and gear such as down-riggers. Several studies show an increased movement and catch rate during dusk and dawn (Kobler et al., 2008, Beaumont et al., 2005, Kuparinen et al., 2010). Prey fish also increase the movement at dusk and dawn and use the open waters (Jacobsen et al., 2004, Pitcher and Turner, 1986). As the results from this study demonstrate, large pike are more active than small pike and utilize a larger lake area. Because prey fish move more and use open waters at dusk and dawn, large pike might benefit from preying closer to the surface. This might explain why large pikes, and not small pikes, move up in the water column at dusk and dawn.

At increasing air pressure the pike UD50 decreased, whilst swimming distance and turboness increased. Few studies have explored the impact of air pressure on fish behavior, and even fewer have found it to be significant. For example, Kuparinen et al. (2010) found an effect of air pressure, but the correlation was not valid for further analyses. However, Kuparinen et al. (2010) is the only study that has tested the direct effects of the changing air pressure on pikes' vulnerability. This is in contrast to a study of the effect of barometric pressure on black-tip shark, where behavioral changes were found. As the barometric pressure dropped before a storm arrived, the sharks moved from their shallow nursery area out to deeper waters (Heupel et al., 2003). This is the opposite of what was found in Aremarksjøen, where the movements increased at high air pressure. The effect of air pressure seems to vary greatly between the different fish species (Guy et al., 1992, Cullen and McCarthy, 2003, Jensen et al., 1986). Air pressure is easy to measure, but how it affects the fishes' behavior is difficult to attain (Stoner, 2004).

The various moon phases and distance to moon during the lunar cycle have an impact on the pikes' behavior. The lunar cycle affects UD50, turboness and swimming distance. Both full- and waning moon increase UD50, turboness, and swimming distance the most. In contrast, waxing moon increase the turboness while decreasing the swimming distance. The lunar cycle affects the light condition in the lake and tidal fluxes (most commonly on larger bodies of water) with the different moon phases (Hanson et al., 2008), hence an impact on animals' behavior is to be expected. The pikes' increased activity at full moon is comparable with other studies of the top-predator pike and the related muskellunge (*Esox masquinongy*). According to a catch-and-release study of pike by Kuparinen et al. (2010), increased catch rates were found at full and new moon. However, fishing only occurred during daytime, so any light-dependent factor could not be assessed. A possible explanation is the change of behavior in zooplankton and prey fish at new- and full moon, which in turn alter the predators foraging behavior (Hernández-León, 2008). Another angling study of a close relative to pike, the muskellunge (Raat, 1988), catch rates at night increased the most at full moon. Increased illumination from the moon increase the light condition in the lake and makes it easier for predators to spot prey and may therefore be a plausible reason for the increased movements of pike during such conditions (Vinson and Angradi, 2014, Stevenson and Millar, 2013).

The length of the pike is an important factor influencing most behavior results in this study. Depth use, UD50, swimming distance and turboness all increased with increasing length. Similarly, various studies indicate an increasing activity level and depth use with increasing fish size (Andersen et al., 2008, Skov et al., 2017, Harvey, 2009, Klefoth et al., 2011). In an acoustic telemetry and radio location study done by Chapman and Mackay (1984) in Canada, large pike were found to utilize greater parts of the lake and to be more versatile with habitat use. This behavior may be beneficial because the pikes can exploit a larger area in search for prey. Small pike on the other hand, spend most of the time in vegetated habitats near shore. Another explanation of the increased movement of large pike, might be the need of an increased intake of food. To increase the foraging, the pikes also have to increase the activity level (Kuparinen et al., 2018). These behaviors can be related to the pikes in Aremarksjøen where large pikes swim greater distances and uses deeper parts of the lake than the smaller pikes. Cannibalism is a well-known threat to pikes (Giles et al., 1986, Nilsson et al., 2014), and may explain the spatial distribution difference between large and small pikes. Larger pikes utilize bigger parts of a lake, while small pikes stay near shore and seek refuge in vegetation in order to avoid predation (Nilsson, 2006). Also, the habitat use and activity level of small and medium sized pikes might be restrained by larger pikes due to the fear of being predated, and therefore affect the growth and survival of the smaller pikes (Haugen and Vøllestad, 2018a, Haugen and Vøllestad, 2018b). In the predictive plots of the pikes' turboness, male pikes increase the turboness much more rapid with increasing length than females do. This is an interesting result, however, the total number of pikes studied is low and the number of males and females are not evenly distributed. Besides, it does not seem to be any similar results in other research. Nevertheless, the results may be right, but with the low total number of individuals, more research is needed before a conclusion can be drawn.

Water temperatures affect the UD50, turboness and swimming distance in different ways. Smaller female pikes increased their UD50 at low and high water temperatures and male pikes increased the UD50 with increasing water temperatures. Large females on the other hand increased their UD50 the most at medium water temperatures. However, both turboness and swimming distance indicated a decreasing trend at increasing water temperatures. In a German acoustic telemetry study, increasing water temperatures was found to decrease the swimming distance (Czapla, 2017). Similarly, Kuparinen et al. (2010) found a declining catch rate as the water temperature increased from 14 degrees. Two possible reasons were proposed, firstly, the need to restore energy reserves in springtime after spawning increase the foraging. Secondly, at high water temperature, pike might experience physiological stress and reducing the activity level and foraging may be beneficial (Kuparinen et al., 2010). In addition, a study done by Jepsen et al. (2001), an increase of movement during winter as a consequence of increasing water temperature from approximately 0 degrees to 5 degrees Celsius. In contrast, some studies show greater activity at higher water temperature (Skov et al., 2017, Vehanen et al., 2006, Casselman, 1978), while others show no change in activity at various water temperatures (Jepsen et al., 2001, Diana et al., 1977). In this study alone, the effect of water temperature on the pikes' UD50 varied considerable with sex and size. The different outcomes of the pikes behavior studies might be explained by behavior variations within the different pike populations or different methods used in the studies (Klefoth et al., 2008).

As seen in the results, all the environmental factors affected the pikes' behavior. However, the factors were almost always involved in interactions with each other. Discussing the factors separately can be negative because of the strong interaction effects. The density and structure of a pike population is strongly influenced by complex interactions between environmental factors (Haugen and Vøllestad, 2018a, Haugen and Vøllestad, 2018b). Therefore, if the goal is to increase the knowledge about the impacts environmental factors may have on the population-level, assessing such interactions between the factors are crucial.

For further analysis, factors such as wind and sun light should be included in the study to get a broader specter of environmental factors which may affect the pikes' activity behavior. Vegetation have an important role serving as habitat, refuge, feeding and spawning area (Bry, 1996). Mapping the vegetation and depth of the lake would contribute to a more detailed utilization distribution of the pikes.

5.2 Acoustic telemetry

Acoustic telemetry is an effective, low-cost method used to monitor the movements of tagged animals out in the field (Donaldson et al., 2014). Furthermore, this technology is suitable for long-term studies in large water systems (Heupel et al., 2006). By using triangulated stationary receivers in the water, detections from the transmitters can be received at all times. This is in contrast to active acoustic telemetry where tracking and receiving data is only possible when following signals from the acoustic tags, which acquire many laboring hours (Kessel et al., 2014). Receivers and transmitters have a detection range which can be exceedingly variable (Clements et al., 2005). Conditions of the study site affect the detection range, hence placement of the receivers are crucial. A mooring system can block signals from transmitters, receivers moored too deep or too shallow in the water column, and physical- and noise disturbance such as high flow, waves and air bubbles, are all examples of what can affect and decrease the detection range (Heupel et al., 2006, Donaldson et al., 2014). In the same way, the transmitters' detection range can be altered by water conditions such as temperature, salinity, substrate and turbidity (Kessel et al., 2014). A range test of the receivers is therefore important to determine where the detection ranges overlap and which areas fish can inhabit without being detected (Heupel et al., 2006). The detection range in Aremarksjøen was very good under ideal conditions of the lake. However, if the fish is deep down beneath the receivers, the range may decrease (Heupel et al., 2006). At summer when the lake is stratified, the detection range of pikes beneath the thermocline may reduce. The detection range of large pikes are therefore more vulnerable than small pikes because the probability of finding large pike beneath the thermocline is higher.

One receiver from the study area was lost, but later found by the shore still attached to its buoy, most likely cut loose by a passing boat. As the receiver have floated past other receivers in the area, the data may have been affected. Not knowing about the detection range may cause errors which can lead to wrong conclusions about the pikes' movement and incorrect management measures (Kessel et al., 2014). An additional drawback was the development of an ice layer early in December. The ice was too fragile to walk on, so collecting data from the last three receivers (TBR ids: 386, 394, 397 – Figure) were impossible as they were inaccessible, and the missing data may have affected the results.

5.3 Relevance for angling vulnerability

All fishing gear are selective in some way (Jørgensen et al., 2009). Different fishing methods select for various behavioral- and physical features, hence fish sampling for studies will never be entirely random. Fish gears are categorized in two main categories; active and passive. Active gear is physically moved around, such as trawling, while passive gear is stationary, such as angling and trapping (Portt et al., 2006, Arlinghaus et al., 2017b). Gill-nets used in this study is another example of a passive gear. The nets are stationary, so fish must actively swim into the net by itself. However, fish were also scared into the nets by persons in this study. Because the fish sampling was done during spawning season, the pike were generally more active than during feeding season, driven by other motivation than feeding.

In many freshwater ecosystems, recreational angling is common and has replaced commercial fisheries (Arlinghaus et al., 2007). This is also the case for Aremarksjøen, which have an increasing focus on pike fishing tourism (Utmarksavdelingen for Akershus og Østfold, 2017). Pike is a popular trophy fish and many anglers strive to catch the largest individual (Schroeder and Fulton, 2013). However, this may have negative consequences for the pike stock and the freshwater ecosystem. Increasing fishing pressure from recreational angling can create trophic changes, evolutionary alterations, biomass reductions and change the composition of size and age of the fish population (Arlinghaus et al., 2007). If there is no or little harvest regulation in a lake, the population may be over-exploited, and a recruitment overfishing may occur. This happens if the fishing mortality exceeds the per capita recruitment rate. Not only harvest anglers can over-exploit a fish stock, but also trophy anglers can add to further over-exploitation when the caught fish perish due to hooking mortality (Kuparinen et al., 2018). Mature fish must be protected to prevent recruitment overfishing, and a minimum size-limit may therefore be a proper measure (Johnston et al., 2013).

Pike populations are found to have three behavioral types, where two of these mainly utilize vegetated areas, while a third type is more active and exploit the whole lake (Kobler et al., 2009). Results from this study show that larger individuals are more active and make these an easier target for recreational anglers. When these large and active individuals are taken out of the stock, a timidity induced population may occur, with shy individuals that spend more time in refuge and less time out in the water actively searching for food (Arlinghaus et al., 2017b). Furthermore, when large individuals are taken out of the population, small fish will dominate and there will be an unintended selection for slow growing fish which maturate early (Pauli and Sih, 2017). In short, the catch rate may reduce, and the size of the fish caught smaller. To prevent timidity, maximum size-limit is a measure to conserve large pikes in the fish stock (Pierce, 2010). The results also show how larger pikes utilize a deeper depth than small pikes. An alternative method of conserving large pikes may be to avoid fishing in deeper waters. To moderate the use of deep water fish gear, such as downriggers (Sitar et al., 2017), may be a good preventative measure to shield the large pikes.

To minimize the consequence of angling, catch-and-release is a way of conserving the fish population by reducing the fish mortality (Arlinghaus et al., 2007). However, because of the fishes' plasticity, catch-and-release may alter the behavior and make it more timid (Arlinghaus et al., 2017b). In a catch-and-release study done on rainbow trout (*Onchorhynchus mykiss*), results showed that the fish learned to avoid the hooks after being caught, which decreased the catchability (Askey et al., 2006). However, different studies on the pikes physical and behavioral recovery after being fished then released again, indicated poor learning, fast recovery and little influence on the behavior (Arlinghaus et al., 2008, Pullen et al., 2017, Arlinghaus et al., 2009, Kuparinen et al., 2018). In spite of this, Klefoth et al. (2011) found that catch-and-release reduced both growth and swimming.

Aremarksjøen as a destination for pike anglers is increasing in popularity. With an increasing fishing pressure, proper management of the fish stock is important to protect and preserve the pike population. Catch-and-release of fish that are not used as food, maximum size-limit, and bag limit are regulations already implemented in the lake. Minimum size-limit and reduced deep water fishing with downriggers may also be suitable regulations to implement in the management strategy of Aremarksjøen.

6 Conclusion

This study has found evidence that pikes increase movement activity during twilight with full or waning moon and high-intensity precipitation, cold water temperature, high air pressure and at days closer to winter. This is particularly pertinent to large pike as they are more active than small pike.

Aremarksjøen has an increasing number of pike angling tourists, especially trophy fishers. Under situations with limited regulations for both harvest- and trophy fishing, the pike population may over time become timid with small, and early matured individuals. Minimum size-limit and reduced deep water fish gear may contribute to a sustainable pike stock along with the previously implemented regulations bag limit, catch-and-release of pike not used for food, and maximum size-limit. The current regulations in operation in Aremarksjøen seem relevant for protecting a broad size composition of pike in the lake, however, if time show otherwise, this study has provided knowledge on size-specific habitat segregations in terms of depth use that open for further regulation opportunities if necessary.

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8 Appendix

Table A 1. The top 10 models fitted to estimate effects on depth use ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	K	AICc	ΔAICc
Time of day * length * day of year	10	2640410	0.00
Sunrise and sunset * length * day of year	18	2640451	41.33
Sunrise and sunset * length + sex * day of year	13	2641509	1098.98
Sunrise and sunset * length + sex * datetime	13	2641526	1116.09
Sunrise and sunset * length + day of year	11	2641545	1134.78
Sunrise and sunset * length + sex + datetime	12	2641549	1138.37
Sunrise and sunset * length + sex + day of year	12	2641566	1155.41
time of day * day of year + length	7	2641655	1244.69
Sunrise and sunset * length + sex + week of year	12	2641656	1245.91
Sunrise and sunset + day of year	7	2641677	1266.73

Table A 2. The top 10 models fitted to estimate effects on utilization distribution ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	K	AICc	ΔAICc
Temperature2 * length * sex + moon distance * moon phase + air pressure + precipitation	23	11005.88	0.00
Temperature2 * length * sex + moon phase + precipitation	18	11007.05	1.17
Temperature2 * length * sex + moon phase + air pressure + precipitation	19	11007.30	1.42
Temperature2 * length * sex + moon distance * moon phase + precipitation	22	11007.40	1.52
Temperature2 * length * sex + moon distance * moon phase + air pressure + precipitation + length year 4	24	11007.83	1.95
Temperature2 * length * sex + moon distance * moon phase + air pressure + precipitation + length year 2	24	11007.90	2.02
Temperature2 * length * sex + moon distance * moon phase + air pressure + precipitation + length year 3	24	11007.92	2.04
Temperature2 * length * sex + moon distance + air pressure + precipitation	17	11010.58	4.70
Temperature2 * length * sex + moon distance * moon phase + air pressure	22	11014.99	9.11
Temperature * length * sex + moon distance * moon phase + air pressure + length year 1	23	11016.90	11.02

Table A 3. The top 10 models fitted to estimate effects on turboness ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc.

Models	K	AICc	ΔAICc
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year	17	645176.6	0.00
Length + temperature + air pressure + precipitation + moon distance *moon phase + day of year + length year 1	16	645176.7	0.08
Length + temperature + air pressure + precipitation + moon distance * moon phase + day of year	15	645176.9	0.32
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 1	18	645177.1	0.42
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 3	18	645178.1	1.43
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 2	18	645178.5	1.86
Length * sex + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 4	18	645178.5	1.86
Length + temperature + air pressure + precipitation + moon distance * moon phase + day of year + length year 4	16	645178.8	2.23
Length * sex + temperature + air pressure * precipitation + moon distance * moon phase	17	645308.7	132.12
Length * sex + temperature + precipitation + moon distance * moon phase + day of year	16	645351.0	174.37

Table A 4. The top 10 models fitted to estimate effects on swimming distance ranked according to AICc. K = number of estimated parameters, AICc and ΔAICc

Models	**K**	**AICc**	**ΔAICc**
Length + air pressure * water temperature * moon distance * moon phase + precipitation	36	1303625	0
Length + sex + air pressure * water temperature * moon distance * moon phase + precipitation	37	1303627	1.907708
Length + sex + air pressure * water temperature * moon distance * moon phase + precipitation	37	1303627	1.907708
Length + air pressure * water temperature * moon distance * moon phase + length year 1 + precipitation	37	1303627	1.984426
Length + air pressure * water temperature * moon distance * moon phase + precipitation + length year 4	37	1303627	1.993712
Length * sex + air pressure * water temperature * moon distance * moon phase + precipitation	38	1303629	3.909466
Length + air pressure * water temperature * moon distance * moon phase + length year 1	36	1303738	113.2077
Length * sex + air pressure * water temperature * moon distance * moon phase	37	1303740	115.1384
Length * sex + air pressure * water temperature * moon distance * moon phase + length year 1	38	1303742	117.126
Length * sex + air pressure * water temperature * moon distance * moon phase + length year 1	38	1303742	117.126

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