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Master Thesis (45 ECTS)

Pike (*Esox lucius*) in River Tryggevælde

- focusing on population structure, habitat choice and movements.

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Abstract

This study was carried out from March 2014 to June 2015 in the Danish River Tryggevælde near Køge, Zealand. This river has long been famous amongst anglers for its population of pike with very big individuals. An increased knowledge about the ecology of the pike in River Tryggevælde is needed in order to protect and preserve the population. Furthermore this knowledge might reveal the dynamics affecting a pike population with many large individuals. A more detailed understanding of the activity patterns and habitat choices displayed by river pike will improve the knowledge which management actions are based on. In a socio-economic aspect which desire these types of populations this would be valuable information.

In this study the population structure of the adult pike (two years and more) in River Tryggevælde was described in order to assess the condition of the population both in terms of growth and density (part 1). An estimated population size was found by capture-mark-recapture and from this a total biomass and density of the pike was deduced. The growth of the pike population was evaluated by scale reading and assessment of the relationship between weight and length. Furthermore recaptures were used to calculate the change in condition factor of the pike during the study period and thereby assess the conditions experienced through this time. The diel and yearly activity and habitat choice of thirty pike was studied by using acoustic telemetry in order to investigate the factors influencing their behavior (part 2). Furthermore it was determined to which degree the pike population uses the brackish coastal areas in Køge Bay (part 2).

Part 1 showed that the pike in the river have a high growth rate and condition factor caused by good conditions in the river in terms of food and suitable habitat. The pike in the river had a mean weight of 5.54 kg. The density was estimated to 12 pike per hectare and the biomass to 68.6 kg per hectare. Both are high compared with other European rivers. It is suggested that the pike population is very close to the maximum capacity of the river. However the conditions in the river during 2014 were poor and as a result pike decreased their condition factor. Few smaller pike were observed and it is likely that either eggs or new hatched pike are exposed to a high predation pressure. No pike of more than 10 years was observed which corresponded well with the high growth rate which tends to cause a shorter life span.

Movements in this study were mainly considered as a result of pike feeding activity. Part 2 showed that pike generally were mobile and that each individual pike utilized a large proportion of the river with home ranges between 44.6 - 100 % of the studied river stretch. The general activity was between 143.6 - 748.1 m/day (mean = 352.8 m/day). The population could not be divided into sedentary and mobile individuals. Movements peaked at about 17 ^{O}C. There was no correlation between the activity measured on a small daily scale and a large yearly scale. It was suggested that pike changed between an active and static hunting strategy through the year. A positive effect on movement of increasing salinity at the outlet was found - possibly explained by new prey fish entering the river causing the pike to be more active. Indication of a diel activity pattern was found on a larger and coarser scale but not on the standardized small-scale 24-hour trackings. The first mentioned indicated that the diel activity may change according to seasons with a daily peak in winter and crepuscular peaks in April/May, June/July and October/November. The 24-hour trackings indicated an effect of size on movement which was supported by the distribution of general activity but could not be confirmed on a larger scale. Habitat choice varied between individual traits (sex, condition factor and length) and depended on temperature and discharge. A critical period in August showed that the individual choices of movement and position in the river were very important. Furthermore it seemed that heavier pike with a higher condition factor had a better chance of surviving lethal river conditions. Pike did visit the bay but only for a short amount of time. It was possible that pike moved to the bay to avoid poor conditions in the river. Furthermore the bay is likely to allow a greater production of prey fish which can forage in the bay and bring the production into the river.

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Contents

General introduction

The northern pike

The northern pike (*Esox lucius*) belongs to the genus *Esox* which contains five species totally (Harvey 2009, Berg 2012). The distribution of the northern pike is circumpolar (Caspers 1976, Craig 1996, Harvey 2009) and it is the only species of the genus that lives in Europe (Berg 2012). The northern pike will in the following report be referred to as "pike". The pike is one of the most widely distributed fish species in Denmark (Berg 2012). It is a pronounced predator who can reach a size of more than 130 cm and 20 kg (Berg 2012).

Pike biology

The pike is typically found in lakes and slow moving rivers but is also widespread in areas with brackish water (Berg 2012). Here it thrives in coastal waters with an accordingly low salinity of up to 12-15 ‰ (Berg 2012). As a top predator the pike can play a significant and very important role in aquatic ecosystems (Craig 1996, Berg 2012). It is opportunistic in its feeding choice and seems to eat whatever prey is present (Raat 1988, Harvey 2009, Berg 2012). Thus, the pike have a great impact on the structure and amount of prey fish in the system (Johnson 1966, Berg 2012). Furthermore studies have shown that the presence of pike has an impact on the behavior, habitat choice and movements of prey fish which reduces their foraging on zooplankton and thereby affects the whole ecosystem (Jacobsen & Perrow 1998, Skov et al 2011).

Habitat requirements

Generally pike is associated with shallow and vegetated areas (Chapman & Mackay 1984b, Chapman & Mackay 1984a, Cook & Bergersen 1988, Casselman & Lewis 1996, Vehanen et al 2006, Rasmussen 2007, Kobler et al 2008). Spawning occurs during spring when the water temperature reaches 8-12 ^{O}C (Casselman & Lewis 1996): In Denmark typically in March/April (Berg 2012). The pike prefer to spawn at shallow, sheltered and vegetated areas (Casselman & Lewis 1996, Craig 1996, Berg 2012). The optimal spawning vegetation is moderate densities of grasses and sedges that are capable of keeping the eggs suspended above the bottom where the water is better oxygenated (Casselman & Lewis 1996). Especially vegetation seems to be very important for the pike (Grimm & Klinge 1996). Juveniles prefer all kinds of dense vegetation while adult pike are more linked to intermediate densities of submergent vegetation (Casselman & Lewis 1996, Craig 1996). This is most likely linked to the smaller pike using vegetation both as a cover to hunt more effectively but also a refuge from predators while the adult pike only has to take the first mentioned into consideration (Craig 1996). This may also explain the fact that larger pike have found to be more versatile in their habitat requirements (Chapman & Mackay 1984b). In Craig (1996) it is mentioned how larger pike, as a top predator, probably has an advantage in being versatile in their habitat selection depending on the availability of suitable prey, season and other factors.

Pike in rivers

Many rivers have a standing stock of pike that thrive and spend their whole life in the river (Ovidio & Philippart 2003, Masters et al 2005, Sauvanet et al 2013). Pike inhabit the lower river areas and are found in the slower-flowing parts of the river (Paragamian 1976, Inskip 1982, Berg 2012). The biotic and abiotic characteristics fluctuate widely in the river through the season and the pike is adapted to this kind of environment because the species has a remarkably wide tolerance range of abiotic factors (Craig 1996). Rivers have shown to be more productive than lakes regarding to fish biomass and this ensures plenty of food for the pike (Randall et al 1995). Several studies have shown how pike living in rivers make spawning migrations to reach their spawning grounds further upstream (Ovidio & Philippart 2003, Koed et al 2006, Pauwels et al 2014). In rivers suitable spawning habitat is especially found on flooded fields (Craig 1996).

Pike in brackish coastal areas

With the pike being an adaptive and opportunistic predator living at the lower stretches of the rivers it is an obvious choice to explore the productive brackish coastal areas adjacent to the river outlet. At least one study has shown how pike that spends most of their life in the river occasionally swim into brackish water (Koed et al 2006). Other populations of pike spend all or most of their life in the brackish coastal areas. Some of these spawn in brackish water (Westin & Limburg 2002, Lappalainen et al 2008, Jørgensen et al 2010). Others migrates upstream rivers to spawn before they return to the brackish areas again shortly after (Johnson 1982, Müller & Berg 1982, Westin & Limburg 2002, Engstedt 2011). It is beneficial to spawn in the rivers because of the shallow, flooded areas that heats up quickly and thereby provides an ideal and food rich environment for the eggs and hatched pike (Müller 1986). Furthermore the risk of predation is smaller compared with the brackish areas (Nilsson 2006a).

Pike in focus

Lately the coastal pike have received a lot of attention. In the Baltic Sea including Denmark the catches of pike have been declining drastically in the past decades and this has been interpreted as a decline in the population of Baltic pike (Jacobsen et al 2008, Lehtonen et al 2009). The reason for this is unknown but it is possibly caused by poor recruitment (Nilsson 2006a) or anthropogenic activities such as habitat changes, eutrophication and/or overfishing (Jacobsen et al 2008, Lehtonen et al 2009, Larsson et al 2015). There has been focus on the Danish populations of pike in recent years. The recreational value of the pike as a sport fish have resulted in a five-year protection plan of pike in certain important brackish areas. Furthermore the nationwide minimum length of pike have been raised from 40 cm to 60 cm and different projects focusing on improving local pike populations are in the making. Hence pike and especially coastal pike are acknowledged as a socio-economically important fish. But in order to manage the populations, there is a need for more knowledge about the biology and status of the pike populations.

Aim of the study

Both pike in rivers and brackish areas use rivers for reproduction and in order to manage these populations it is crucial to gain knowledge about their behavior in this environment. Regardless of whether the pike lives in the river or only utilizes the river during spawning an understanding of the different factors effecting their movements and habitat choice in the river will contribute to the management of the populations.

This study is carried out in the Danish River Tryggevælde near Køge, Zealand. This river has long been famous amongst anglers for its population of pike with very big individuals. Anglers have caught pike of more than 16 kg and pike of more than 10 kg is caught every year. This indicates a high growth rate of the pike which possibly could be a result of the pike using the large areas of brackish water at the river's outlet. The fact that the population consists of large pike is relevant for the socio-economic aspect where large individuals represent a larger value than smaller individuals. The pike angling is mostly carried out in the spring a couple of months before and after the spawning (which often occurs in March/April) on the last 4 kilometers of the river before its outlet in Køge Bay. The anglers typically experience an increase in the amount of pike on this stretch in the spring but it is unknown whether some or all of the pike migrates from the brackish water into the river to spawn. An increased knowledge about the ecology of the pike in River Tryggevælde is needed in order to protect and preserve the population. Furthermore this knowledge might reveal the dynamics affecting a pike population with many large individuals. In a socio-economic aspect which desire these types of populations this would be valuable information.

Based on the angling records it was expected that River Tryggevælde contained a large population of large pike (compared with other studies) with a high growth rate. It was hypothesized that at least some of the pike migrated to Køge bay during the summer. The bay would provide the pike with plenty of food and a water temperature optimal for growth (19-21 ^{O}C). The combination of a high water temperature and brackish water have shown to be beneficial for the metabolic rate of perch (*Perca fluviatilis*) (Christensen 2015) and it is possible that it was applicable for pike too. It was also expected that the summer oxygen levels at the bay would be higher than in the river. River Tryggevælde has a discharge that is ten times smaller in summer compared with winter (Sand-Jensen 2013). This indicates a very low exchange of water in summer. At the same time the river is known to be covered in duckweed (*Lemna sp.*) and decaying vegetation during the summer possibly causing very low oxygen levels.

According to angling records it was hypothesized that the pike mostly inhabited the lower stretches of the river during fall, winter and spring while they moved to either brackish water or further upstream during the summer. Based on other studies of pike in rivers it was expected that the pike in general primarily moved smaller distances within a restricted area (Ovidio & Philippart 2003, Beaumont et al 2005, Masters et al 2005, Koed et al 2006, Pauwels et al 2014). This could possibly be replaced by migrations to certain spawning areas during early spring (Ovidio & Philippart 2003, Koed et al 2006, Pauwels et al 2014). It was expected that the pike would be more active with increasing temperature (Casselman 1978) and that increasing salinity levels in the river (brackish water being pushed into the river) would result in the pike moving further upstream to avoid lethal salinity levels. At last it was expected that the activity would decrease with increasing discharge since the pike is not suited for high currents (Jones et al 1974, Raat 1988, Pauwels et al 2014). On a diel basis it was expected that the pike would show activity peaks at dusk or dawn (Cook & Bergersen 1988, Beaumont et al 2005, Rasmussen 2007, Kobler et al 2008, Baktoft et al 2012).

In this study the population structure of the pike in River Tryggevælde is described in order to assess the condition of the population both in terms of growth and density. This will give insight to the kind of population that is found in River Tryggevælde as well as confirm whether or not the river has a large population of pike with a high growth rate. The diel and yearly activity and habitat choice of the pike is studied in order to investigate the factors influencing their behavior. This will increase the knowledge of river pike ecology which still is sparse and contribute with valuable knowledge for the decision making when management actions are considered. Furthermore it will create valuable knowledge about the type of pike population that is desired in a socio-economic perspective. Another aim of this study is to determine to which degree (if any) the pike population uses the brackish coastal areas in Køge Bay. This is done in order to investigate how important the brackish areas are for the pike in the river including how they contribute to the apparent high growth rate. This gained knowledge will provide a better basis for the conservation of the population.

Part 1: Population structure and growth of pike in a Danish lowland river

Introduction

Population structure and growth

The structure, age distribution and growth are important characteristics of a pike population and tell a lot about the environment the pike lives in. The age distribution is influenced by important biological factors such as recruitment, competition and mortality. This explains the wide variation in age found in different pike populations (Frost & Kipling 1967, Mann 1976, Bregazzi & Kennedy 1980, Mann 1980, Roche et al 1999, Žiliukienė & Žiliukas 2012, Sauvanet et al 2013). The growth of pike depends on both abiotic and biotic factors (Raat 1988). Juvenile pike grow fast and will typically reach about 20 centimeters during their first year (Craig 1996, Berg 2012) but in very productive areas the small pike can even reach 35 cm (Craig 1996, Jacobsen et al 2008). Female pike typically reaches a length of about 100 cm at an age of 9-11 years while male pike typically reaches 75 cm at 10 years of age (Frost & Kipling 1967, Mann 1976, Bregazzi & Kennedy 1980, Roche et al 1999). Especially temperature affects the growth which has been found to be optimal at 21 ^{O}C (Casselman 1978). Below 4 ^{O}C the growth is slow but positive and at 27.5 ^{O}C the growth ceases (Casselman 1978). An insight into the growth of the pike will reflect the environment they live in as well as the conditions experienced by each individual. Factors affecting recruitment, growth and mortality will influence how many pike a certain biotope can hold. The theoretical maximum capacity of pike has been calculated to 80-150 kg per hectare vegetated area (Craig 1996). Different studies have tried to estimate the size of a river pike population by capture-mark-recapture and the results differ widely which indicates a great variation in both biomass, number and mean weight between different rivers (Hart & Pitcher 1973, Paragamian 1976, Mann 1980, Taugbøl et al 2004, Sauvanet et al 2013). This variation is probably caused by differences in recruitment (quality of spawning areas, predation), mortality (predation, fishing, abiotic factors) and growth (food, abiotic factors). In most lakes the population size often does not exceed 25-30 fish per hectare or 20-30 kg per hectare (Bregazzi & Kennedy 1980, Craig 1996, Berg 2012). An insight into the structure of a pike population will contribute to a better understanding of the dynamics affecting the population especially in terms of intraspecific interactions. This insight is important if management actions are to be considered.

Aim of this study

During a tagging study of pike in River Tryggevælde (see part 2) the population structure of the pike was investigated. This was done in order to give insight to the dynamics of the pike population that is found in the river as well as give a possible explanation to why the pike in the river grows so big. The structure of a population is important in the evaluation of movements and habitat choice because these are likely to be affected by intraspecific factors such as competition, cannibalism or reproduction. Furthermore it is possible that knowledge of the growth and condition factor during the study period can explain some of the behavior observed. Based on the angling records it was expected that River Tryggevælde contained a large population of large pike (compared with other studies) with a high growth rate. The objective of this part of the study was to determine the size, distribution and condition of the pike population. Knowledge of the size of the pike was obtained by regularly catching pike from the population. An estimated population size was found by capture-mark-recapture and from this a total biomass and density of the pike was deduced. The growth of the pike population was evaluated by scale reading and assessment of the relationship between weight and length. Furthermore recaptures were used to calculate the change in condition factor of the pike during the study period and thereby assess the conditions experienced through this time. All of this increased the knowledge and understanding of the population investigated in the other part of this study which covered the movements and habitat choice of the pike in the river according to environmental factors (see part 2). The two parts compliments each other and each part contribute to the understanding and discussion of the other.

Method

Study area

River Tryggevælde is approximately 35 kilometers long and originates from Lake Ulse, Haslev (Tryggevælde Ådal 2015). From there it runs north-east to St. Heddinge where it flows into Køge Bay (Olsen 2002, Kuhlman & Serritslev 2013). Køge Bay is described by the Danish Nature Agency as a shallow mesohaline bay with salinity between 5 - 18 ‰. A sluice is placed at the outlet to stop brackish water from Køge Bay to be pushed into the river and cause floods. On its way the river amongst others receive water from River Stevns and Storkebæk (Olsen 2002). The catchment area is about 300 km^2 (Olsen 2002, Kuhlman & Serritslev 2013) and consists of about 80 % agriculture and 15 % forest (Olsen 2002). The soil is mostly clay which means the precipitation during fall and winter has difficulties permeating to the groundwater and instead run off to the river. At summer the clay holds the precipitation better making the evaporation greater and by that the summer discharge very small (Sand-Jensen & Lindegaard 2004). The mean monthly discharge is thus 10 times greater in winter compared with summer (Sand-Jensen 2013). On the outer stretches the river is surrounded by wet meadows which are flooded when the river is high. The river's course is highly regulated (Kuhlman & Serritslev 2013).

The study was carried out in the lower 12 kilometers of River Tryggevælde on Stevns, Zealand, Denmark (55°22'48.71"N; 12°15'26.66"E) and in Køge Bay. The area of the studied river stretch was 14.8 hectares. In the following report a position in the river will be written as p.xxxx where p is position and xxxx is how many meters from the outlet the position is.

In the study area the river's width varies from about 5-20 meters at normal water levels and the deepest parts are about 3 meters. At p.12000 the bottom is hard and gravelly. From about p.10000 the bottom changes to very soft and silty until about p.4000 where the bottom changes again and becomes dark and hard. On the lower stretches the velocity and water level is very much determined by the water level in Køge Bay (own observations). Despite of the sluice brackish water can travel more than three kilometers up the river and the salinity can in periods exceed 10 ‰ (own data). In the summer months the river has a great amount of vegetation and especially the stretch at p.6000 to p.12000 can be very difficult to access by boat due to huge amounts of yellow water lily (*Nuphar lutea*), duckweed (*Lemna sp.*), common mare's tail (*Hippuris vulgaris*) and different species of pondweed (*Potamogeton sp.*). The weed is cut twice a year.

The fish population is diverse and 20 different species have been registered. During the electro fishing in this study the most common species seemed to be eel (*Anguilla anguilla*), bream (*Abramis brama*), ide (*Leusciscus idus*), tench (*Tinca tinca*), roach (*Rutilus rutilus*) and pike (*Esox lucius*). Besides these the following species have been registered in the river: Perch (*Perca fluviatilis*), rudd (*Scardinius erythrophthalmus*), trout (*Salmo trutta*), grass carp (*Ctenopharyngodon idella*), carp (*Cyprinus carpio*), bleak (*Alburnus alburnus*), European flounder (*Platichthys flesus*), crucian carp (*Carassius carassius*), goldfish (*Carassius auratus*), salmon (*Salmo salar*), three-spined stickleback (*Gasterosteus aculeatus*), rainbow trout (*Oncorhynchus mykiss*), ninespine stickleback (*Pungitius pungitius*) and spined loach (*Cobitis taenia*) (Carl 2014).

Several fish eating predators such as mink (*Neovison vison*), cormorant (*Phalacrocorax carbo*), osprey (*Pandion haliaetus*), kingfisher (*Alcedo atthis*) and white tailed eagle (*Haliaeetus albicilla*) can be found along the river (own observations).

Data collection

The field work was carried out using a small boat with both a gasoline engine and an electrical engine. The gasoline engine was used when travelling longer distances on the river while the electrical engine was used during angling and electro fishing.

Pike from the river was caught on several occasions. This was done in order to keep registering fish for the capture-mark-recapture (see below) analysis and to get scale samples for the age determination. Furthermore it was done to assess the growth and change in condition factor through the study period and obtain a size distribution of the pike in the population so an estimate of the biomass could be calculated. From March 9th to March 12th 2014 thirty pike from River Tryggevælde was caught by electro fishing (18) or angling (12). Each pike was tagged with a floytag and a pit-tag and had an acoustic transmitter inserted in the body cavity in order to follow its movements through the study period (see part 2). During the study period (March 2014 - June 2015) pike were regularly caught by angling or electro fishing. The angling was done in a standardized way by sailing up and down the study area of river with one or two rods fishing a live bait suspended under a float. The angling typically lasted 6-10 hours and covered about 30 - 70 % of the river each time. The angling could not be carried out in summer and early fall due to large amounts of vegetation. In total 21 days of angling were carried out through the study (six in spring 2014, two in fall 2014, four in winter 2014/2015 and nine in spring 2015). The electro fishing was carried out for a whole day twice in the fall 2014 and twice in the spring 2015. This was done by sailing up and down the investigated stretch of the river and fishing the margins. In the fall 2014 it was only possible to fish from p.7000 and upstream due to very high conductivity further downstream. When a pike of more than 50 cm was caught by angling or electro fishing it was placed on a protective and wet unhooking mat in the boat. The total length was measured and the pike was weighed in a wet carp sack with a fitting Super Samson weight from Salter - typically the 5 or 10 kg version but sometimes with the 2 or 25 kg version. A scale sample of 3-8 scales were taken from just above the lateral line at about half way down the body. These were placed into a small paper envelope for later investigation. A picture of both sides of the fish was taken for later identification before the pike was carefully released back into the river. The handling of a pike was kept at a minimum of time (2-5 minutes). The pike with a transmitter were targeted during electro fishing in 2015 but it showed to be more difficult to recapture them than first thought and only one of the tagged pike was caught under electro fishing.

Data treatment

The mean weight of the total number of pike at their first capture (123 individuals) was calculated. The relationship between weight and length of the pike caught during the study were modeled to give an estimate of the growth and condition of the population. The model was also used to compare the population with pike populations from other studies. The relationship between weight and length in fish can be described as:

$$W = aL^b$$

where W is the weight in kg and L is the length in cm. A and b are constants with b being approximately 3 (Frost & Kipling 1967). The equation parameters were found by making a plot of the caught pike in excel and fitting the power trend line.

Growth in length during the study period were calculated for 19 pike (15 females, 4 males) that were caught in spring 2014 and recaptured in spring 2015 (February - May). The growths of the 15 females were assessed by the relationship between age and length found by scale reading. The expected growth was calculated by:

$$Expected\ length\ = 37.047\ \cdot \ln(x+1) +\ 28.635$$

, where x is the expected mean age of the 15 females. This was compared with the observed growth.

All of the recaptured pike were caught before spawning time at their first capture. For the pike that were recaptured before spawning time in 2015 (mid April) it was possible to assess the change in condition factor through the study. Since the condition factor decreases as a result of spawning the pike caught after spawning was not included in this analysis. The change in condition factors of the pike were assessed using the relationship of weight and length to evaluate whether the growth has been as expected for the population (or better/worse). Furthermore the condition factors of the pike were calculated in order to compare the change through the study. This would give an indication of the conditions experienced by the pike during the study. The condition factor was calculated by using the formula for Fulton's K:

$$K = \frac{W}{L^3}$$

, where K is condition factor, W is the weight of the pike in grams and L is the length in cm. Then the condition factor in 2014 and 2015 were compared with a paired t-test. Fulton's K was also used to give an overview of the condition factor of pike through the year. Here the condition factor was calculated for every pike caught a given month through the study.

Population size

The capture-mark-recapture method is carried out by catching a certain number of individuals from a population. These are marked in some way so they can be recognized should they be recaptured. After marking they are released to the population again where they are allowed to be fully mixed. Here after a number of samples are taken where individuals from the population are caught and the number of marked and unmarked individuals is registered. There are several methods that can be used to calculate an estimate of the true population size depending on the given conditions. In this study the Schnabel-method as described by Greenwood and Robinson (2006) was applied. The Schnabel method is used when more than two samples are taken. The number of marked and unmarked individuals are registered and the unmarked animals are marked before being released again (Greenwood & Robinson 2006). The marking of the individuals can be done in many different ways. Pike have unique body coloration and color patterns and these are specific for each individual fish. Therefore it is possible to distinguish between different fish by comparison of body coloration and patterns (Raat 1988). In this study the marking consisted of these unique body colorations and patterns and the identification was done by taking a picture of both sides of the pike. Whenever a pike was caught the picture was compared with pictures of previously caught pike in order to identify recaptures. Especially the patterns near the tail were very useful for this method (Figure 6, Figure 7, Figure 8 & Figure 9).

The Schnabel-method has the following assumptions:

- The tagged animals are unaffected in behavior and survival and the tags are not lost.
- The tagged animals are completely mixed with the rest of the population.
- The likelihood of catching a tagged animal is as big as the likelihood of catching any other individual from the population, i.e. the samples are taken completely random in relation to tag-status, age, sex and size.
- Every tag is registered at recapture.
- The population is closed - no migration, death, immigration or births happens during the study period.

$\hat{N}$	The estimated size of the population just before the first sample.
k	The number of samples in the study (i = 1…k).
n_i	The number of fish in the i'th sample.
M_i	The number of marked fish in the population just before the i'th sample ($M_1 = 0$).
m_i	The number of marked fish in the i'th sample ($m_1 = 0$).
A	$\sum_i^k n_i M_i^2$
B	$\sum_i^k m_i M_i$
C	$\sum_i^k \frac{m_i^2}{n_i}$

The estimate of the population is made by:

$$\hat{N} = \frac{\sum_i^k n_i M_i^2}{\sum_i^k m_i M_i} = \frac{A}{B}$$

The 95 % confidence limits are calculated:

$$\frac{A}{\left[B \pm t\sqrt{\frac{AC - B^2}{k-2}}\right]}$$

, where t is Student's t for k - 2 degrees of freedom for a significance level of p = 0.05.

In order to detect possible biases the proportion of marked pike in each sample was plotted against the number of marked pike in total prior to each sample (Greenwood & Robinson 2006). Also to test the model-assumptions a goodness-of-fit test were made as described by Greenwood and Robinson (2006).

The pike population was probably reduced due to very poor conditions in the river during the summer 2014 (see further below and part 2). Therefore only catch-data from November 2014 and forwards were used to estimate the population size in order not to violate the Schnabel-method's assumption of no deaths.

The picture of the caught pike was compared with previously caught pike of similar size (with a margin of + 3 cm to -15 cm taken growth and variation in measuring into account). If a pike had been caught previously it counted as a recapture, if not it counted as a new fish in the population estimate. Every whole fishing day counted as a capture-event. Generally only pike of more than 50 cm was included in the population structure. This was done with regards to the selectivity of the angling which probably would severely underestimate fish of less than 50 cm. Also pike of less than 50 cm must be considered more in risk of predation and this would therefore violate the model assumption of no deaths. The population estimate should therefore be seen as an estimate of adult pike in the river (pike > 50 cm).

Age determination

The age of a pike can be determined by studying the calcified structures such as otoliths, bones or scales. Age determination by scales is the only one of these methods that does not require for the fish to be killed and therefore this was the method chosen for this study. Several studies have used scales to determine the age of a pike (Frost & Kipling 1959, Mann 1980, Wright 1990, Žiliukienė & Žiliukas 2012, Sauvanet et al 2013). This is possible due to the growth bands that are created on the structures when the fish grow. These growth bands are close to each other in periods with slow growth and wider apart in periods with fast growth. In Denmark the slow growth is expected to occur during winter and since this is an annual event it is expected that the clustering of the growth bands is too. Therefore the number of clusters should equal the number of years the fish have lived. Unfortunately there are pitfalls since slow growth can occur outside winter due to lack of food or stress caused by poor physical conditions. In this study the scales were studied under a microscope in order to estimate the age of the fish. As a way of checking the accuracy a colleague made independent estimates of the age and the results were compared showing similar results with the widest disagreements being ± 1 year. Because of the relative uncertainty of the age the estimations should be considered as an approximate assessment of the age of the pike in the population. It was assumed that the thirty pike with a transmitter were representative of the adult pike population and the age of these were used to determine the age distribution in the population. More scale samples were included to give an indication of the growth over years and in this analysis scales from 54 pike were used. These were chosen non-randomly in order to have a certain amount of fish in each age group. This also explained why these scale readings was not representative for the age distribution in the population.

Results

Population - structure and condition factor

Through the study 26 capture events were made (21 angling, 4 electro fishing and 1 combined). On these events 123 different individuals of pike were caught (mean weight 5.54 kg; mean length 86.6 cm, see **Figure**

1). At all occasions there were long stretches without any pike followed by smaller areas with larger concentrations of pike. The electro fishing seemed to be effective towards catching smaller pike. All though these were not included in the population analysis it seemed that the amount of smaller pike less than 50 cm was small (< 50 pike during all electro fishing events). The relationship between weight and length of the pike in the river follow a power regression (**Figure 2**). The scattering increases as the pike grows which is caused by different growth rates. The condition factor of the pike is highest in the months of early spring (before spawning) and decreases hereafter until the next spawning time (**Figure 3**).

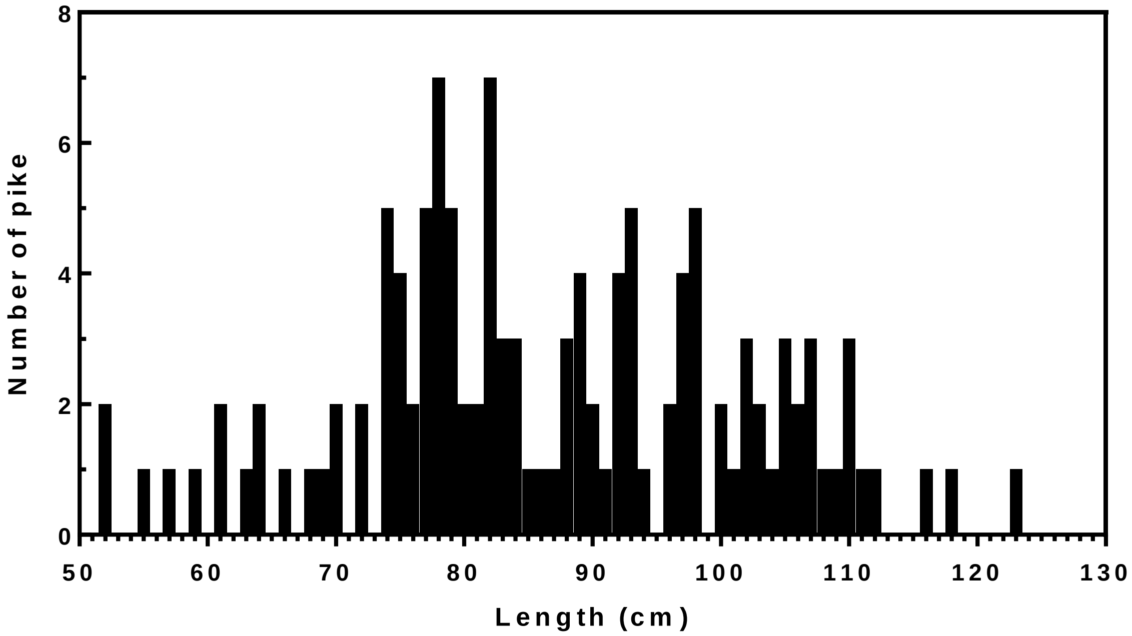


Figure 1: Length distribution of 123 pike caught in River Tryggevælde.

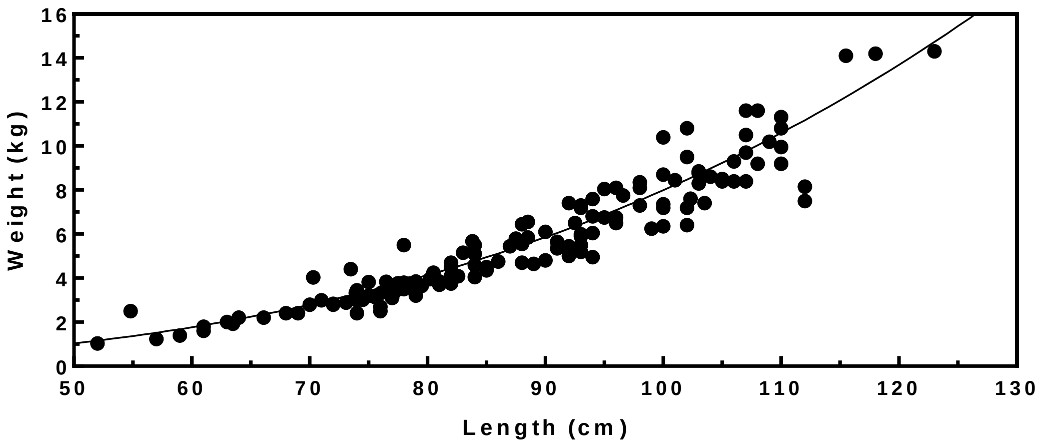


Figure 2: Relationship of weight and length of pike caught in River Tryggevælde.

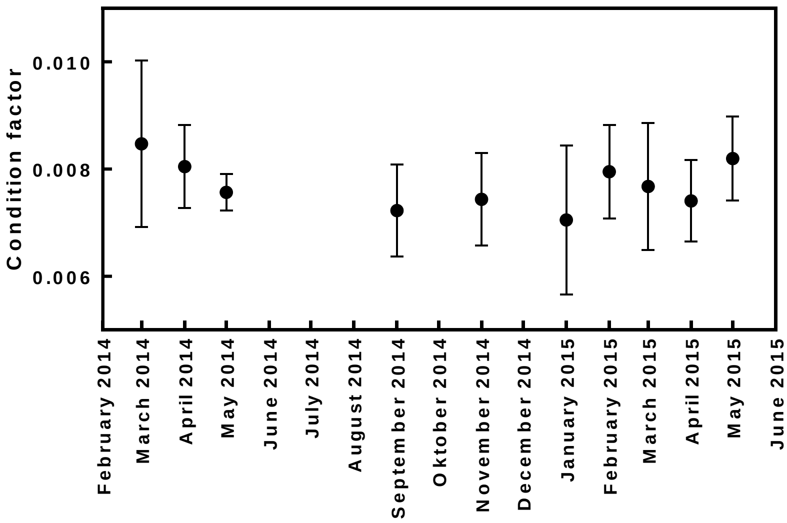


Figure 3: The condition factor (Fulton's K) of pike over months during the study period with standard deviation.

Growth

The 19 pike that were caught in spring 2014 and recaptured in spring 2015 grew between 0 and 13 cm with a mean of 4.5 cm (**Table 1**). Four of these were male pike which according to the literature were close to their maximum length (Frost & Kipling 1967, Mann 1976, Bregazzi & Kennedy 1980, Roche et al 1999). Therefore it would make sense only to look at the growth for females. The observed growth in length of the 15 females was 5.7 % while the expected growth was estimated to be 6.55 %. The relationship between weight and length of the 17 pike that were recaptured before the spawning time in 2015 generally seemed to show a decrease in grams per cm (**Figure 4**). This trend was confirmed by the fact that the change in condition factor of the 17 pike decreased significantly from 2014 to 2015 ($p = 0.0036$, see **Table 2**).

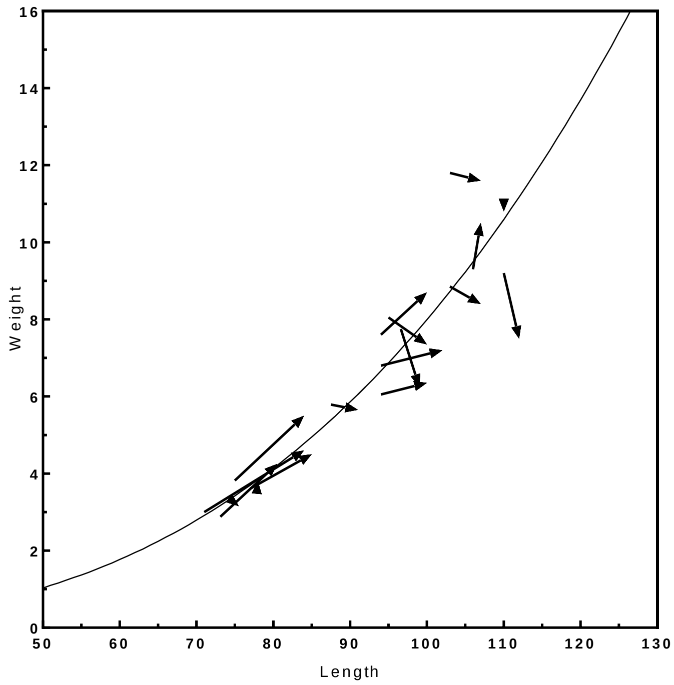


Figure 4: Change in W/L-relationship for the 17 pike recaptured in spring 2015. The line represents the expression of W/L of pike in the river shown in Figure 2. The arrows show the change of the pike's position on the graph.

Table 1: Growth of 19 recaptured pike caught in spring 2014 and 2015. M = Male, F = Female.

Pike no.	Sex	Length 2014 (cm)	Length 2015 (cm)	Growth (cm)
1	F	87.5	91	3.5
4	F	77	85	8
7	M	76.5	79	2.5
9	F	71	84	13
10	F	75	84	9
13	F	96.6	99	2.4
16	M	76.1	78	1.9
23	F	94	100	6
24	F	73.1	80.5	7.4
30	M	77.9	78	0.1
43	F	110	112	2
60	F	95	100	5
61	F	103	107	4
62	F	94	102	8
63	F	94	100	6
65	F	106	107	1
66	M	74	75.5	1.5
109	F	110	110	0
113	F	103	107	4
Mean				4.5
Mean (females)				5.3

Table 2: Condition factor (Fulton's K) of pike caught in both spring 2014 and spring 2015.

Pike no.	Condition factor 2014	Condition factor 2015	Change
1	0.864	0.750	-0.115
4	0.791	0.733	-0.058
9	0.838	0.776	-0.062
10	0.905	0.928	0.022
13	0.860	0.644	-0.216
23	0.728	0.635	-0.093
24	0.737	0.815	0.077
30	0.768	0.801	0.033
43	0.691	0.534	-0.157
60	0.939	0.735	-0.204
61	0.810	0.686	-0.124
62	0.819	0.678	-0.140
63	0.915	0.870	-0.045
65	0.781	0.857	0.076
66	0.839	0.732	-0.107
109	0.826	0.811	-0.015
113	1.080	0.947	-0.133
Mean	0.835	0.761	-0.074
Std. dev.	0.092	0.108	0.090
95 % C.L.	0.044	0.051	0.043

Population size

Due to a long period with strong winds from W and NW saline water was pushed into the river in the end of August 2014. Several hundred ide and roach were found dead as well as nine pike from 1 to 7 kg. In the same time four of the pike with a transmitter (see part 2) presumably died too probably due to the combination of high water temperature and low oxygen content. The Schnabel-method assumes a closed population and since the pike population was reduced in the summer of 2014 only capture events from November 2014 and forward were used to estimate the population. The coloration and pattern on the body of the pike were used for identification. Especially the patterns on the tail and on the lower belly were very different and unique for each individual pike (**Figure 6, Figure 7, Figure 8 & Figure 9**). On 16 capture-events (14 angling and 2 electro fishing) 94 pike were caught for the population analysis and of these 20 (one pike was recaptured twice) were recaptures (21.3 %). This gave an estimated population size of 183 adult pike (95 % CL: 132 - 296). This corresponds to an average of about 12 adult pike per hectare on the studied river stretch (95 % CL: 9 - 20). With regards to the mean weight of pike caught in the study the density corresponded to a biomass of adult pike on the studied river stretch of 1013 kg or 68.6 kg per hectare (95 % CL: 50 - 111). To assess the quality of the population estimate the proportion of recaptured pike in each sample was plotted against the number of marked pike prior to each sample as described by Greenwood and Robinson (2006) (**Figure 5**). This showed a scattering around the regression line. This is probably caused by variation in catchability but since it is not a curved distribution which could indicate a trend such as gear avoidance this is satisfactory (Greenwood & Robinson 2006). Also a goodness-of-fit test were made of the capture-mark-recapture data which did not turn out to be significant (G-test, α = 0.95, DF = 16, G = 15.94, $\chi^2 = 23.68$). This indicates that the expected values fit the observed values which makes it acceptable to use the Schnabel-method on this data set (Greenwood & Robinson 2006).

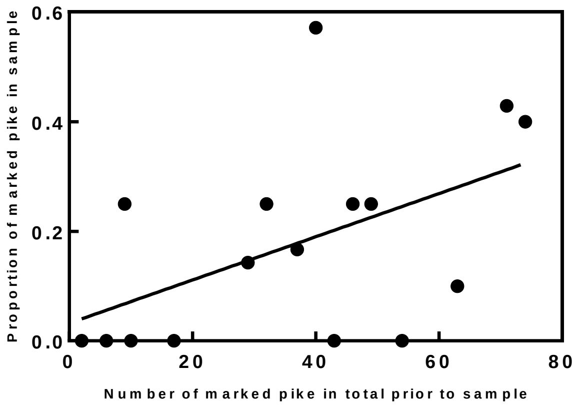


Figure 5: Plot of the proportion of marked pike in each sample against the number of pike in total that previously had been marked.

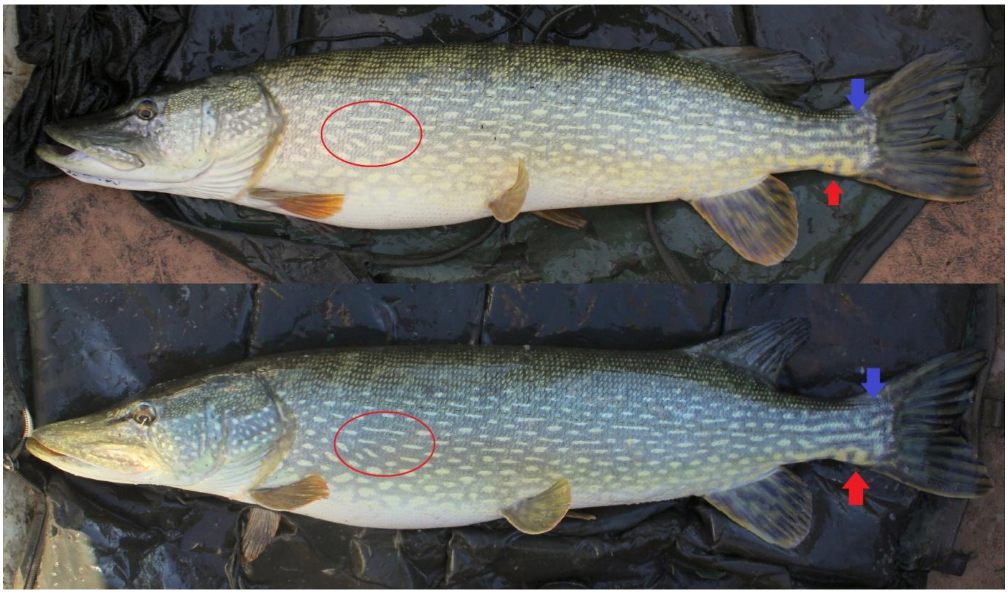


Figure 6: Left side of pike no. 96 caught 19/2-15 and 12/3-15

Figure 7: Right side of pike no. 96 caught 19/2-15 and 12/3-15

Figure 8: Left side of pike no. 63 caught 29/3-14 and 12/3-15.

Figure 9: Right side of pike no. 63 caught 29/3-14 and 12/3-15.

Age determination

The age of the thirty pike with a transmitter was determined in order to show the age distribution of the adult (> 50 cm) pike population. The determination of age by scale reading showed that the adult pike investigated approximately were between three and nine years old with most fish between three and six years of age (**Figure 10**). The scales from 54 pike were read in order to show the growth over time. The ages of these were between two and nine years. The relationship between age and length showed that growth ceases over time and that some pike reaches 100 cm at five years of age but that the trend is to reach this length at six or seven years of age (**Figure 11**).

Figure 10: Age distribution of thirty adult pike in the river.

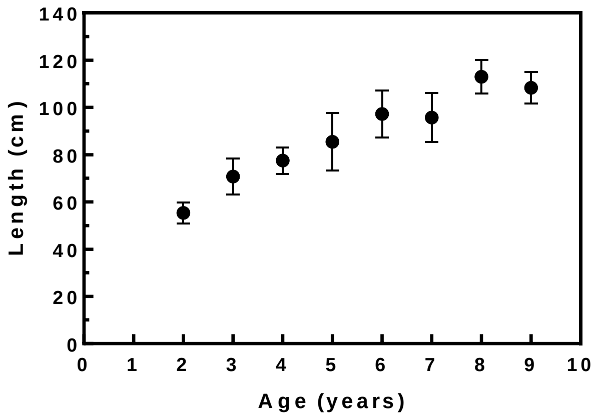


Figure 11: Plot of the age and length of adult pike in the river with std. dev.

Discussion

Growth

The mean weight of the pike in River Tryggevælde (5.54 kg) is extremely high compared with other river pike studies (**Table 3**). This study did not include pike aged 0-1 years and data for similar studies are not available. Compared with studies including one more or one less of the lower age groups the mean weight in this study is 2 - 10 times larger (**Table 3**). By comparing the W/L-relationship of the pike in River Tryggevælde with the relationship of other river pike it is apparent that the large mean weight could be a result of an extreme high condition factor (**Figure 12**). The W/L-relationship is higher than in the European rivers Allier and Stour but lower than in River Nene.

The large mean weight could also be explained by a very high growth rate. The 15 females recaptured in 2015 increased their length with 5.7 %. It must be taken into consideration that this growth was experienced in a year where conditions in the river were poor and the general condition factor decreased (see below). This is also expressed through the expected growth which was calculated to be 6.55 %. The growth of five female pike from River Gudenå with a similar mean length (92.8 cm) showed an increase in length of 3.4 % (Koed et al 2006). This indicates that the pike in River Tryggevælde has a high growth rate all though the increase in lengths found in the two rivers were not significantly different (un-paired t-test, $p = 0.23$). It must be stressed that the study compared with was carried out in River Gudenå which are very famous for its many, large pike (Sørensen 2008, Lyngby 2011). The high growth rate is also apparent when comparing data of length and age with other rivers (**Figure 13**). Here River Tryggevælde clearly has a higher growth rate than River Frome, River Nene, River Allier and River Stour.

An explanation for the high condition factor and growth rate could be large quantities of quality food in all sizes. River Tryggevælde has a large number of many different prey fish and pike is the only predatory fish found in greater numbers which means the competition for food is sparse. Furthermore it is possible that the pike occasionally swims into the bay to forage (see part 2). It is also possible that prey fish like ide and bream in some periods forage in the productive environment that is found in the bay and later bring this production into the river as they swim into it again. However it is interesting that several pike were located at the upper stretch during summer when this stretch seemed to hold only few prey fish during the electro fishing in September. This is further discussed in part 2. Another explanation of the high growth rate and condition factor could be the large amount of vegetation that is found in the river. Vegetation is considered a major factor in the density, abundance and structure of pike populations (Raat 1988). The vegetation provides the prey fish with optimal spawning habitat as well as plenty of food. At the same time it is possible that the pike which is an ambush predator (Berg 2012) achieves a higher hunting efficiency in the cover of the vegetation where it is well camouflaged (Raat 1988). Furthermore it is possible that the large proportion of floating-leaf plants reduces the light intensity in the river (Raat 1988). This will create ideal hunting conditions for the pike which have been shown to be optically superior to its prey at low light levels (Dobler 1977).

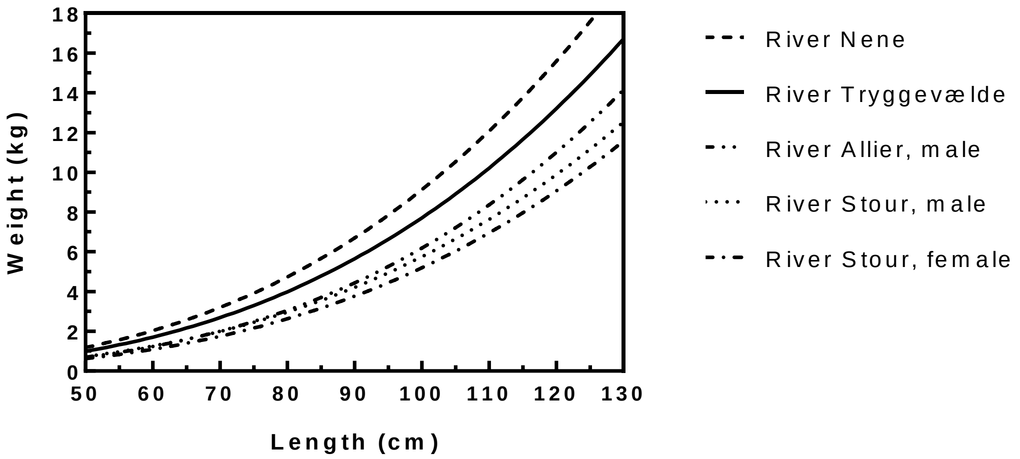


Figure 12: Relationship between weight and length of pike in River Tryggevælde, River Allier, River Nene and River Stour. Lines created from the model of the relationship between weight and length calculated in each study.

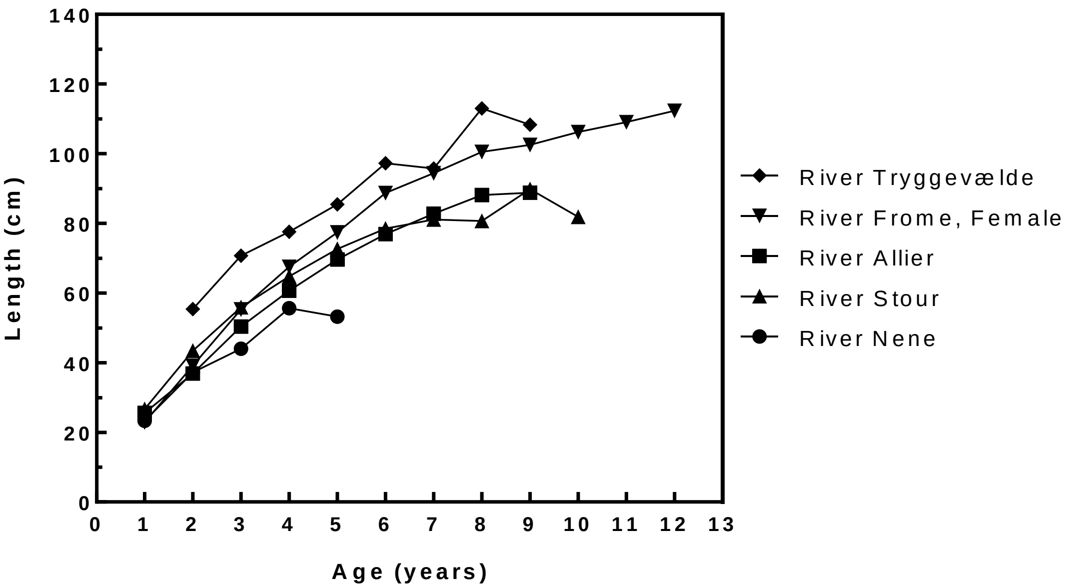


Figure 13: Age and length of pike in River Tryggevælde as well as in four other European rivers.

Condition factor and conditions in the river

The relationship between weight and length show a trend where the increase in weight is larger than the increase in length as the pike grows. This means that the condition factor generally increases with increasing length of the pike. This shows that the pike in the river do not experience any kind of limitation as they grow bigger. If this was the case it would be expected that the gain in weight would slow down. Thus, the river as a habitat provides the pike with plenty of opportunity to grow as large as possible. The W/L relationship show an increasing scattering of the points with increasing length. This show that the condition factor of a pike in the river will vary more as the pike grows. This can partly be the result of a difference in growth which naturally will be more apparent over time. Furthermore it must be expected that the proportional increase in weight during spawning increases with increasing length which makes it possible for the relationship between weight and length to fluctuate more in larger pike.

The gonad weight can form 2-4 % of the body weight in male pike and 18-20 % in female pike (Raat 1988). This explain why some studies have shown the highest condition factor to be just before spawning time (Mann 1976, Bregazzi & Kennedy 1980). This is similar to the result found in this study. However this study does not show the gradually increase in the condition factor during fall as other studies have (Mann 1976, Bregazzi & Kennedy 1980). However the data in this study show wide variations in the condition factor and data are missing for several months during summer and fall which makes it insufficient to base conclusions on.

Food intake and hence growth in pike can be inhibited by abiotic factors such as high temperature (Casselman 1978, Raat 1988). The significant decrease in condition factor from 2014 to 2015 indicates that the conditions in the river have been harsh. This is further confirmed by the growth being lower than expected. Generally 2014 was the warmest year since 1874. The summer mean temperature was 1.6 ^{O}C above the mean and it was the hottest summer in eight years (DMI). At the same time the summer precipitation was 7 % lower than the decade value which is the mean precipitation measured from 2001-2010 (DMI). In late August there were indications that the oxygen level at the lower and middle stretch was very low. The water was black and smelly and in the beginning of September a point measurement showed an oxygen content of just 12 % (see part 2). The lethal oxygen level for a pike at 24 ^{O}C is 12.2 % (Raat 1988) and it is likely that the lower condition factor is caused by poor conditions with regards to oxygen levels and temperature. This information is of great importance for the second part of this study. If the conditions in the river have been really bad it possibly explains the movements and behaviors of the pike in certain periods where it probably is more important to avoid poor or even lethal conditions than to hunt and grow. Furthermore saline water was pushed into the river in late August resulting in the death of several hundred large ide and roach. This reduction in prey fish could also have affected the condition factor of the pike.

Population structure - length and age

The large number of pike between 74 - 98 cm is probably caused by a stunting in growth of male pike at around 75 - 80 cm which increase the proportion of pike in this length class. Furthermore it must be assumed that only a small proportion of the pike population reaches a size of more than 100 cm due to increased mortality with age. The decreasing number of pike smaller than 74 cm could partly be explained by the catching methods being selective towards pike of more than 50 cm. However the low number could also be explained by a high predation pressure by larger pike. Cannibalism can affect the number of 0+ pike and an inverse relation between 0+ pike and older pike have been shown (Craig 1996). In River Frome it was found that smaller pike made up 13 % of the annual weight of the prey fish eaten by pike of 4 years and more (Mann 1982). In the same study cannibalism accounted for most of the natural mortality found in pike aged 6 months - 2 years. During the electro fishing small pike were caught with ease but there did not seem to be many smaller pike in the river (< 50 pike during the electro fishing). There is plenty of large "mature fish" and it does not seem that the river is in lack of suitable spawning habitat due to the generally shallow depths and heavy vegetation cover. Thus, the low number of smaller pike indicates a high selection during the first years of the pike's life. If this selection is caused by predation on eggs it will create less competition for the hatched pike which in turn will grow fast. If the selection is caused by cannibalism from larger pike a high growth rate will be beneficial and awarded since it will reduce the risk of predation (Nilsson 2006b).

The youngest pike in the age distribution was three years old. This is due to the fact that only pike of more than 60 cm was chosen for the tagging study in order to decrease the risk of predation (see part 2). The age distribution is therefore a representation of pike older than two years of age. The range in age found in River Tryggevælde was very similar with the ones found by Mann (1976) and Sauvanet et al (2013). No pike of more than nine years of age were found but the two nine year old pike with a transmitter survived through the whole study and thus reached ten years of age during the study. However it seems that pike in River Tryggevælde rarely exceeds ten years of age. Thus, the large pike in the river is not a result of the pike growing really old. The low number of really old pike corresponds well with the fact that a high growth rate is found to be associated with a shorter life span (Raat 1988, Berg 2012). It must be expected that the number of pike at a specific age decreases with increasing age due to mortality. This trend is also seen in this study where the youngest pike of three years of age are the most numerous and the next three age groups seem to show a linear decrease which is caused by an equal mortality each year. No pike aged 7 is present which could indicate a weak cohort. This could be due to the spawning failing or poor conditions in the river for the newly hatched pike. The number of 8 year old pike follows the linear decrease while the number of 9 year old pike is larger than what would be expected. This could be caused by this cohort being particularly strong. It seems that pike of 3-6 years of age is most frequent in River Tryggevælde which is very similar to the result found in a Belgian river by Sauvanet et al (2013) who found that 73 % of the pike were between 4 -7 years of age. Contrary the pike in the study made by Mann (1976) were most frequent at 1-4 years of age with fewer pike older than this.

Table 3: Density, biomass and mean weight of pike found in different studies.

Author	River	Age group (years)	Pike ha-1	Kg. pike ha-1	Mean weight (kg)
Sauvanet et al (2013)	Allier, France	1-9	15-16	40,3	2.599
Paragamian (1976)	Plover River, USA	0-4	54	28.9	0.54
Mann (1980)	River Frome, Britain	0-10	159	68.6	0.43
Mann (1980)	River Stour, Britain	1-10	61	45.8	0.75
Hart & Pitcher (1973)	River Nene, Britain	1-6	200	115	0.58
Taugbøl et al (2004)	Søndre Rena, Norway	> 2	4	3.17	0.79
Lind & Kaukoranta (1975)	Oulujoki, Finland	> 2	4.5	7.2	1.6
This study	River Tryggevælde, Denmark	> 1	12	68.6	5.54

Population size

The density of pike depends on the suitability of the habitat with regards to both biotic and abiotic factors. Since this study only included adult pike of two years or older it was not possible to compare with a study with the exact same age groups included. However studies with one more or one less of the lower age groups have been made. The densities found in Søndre Rena (Taugbøl et al 2004) and Oulujoki (Craig 1996) of pike aged three years and older both were about three times smaller than the density of 12 pike per hectare found in this study (**Table 3**). Due to the few pike aged two years caught in this study the difference alone could not be caused by the inclusion of this age group. The density found in River Allier (Sauvanet et al 2013) of pike aged one year and older is higher but also includes one more age group. Furthermore it should be stressed that the density in River Allier is calculated for suitable habitat and not for the whole area of the river.

This indicates that River Tryggevælde not only is capable of producing very large pike but also is able to maintain a high density of pike. It is likely that this is explained by the same factors influencing the high growth rate and condition factor (see above). Furthermore the high density is an indication that a large proportion of the river should be considered as suitable habitat - if not the density could not be that high. In general the biomass of pike per hectare was the second largest compared with seven other European rivers which is a result of the extremely large mean weight. The study in River Frome by Mann (1980) had the same biomass of pike per hectare (with two age groups more included) but this was spread out on 13 times as many pike. The population of pike in River Tryggevælde is almost 70 kg per hectare which is close to the range of maximum capacity estimated in Craig (1996) (80-150 kg per hectare). This estimation is based on the amount of suitable habitat. With this in mind it is possible that the population right now is so close to the maximum capacity of the river that it can't be improved in terms of density and biomass. In other words: The river is close of holding as many pike as realistically possible.

Evaluation of methods

The population size estimated with the Schnabel-method was complicated due to the fish death experienced in August. If data from before the fish death was included it would result in the Schnabel-method overestimating the population with about 100 pike because it would assume a greater chance of recaptures than what would actually be. This made it necessary only to use some of the data collected (pike caught from November 2014 and forwards) but in the end this gave a satisfactory estimate of the population size (based on proportion of recaptures and 95 % confidence limits). The method assumes a closed population. Since the data used were for a short time of less than six months and that no dead pike were found during these months it was concluded that it was fair to say that the mortality of pike during the period was equal to zero. The same could be said regarding births - no pike could be expected to hatch and reach a size of more than 50 cm during this period. Regarding the assumption of no migration the other part of this study (see part 2) showed that the pike mainly stayed in the river and never left the river or swam upstream the study stretch for longer periods. It is possible that new pike could have migrated from upstream or from the bay. However there does not seem to be a large pike population in the bay and the net fishers only rarely catches pike. The nearest river is River Køge and it is not known to have a big pike population - especially not on the lower stretches. Furthermore the stretch upstream the study area is narrow, shallow and fast flowing and is most likely not an ideal place for pike to live in. This is further supported by the fact that the pike with a transmitter only rarely visited the upper three kilometers of the study area. With this in mind the chance of new pike entering the population in a larger degree during the study period was considered small. The method also assumes an equal likelihood in catchability between tagged and not-tagged animals. The plot of the proportion of marked animals against the number of marked animals shows that there is a variation in the catchability between samples. However since the points are not distributed on a curve it also indicates that this variation is not caused due to gear avoidance or even gear affinity (Greenwood & Robinson 2006). Furthermore two methods were used for catching the pike (electro fishing and angling) which allowed pike that somehow was difficult to catch with one method had a chance of being caught with the other method. Both electro fishing and angling was considered non-selective with regards to pike of more than 50 cm meaning that the methods was not more likely to catch pike of a specific size in the range of 50+ cm pike. In terms of the method used for identification it was chosen to take a picture of both sides of the pike and distinguish between the individual fish by looking at the unique patterns on their sides. This method has an advantage instead of tags which could be lost or cause a change in the behavior of the animal. A recaptured pike should be easy to identify and with a little experience it was pretty straightforward to recognize pike as well as distinguish between different pike. All pike was checked for several characteristics so two pike with a similar pattern at e.g. the tail still was distinguished.

Conclusion - Part 1

The pike population in River Tryggevælde is large both in terms of density and biomass. The pike have a high growth rate and a high condition factor which causes a large mean weight. All of this is caused by good conditions in the river in terms of food and suitable habitat all though there seemed to be fewer prey fish in the river during summer. It is likely that the pike population in the river currently is very close to its maximum capacity and therefore can't be improved in terms of neither density nor biomass. However 2014 was a difficult year for the pike which showed a decrease in condition factor probably due to poor abiotic conditions and a reduction in prey fish. This study indicated a low number of smaller pike in the river which could be caused by a strong predation pressure on the eggs or younger pike. An interesting future study could focus on the young pike in terms of determining the number and condition of these. This knowledge would first of all allow a comparison of the population with more studies. Furthermore it would reveal the factors affecting the pike in its first years which in this study seems to be either predation on eggs or cannibalism from larger pike. Predation on eggs would decrease the competition of hatched pike which would display a high growth rate. Since pike are gape limited predators cannibalism would be selective towards a high growth rate which could further explain the very high growth rate found in the river (Nilsson 2006b). The high growth rate is likely to explain that no pike of more than 10 years of age were found since a high growth rate is associated with a shorter life span.

Part 2: Movements and habitat choice of pike in a Danish lowland river with possible seawards migrations

Introduction

Knowledge about the activity and behavior of pike is of great ecological importance (Beaumont et al 2005) but most studies of pike activity have been made in still waters. Increased knowledge about pike in rivers will give a more detailed understanding of the behavior of these pike according to habitat choice, movements and activity patterns. Furthermore this knowledge may give insight to the mechanisms affecting the pike in this dynamic environment. The local movements of pike may be of significance for the conservation of populations since important habitat requirements and swimming routes can be revealed (Lucas & Baras 2001). Moreover studying the movements of the pike through extensive time will expose valuable information of habitats prefered according to different conditions and seasons. Besides expanding the general knowledge of river pike ecology this information is especially important if management actions are considered.

Rivers as an important habitat

Numerous studies have shown spawning migrations of pike. This phenomenon is both found within freshwater such as lakes and rivers (Clark 1950, Ovidio & Philippart 2003, Koed et al 2006, Vehanen et al 2006) and from brackish coastal water where pike migrate up rivers during spring (Johnson 1982, Müller & Berg 1982, Müller 1986, Engstedt 2011). Furthermore pike spawning in brackish water has also been shown (Westin & Limburg 2002, Jørgensen et al 2010, Engstedt 2011). Often the pike show a degree of homing where the pike returns to the same spawning sites every year (Johnson 1982, Müller & Berg 1982, Müller 1986, Karås & Lethonen 1993, Miller et al 2001, Westin & Limburg 2002, Vehanen et al 2006, Engstedt 2011). The pike in the Baltic Sea have two reproduction strategies: Either they spawn in shallow, brackish water or they migrate up through coastal streams (Engstedt 2011). By analyzing the Sr:Ca in otoliths Engstedt (2011) showed that 45 % of the pike in the Baltic Sea originated from freshwater. The same study suggested that restoration plans for improving the pike populations in the Baltic sea focused on the populations in individual streams and rivers (Engstedt 2011). Thus, the rivers play an important role in the pike's reproduction and the time spent in the river is crucial for the population. This magnifies the importance of understanding the behavior and requirements of the pike when they are located in the river.

River pike ecology

Movement rates of pike are often considered as an expression of feeding activity (Beaumont et al 2005, Kobler et al 2008, Baktoft et al 2012). Other incentives could be to avoid or search for specific environmental conditions, avoid or seek conspecifics due to either cannibalism/competition (Nilsson 2006b) or reproduction or to search for suitable spawning areas (Koed et al 2006, Pauwels et al 2014). The pike is considered an ambush predator (Berg 2012) but it has not been established whether the pike hunts from a single ambush site or move between several potential ambush sites (Beaumont et al 2005). Furthermore there are indications that pike may also display a more active hunting strategy (Turesson & Brönmark 2004) maybe in order to increase the chance of encountering prey. Since the pike are build for short bursts of rapid acceleration rather than prolonged swimming it has been hypothesized that pike in rivers moved less than pike in lakes due to the increased effort needed for swimming in flowing water (Beaumont et al 2005). Previously the pike were considered a mainly sedentary fish - a view confirmed by a study made by Diana (1980) who showed that the pike were inactive in 80 % of the study. This view of the pike has shown to be more diverse and already in 1984 Chapman and Mackay (1984b) suggested that the pike were more mobile than first thought. Several studies show a diverse pike population where some individuals are very static while others are very mobile (Cook & Bergersen 1988, Masters et al 2005, Vehanen et al 2006, Rasmussen 2007, Kobler et al 2008). This difference has sometimes been correlated with sex (Lucas 1992, Koed et al 2006) or size (Masters et al 2005, Vehanen et al 2006, Kobler et al 2008). In the case of variations between sexes the difference have only been shown in the spawning season but both males and females have shown to be the most mobile sex (Lucas 1992, Koed et al 2006). In studies where larger pike moved more than smaller pike it is thought to be due to a decreased risk of predation (Masters et al 2005). In rivers movements usually have a longitudinal and/or lateral component rather than a vertical component which is more common in lakes (Lucas & Baras 2001). How much the pike actually moves can be very different and especially depend on whether the pike make spawning migrations or not.

Diel activity patterns

Most studies of the diel activity of pike have shown a peak in activity at dusk and/or dawn (Cook & Bergersen 1988, Beaumont et al 2005, Rasmussen 2007, Kobler et al 2008, Baktoft et al 2012). An experiment of pike without conspecifics and prey showed a peak in activity during dusk. This indicated a routine response in the pike due to low light levels (Nilsson et al 2012). It seems that whether the pike are active at night or not can vary with some studies showing a decent activity during night (Beaumont et al 2005, Rasmussen 2007, Kobler et al 2008, Baktoft et al 2012, Nilsson et al 2012), while others do not (Diana 1980, Lucas 1992). Knowledge of the diel activity patterns displayed by the pike contributes to the interpretation of the important mechanisms influencing the pike. By determining the patterns shown by the pike according to different seasons it is possible to specify the most important factors affecting the pike.

Environmental factors

The influence of temperature on the pike's activity levels can vary. Some studies have observed a greater activity or increased movement during summer compared with winter (Cook & Bergersen 1988, Ovidio & Philippart 2003, Vehanen et al 2006, Kobler et al 2008). In an *in situ* experiment (data from CPUE) Casselman (1978) found that pike maximum swimming activity occurred at 15-17 ^{O}C. However Pauwels et al (2014) found that pike moved most in the colder months and all though Cook and Bergersen (1988) found that distances swam in winter was shorter than in summer they found an increase in activity (number of relocations) probably caused by more active foraging. At last Diana (1980) found no difference in activity between summer and winter. Some studies have shown a decrease in activity when the temperature exceeds 19-20 ^{O}C (Vehanen et al 2006, Rasmussen 2007). A study made over different months by Baktoft et al (2012) showed no effect of temperature on the pike's activity indicating that a change of temperature in the lower levels (1-17.3 ^{O}C) did not have an effect on the pike's activity. This is contrary to the lab experiment made by Casselman (1978) who showed that pike were significantly less active at temperatures below 6 ^{O}C than at temperatures greater than 9 ^{O}C. Pike is not suited for high currents (Jones et al 1974, Raat 1988) and it has been shown that the activity of pike decreases with increasing flow (Pauwels et al 2014).

Aim of this study

A more detailed understanding of the activity patterns and habitat choices displayed by river pike will improve the knowledge which management actions are based on.

This study is carried out in the Danish River Tryggevælde near Køge, Zealand which long have been famous for its many large pike. Knowledge of the pike population in the river is especially interesting in a socio-economic aspect since it is pike populations like this current management actions hopes to form and preserve. The time spent in the river is of great importance for both river pike and coastal pike which enters the river to spawn. Thus, a further understanding of the factors influencing the activity and habitat choice on a timely scale may enhance the future conservation of important pike populations.

Since pike are found on the lower stretch of the river which runs into Køge Bay it was hypothesized that at least some of the pike migrated to the bay during the summer. The bay was expected to contain plenty of food as well as a water temperature optimal for growth (19-21 ^{O}C). The combination of a high water temperature and brackish water have shown to be beneficial for the metabolic rate of perch (*Perca fluviatilis*) (Christensen 2015) and it is possible that it was applicable for pike too. It was also expected that the pike during summer was able to find more favorable oxygen levels in the bay than in the river. The discharge in the river is much smaller in summer compared with winter (Sand-Jensen 2013) which indicates a low exchange of water during summer. In addition to this the river is known to be covered in decaying vegetation during summer which probably causes very low oxygen levels. It was expected that the combination of high water temperatures and low oxygen levels in the river would be a reason for the pike to move into the bay.

Based on angling records from the river it was expected that the pike mostly inhabited the lower 3 kilometers of the river during fall, winter and spring while they moved to either brackish water or further upstream during the summer. Other studies of river pike had shown that the pike in general primarily moved smaller distances within restricted areas (Ovidio & Philippart 2003, Beaumont et al 2005, Masters et al 2005, Koed et al 2006, Pauwels et al 2014). Coupled with the general assumption of the pike being an ambush predator it was expected that the pike generally displayed a static movement pattern maybe replaced by movements of longer distances during spawning (Koed et al 2006, Pauwels et al 2014). It was expected that the pike were affected by the environmental factors in the river. Especially temperature was hypothesized to have a positive effect on the activity of pike (Casselman 1978). Furthermore a connection with light intensity was expected with activity peaks at dusk or dawn probably caused by increased feeding activity (Cook & Bergersen 1988, Beaumont et al 2005, Rasmussen 2007, Kobler et al 2008, Baktoft et al 2012).

In this part of the study the diel and yearly movements and habitat choice of the pike is studied by using acoustic telemetry in order to investigate the factors influencing their behavior. This will increase the knowledge of river pike ecology which still is sparse and contribute with valuable knowledge for the decision making when management actions are to be considered. Another aim in this study is to determine to which degree (if any) the pike population uses the brackish coastal areas in Køge Bay and to investigate these areas' contribution to the apparent high growth rate of pike in the river (see part 1). This gained knowledge will provide a better basis for the conservation of the population.

Methods

Study area

The study was carried out in the lower 12 kilometers of River Tryggevælde on Stevns, Zealand, Denmark (55°22'48.71"N; 12°15'26.66"E) and in Køge Bay (Figure 14). This stretch contained one small tributary (Krogebæk) and three ditches occasionally holding enough water for a pike to swim into. Further upstream the river receives water from the larger River Stevns and it was decided to place the upper boundary (PIT-station, explained further below) before this to make sure the pike did not disappear into River Stevns. The area of the studied river stretch was 14.8 hectares (for more information on the study area, see part 1). In this paper a position in the river will be described as p.xxxx where p is position and x is the distance from the outlet in meters.

Capture and tagging

From March 9th to March 12th 2014 thirty pike from River Tryggevælde was caught by electro fishing (18 pike) or angling (12 pike). Angling was carried out by float fishing a live bait. The electro fishing was done from a boat by fishing the margins of the river both up- and downstream. All pike were caught between p. 500 - p. 5000. Each pike had an acoustic transmitter inserted in the body cavity (model V13-1L coded transmitter, VEMCO, Nova Scotia, Canada, 13 mm in diameter, 36 mm in length, 11 g in air, estimated battery life of 465 days). Furthermore it was tagged with a floytag (TBA-1, Hallprint fish tags, Australia) and a PIT-tag (Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, 23.1 mm long, 3.85 mm diameter, 0.6 g in air). The acoustic transmitter transmitted a unique signal approximately once per minute and was chosen in order to determine if the pike moved into the brackish coastal areas where a radio-transmitter does not work because of the conductivity. The floytag was chosen as an external tag so a pike could be recognized if caught by an angler or found dead. The PIT-tag was to make sure that the pike would be registered if it swam to the upper boundary in the river where a PIT-station was build. In an attempt to decrease the risk of predation only pike of more than 60 cm had a transmitter inserted.

Before tagging the pike were kept in carp sacks or livewell placed in the river for up to 24 hours. The tagging took place at the river bank. Here the pike were anesthetized in 0.5 mg/l solution of 2-phenoxyethanol. Before operation the weight and body length (total length and fork length) was registered and a tissue and scale sample was taken. During the tagging and insertion of the transmitter the pike was placed on its back in a water filled tube and water was regularly poured over its gills and body. The incision was closed by two separate sutures using absorbable suture material (Vicryl 3-0 FS-2, ETHICON, Johnson & Johnson Medical Limited, Livingston, Scotland). After the operation the pike was photographed for later identification in the population analysis. Hereafter it was placed in aerated river water to fully recover before being released to the river. Duration of the tagging procedure was 3-5 minutes.

Data collection

The field work was carried out using a small boat with both a gasoline engine and an electrical engine. The gasoline engine was used when travelling longer distances on the river while the electrical engine was used when tracking the pike's locations.

Environmental factors

The water temperature in the river was measured every ten minutes just above the bottom at p.82, p.2818 and p.5389 ("HOBO Pendant® Temperature/Light Data Logger 8K - UA-002-08") or at least one time pr. Hour at p.82 and p.2818 ("HOBO Conductivity Data Logger - U24-002-C"). Water discharge data was obtained from Naturstyrelsen, Miljøministeriet who collect data from the station at Lille Linde at p.16500. Only data until March 17th 2015 was possible to obtain. The data from this station was multiplied with a factor 2.293 (according to COWI) corresponding to the proportional larger catchment area at the outlet compared to the station at Lille Linde. Point measurements of the oxygen level through the river were carried out from the boat (YSI 85 multi parameter probe, Rickly Hydrological Company, USA) and the mean of the whole river was calculated. The conductivity in the river was measured at least once per hour from late June 2014 with a "HOBO Conductivity Data Logger - U24-002-C". This was placed just above the bottom on p.82 and p.2818. The measured conductivity was calibrated to the corresponding temperature with the formula:

$$Calibrated\ conductivity = \frac{Measured\ conductivity}{1 + \frac{(temp. - 20) * 2.14}{100}}$$

The salinity was then calculated in ‰ by multiplying the calibrated conductivity with 0.00064.

Movements

The pike's movements were registered using three methods:

Stationary tracking was carried out by placing twelve automatic VR2-recievers (Vemco, Nova Scotia, Canada) in the river or in the bay (**Figure 14**). Two receivers were placed about 400 meters from the coast in the bay. One north and one south of the outlet to register if the pike left the river and entered the bay. An arrangement of four receivers were placed at the sluice (two on each side) to make sure that pike leaving the river were registered. Further upstream two arrangements with two receivers were placed at about p.3000 and p.5500. The reason for placing the receivers in pairs was to determine the direction swam by the pike. The receivers were placed where the river was straight to make sure that a good range was achieved. The positions of the receivers were based on the experience from angling in the river and were done to divide the river into different stretches. In fall 2014 a receiver was placed at about p. 8000 since several fish often were found in this area. A single receiver was placed just before the PIT-station at about p.12000. All receivers in the river were attached on a two and a half meter wooden pole which was hammered into the river bottom. A metal eye was screwed into the pole and a rope holding the VR2 and a sinker was attached. The VR2 receivers in the river were emptied once or twice per month throughout the study. The two receivers placed in the bay itself was attached with a chain to a heavy anchor and suspended above the bottom with a floating 5 L plastic bottle. At the surface this was connected to a buoy with a rope twice as long as the depth making sure that the assembly did not move during storms and high water levels. This also made it easier to empty the receiver since it was not necessary to lift the heavy anchor each time. The receivers in the bay were emptied after seven months and checked again six months after. Unfortunately both receivers were missing probably due to theft, resulting in missing data for the whole of 2015. At p.12440 a PIT-station was build creating the upper boundary of the study (**Figure 14**). Here the river was about 5 meters wide and 1 meter deep. The PIT-station was build in order to be 100 % sure when a pike crossed the upper boundary. The river is narrow and small at this point which decreases the range of the VR2 receiver and it is possible that the acoustic signal is not registered if a pike moves quickly past the receiver. This would not be a problem with the PIT-tag which is detected as soon as a pike swims through the antennae.

Manually tracking was done by sailing through the river on a regular basis and registering the pike's location with a multidirectional hydrophone attached to a VR60 receiver (Vemco, Nova Scotia, Canada). When the VR60 showed that a pike was present the location was registered with a GPS (Garmin Oregon 300). During the study 49 manually tracking events were completed (**Figure 15**). It was attempted to place the manually tracking events regularly through the year but due to heavy plant coverage in the river it was impossible to make registrations in the last half of July and in the beginning of August. When the boat also was stolen at this time there was a period of about two months where no manually tracking events were made.

To give insight to the diel movements four 24-hour trackings (two in winter and two in spring) were made. During these trackings the same 3 km stretch of river was manually tracked by boat every 4 hours. The same 3 km stretch was chosen for all four events because it would make sure that the physical conditions experienced by the tracked pike would be as similar as possible. Furthermore the chosen stretch generally had the largest concentration of pike and thereby allowed as many pike as possible to be included in the sample. The tracking was done by sailing upstream with a gasoline engine to the 3 km mark. Here an electrical engine was used to sail slowly downstream while the position of every pike received with the VR60 was registered. This was done seven times to make sure that an average of the activity for every four hours through the 24 hours could be estimated. The mean number of pike participating in the measurements was 10 (13 in winter and 8 in spring). The four hour intervals were scheduled so the light intensity were constant at each manually tracking event. In winter this meant that the measurements began at 9, 13, 17, 21, 1, 5 and 9. At spring they began at 8, 12, 16, 20, 00, 4 and 8. Every manually tracking event took approximately two hours to complete.

In the end of the study (ultimo May) electro fishing was carried out to find out if the four pike that have been at the same spot for more than 6 months were dead. This was done by locating the transmitter with the manual receiver and electro fish through the area.

Data treatment

Movements

The waypoints plotted on the GPS during the manual tracking events were uploaded to Google Earth and the position of each fish at a specific time was registered. The data from the VR2-recievers were converted to a .csv format and added to the positions found by manual tracking.

Different estimates of the activity of the pike were made. The general activity of each pike was calculated by adding the total distance moved which had been registered by either a VR2 or a manual tracking. In the expression of total activity the months with no registrations were left out and a general expression of activity in meters per day was calculated:

$$General\ activity\ in\ m/day = \frac{Meters\ moved}{Months\ tracked - Months\ without\ registrations} = \frac{Meters\ moved\ per\ month}{30\ days\ per\ month}$$

In total there were 26 occasions where no registrations were made for a pike in a whole month. 18 of these happened in June, July and August because of the heavy vegetation cover making it impossible to track on large parts of the river. In this calculation the receivers placed in pairs were pooled so a bias of activity was avoided when a pike was registered by both receivers. Movement was registered as the distance between a registration on a VR2 receiver or a manual tracking event to a new registration on either a new VR2 receiver or manual tracking event. It should be noticed that the expression of the general activity is an underestimation since only registered movements counts. Any movement that is not registered by the VR2 receivers or a manual tracking will not contribute to the general activity.

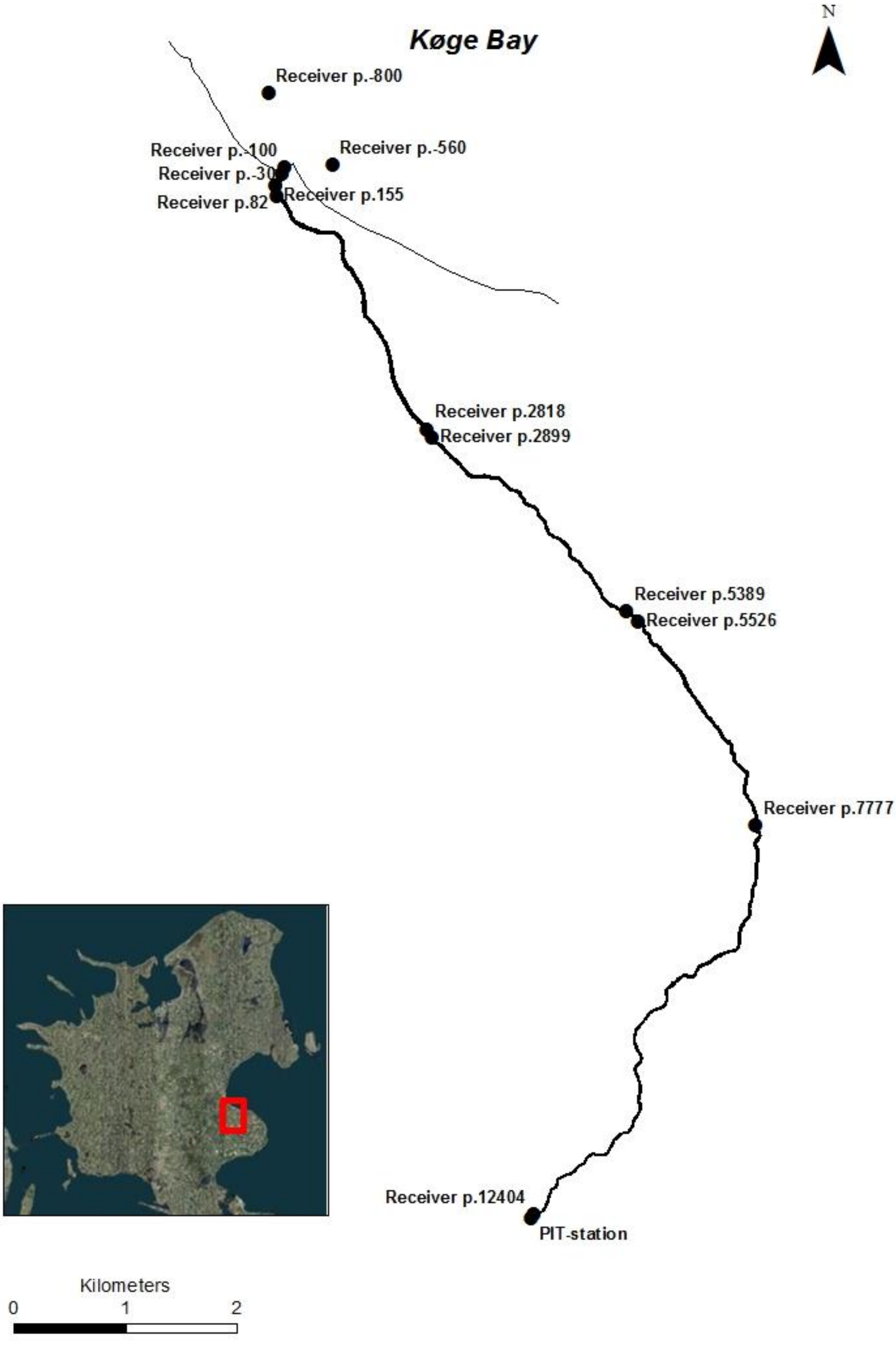


Figure 14: Study stretch in River Tryggevælde.

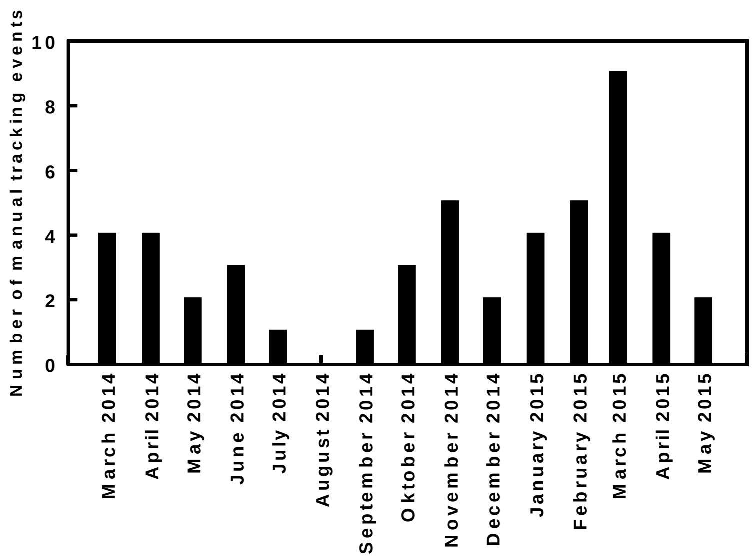


Figure 15 Number of manual tracking events through study

Another way of showing the activity of a fish was to calculate the home range used during the study period (Masters et al 2005). The home range can be defined as the longitudinal distance used by each pike during the study, i.e. the distance between the furthermost upstream and downstream location (Masters et al 2005). In this study the home range was related to the study area by calculating the proportion of the study stretch used by each pike.

Data from the VR2 receivers was also used in order to assess the diel activity made on a yearly basis, i.e. to investigate if the pike showed a diel activity pattern according to different seasons. It was assumed that the first and last time a pike was registered on a receiver was a result of movement since the pike must have either entered or left the range of the receiver. To gain knowledge of the diel activity patterns through the study period the time of the first and last registration (arrival and departure) on a receiver was extracted and divided into intervals of 24 hours. To make the calculation as simple as possible an arrival registration was defined as the first time a pike entered the range of another receiver than the receiver it left. A departure registration was defined as the last time a pike was registered on a receiver before it entered the range of another receiver. Thus, a departure registration was always linked to an arrival registration. The number of registrations at each hour was summed and divided into seasons in order to look for diel activity patterns.

The mean monthly activity of all pike during the study period was calculated by dividing the movements registered by a VR2 receiver or on a manual tracking into months. The movement made by a pike during each month was summed up and the mean for all pike was calculated as a general expression for the activity observed per month. The activity was not measured for the whole of the first and last months (March 14 and June 15) and therefore data was corrected to fit a whole month.

To give insight into the pike's movements in the two weeks of late summer where seven of the pike were last registered by a VR2 receiver the position in the river during these weeks were extracted. The pike were divided into groups that showed a similar behavior according to movements in the river. For the pike on the middle stretch that disappeared or were presumed dead and the pike on the middle stretch that survived a mean position in the river per day was calculated in order to show the general pattern of movement for the two groups.

24-hour trackings

The activity during the 24-hour trackings was calculated for each four hour period during the sampling. This was done by calculating the distance moved since the last manually tracking event and dividing this with the time gone. This gave an expression of the activity for each period in meters per hour. A 2-way ANOVA was made on the two pairs of 24-hour samples to test if it was okay to pool them. For the pike that participated in both measurements the average movement for each 4 hour period was calculated.

Habitat choice

In order to show the stretches occupied by the pike through the study an expression of the pike's position was needed. It was chosen to calculate a mean weekly position for each pike by taking the average of the positions a pike was registered at each week. If a pike was not registered in a week it was presumed that the pike was found on the stretch where it was last located. The river was divided into three parts: A lower (< 2000 m from sea), middle (2000-5450 m from sea) and upper (> 5450 m from sea) stretch. The divisions were made according to the appearance of the river on the different parts as well as in accordance to the position of the VR2 receivers making boundaries for the different stretches.

Statistical analysis

All simple statistics like t-tests and ANOVAs were carried out in GraphPad Prism 6. More complex statistical models were made in RStudio.

To assess if the transmitters affected the pike during the study the change in condition factor of recaptured pike with transmitters were compared with the change in condition factor of recaptured pike without a transmitter (see part 1) by using an unpaired t-test. The same test was used to test if there was a significant difference in the size of males and females as well as to test if the pike with a transmitter differed from the population in terms of length and weight.

Movements

To test whether the activity of the pike was biased by the frequency of manual tracking events two linear models were carried out. The first one tested whether the individual activity of a pike depended on how often it was found on the manual tracking events. The other one tested whether the monthly activity of the pike in general depended on the number of manual tracking events in a given month.

The possible time dependent effect of individual traits and physical parameters on the movement of pike was modeled in R-studio by a linear mixed model including a random individual effect to account for inter-pike variation and an additional Spatial Gaussian serial correlation structure to describe dependency between movement measurements that are close in time. All p-values corresponded to likelihood ratio tests and were evaluated at a 5 % significance level. First a model for the whole study period was made. Since temperature was the only physical parameter that was measured through the whole study the model consisted of the following parameters: sex, length, temperature, max. temperature, min. temperature, temperature^2, max. temperature^2 and min. temperature^2. After reducing this model the result was used to make the full model with all physical parameters. This model consisted of the parameters: sex, length, max. temperature, discharge, salinity at p.0, salinity at p.3000 and max. temperature^2.

Diel movements

The same method was used to look at the effect of individual traits (sex, length, condition factor) on the diel movement of pike but without the time effect included. In this model the parameters investigated were condition factor, length and sex. As a result of the effect of sex on the movement during the spring sample the model was used to test the effect of sex on a larger scale by only using movement data of pike from March 1st to April 30th. The model was also used to test whether there was a correlation between the diel and yearly activity of the individual pike. A 2-way ANOVA was used to test whether the time of day had an effect on the diel activity.

Habitat choice

To investigate which parameters affected the habitat choice of pike in the river different tests were carried out. First a multinomial logistic regression model was used to test whether there were differences in the number of pike on the three different stretches (lower, middle and upper) through time. Hereafter a generalized linear model was used to test which parameters affected the presence on each stretch. Since discharge and salinity data was not available for the whole study period two models were made: one for the whole study with temperature as the only physical parameter and one for a part of the study with temperature, salinity and discharge.

A one-way ANOVA was used to test if there was a difference in individual traits between three of the groups of pike (upstream, middle stretch surviving, middle stretch dead) which were found in the critical period in August. Furthermore pike were divided into surviving and dead pike in the critical period and Welch's t-test were used to test for differences in individual traits (weight, length and condition factor). This test assumes unequal variances between samples and allows for unequal sample sizes.

Results

Background

A range test of the three paired receivers in the river and the two receivers in the bay showed a range of about 100 meters in each direction (**Table 4**). Using a test-transmitter the range of the transmitters to the VR60 in the river was found to be more than 350 meters in each direction. It was possible to determine how close the pike were by listening to the signal received by the VR60. This method was tested in the river by blind testing of a similar transmitter to the one inserted in the pike and here the accuracy of the VR60 was found to be in a range of 13 meters in average.

Table 4: Range test of receivers

Receiver (position in river)	Distance downstream	% of signals received	Distance upstream	% of signals received
p. 5526	135 m	100 %	60 m	100 %
p. 5389	70 m	90 %	80 m	90 %
p.2899	135 m	70 %	*Not measured*	*Not measured*
p. 2818	130 m	80 %	85 m	70 %
p.155	85 m	100 %	85 m	100 %
p.82	70 m	100 %	120 m	100 %
Bay - S	200 m	100 %		
Bay - N	100 m	100 %		

Thirty pike were caught for the study (19 female, 11 male; TL: 63.5 - 118 cm; mean 83.3 cm, **Table 5**). The size of males and females were significantly different ($p < 0.05$). During the study four pike (#114, #116, #118 and #125) disappeared inside the study stretch. #114 disappeared at the upper stretch already in June. #125, #116 and #118 was last registered by a VR2 receiver in the beginning of August. However #116 and #118 was registered on two and one manual tracking event(s) respectively in September and October before disappearing completely. Four other pike (#119, #128, #138 and #142) were presumed dead since their signal was registered at the exact same spot over several months. In late May 2015 electro fishing was tried at the spots and when the signal did not move and no pike appeared they were presumed dead. The signal from the four pike still transmitted at the end of the study. Pike #124 were found dead by an angler after a period with very high salinities at the outlet in late August. The last registration on a VR2 receiver of the four pike that were presumed dead happened in the expand of eight days (29/7-2014 to 6/8-2014) and were all on the same receiver at p.2818. During the study 123 different individuals of pike from the river were continuously caught (see part 1). Thus, it was possible to model a relationship between weight and length. The 30 pike with a transmitter were plotted against this model to assess whether they were representative for the whole population (**Figure 16**). Furthermore un-paired t-tests showed that there was no difference in length and weight between the pike with a transmitter and the rest of the pike caught (p_{weight} = 0.2125; p_{length} = 0.3045, $n_{population}$ = 93). In order to asses any affect of the transmitters on the pike the change in condition factor of recaptured pike with a transmitter and recaptured pike without a transmitter was compared and found not to be different ($t = 1.3$; $DF = 17$; $p = 0.2111$, $\alpha = 0.95$, see Table 6).

Table 5 Overview of the 30 pike in the study

No.	ID	Sex	TL (cm)	Weight (kg)	Faith
1	115	F	87.5	5.79	
2	114	M	74.5	3.02	Disappeared, last registered June 10th at p.7565
3	116	F	80.5	4.03	Disappeared, last registered October 21st at p.3000
4	117	F	77	3.61	
5	118	M	77.5	3.77	Disappeared, last registered October 21st at p.3405
6	119	M	72	2.83	Presumed dead, last registered on a VR2 receiver August 1st at p.2818
7	120	M	76.5	3.83	
8	121	M	78.5	3.76	
9	122	F	71	3	
10	123	F	75	3.82	
11	124	F	92	7.4	Found dead August 24th at p.0
12	125	F	77.8	3.58	Disappeared, last registered August 4th at p.2818
13	126	F	96.6	7.75	
14	127	F	118	14.2	
15	128	M	82.6	4.09	Presumed dead, last registered on a VR2 receiver August 4th at p.2818
16	129	M	76.1	3.34	
17	130	F	63.5	1.93	
18	131	M	66.1	2.2	
19	132	F	73.9	3.33	
20	133	F	79.2	3.59	
21	138	F	80.2	3.95	Presumed dead, last registered on a VR2 receiver June 29th at p.2818
22	137	F	92.5	6.5	
23	134	F	94	6.05	
24	135	F	73.1	2.88	
25	136	M	77.2	3.37	
26	139	F	115.5	14.1	
27	140	F	110	11.31	
28	141	F	102.3	7.61	
29	142	M	79.5	3.65	Presumed dead, last registered on a VR2 receiver August 6th at p. 2818
30	143	M	77.9	3.63	

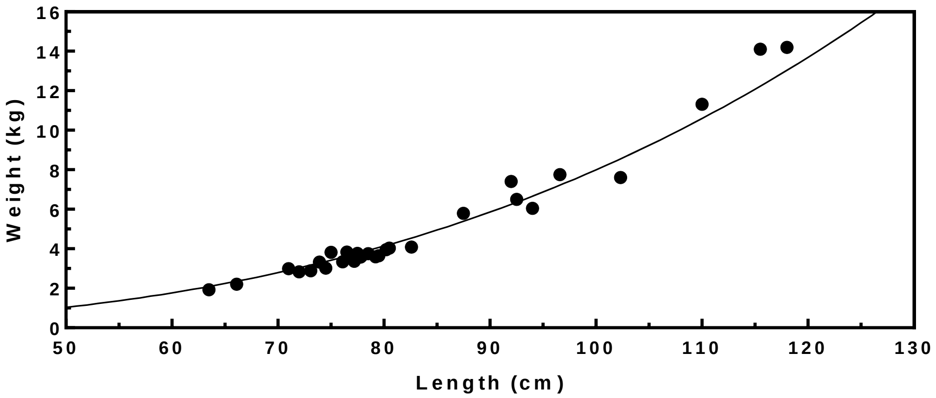


Figure 16: Weight/length relationship of the pike caught in River Tryggevælde. The 30 pike with a transmitter are plotted.

Table 6: Condition factor of pike with and without a transmitter caught in 2014 and recaptured in 2015.

With transmitter				**Without transmitter**			
Pike no.	**Condition factor 2014**	**Condition factor 2015**	**Change**	**Pike no.**	**Condition factor 2014**	**Condition factor 2015**	**Change**
1	0.864	0.750	-0.115	**43**	0.691	0.534	-0.157
4	0.791	0.733	-0.058	**60**	0.939	0.735	-0.204
7	0.855	0.832	-0.024	**61**	0.810	0.686	-0.124
9	0.838	0.776	-0.062	**62**	0.819	0.678	-0.140
10	0.905	0.928	0.022	**63**	0.915	0.870	-0.045
13	0.860	0.644	-0.216	**65**	0.781	0.857	0.076
16	0.758	0.759	0.001	**66**	0.839	0.732	-0.107
23	0.728	0.635	-0.093	**109**	0.826	0.811	-0.015
24	0.737	0.815	0.077	**113**	1.080	0.947	-0.133
30	0.768	0.801	0.033				
Mean	0.810	0.767	-0.044	**Mean**	0.856	0.761	-0.094
Std. dev.	0.058	0.082	0.081	**Std. dev.**	0.104	0.117	0.080

Environmental factors

The spring and summer in 2014 was very warm and the mean water temperature in the river reached a maximum of almost 25 ^{O}C in August (**Figure 17**). The winter was relatively mild with only one short cold period in late December. Spring 2015 was colder than 2014 and the mean temperature was generally 5 ^{O}C lower than the same time the year before. The discharge was very low until the fall of 2014. From the regularly pulses of discharge was seen with the maximum being approximately 18 m^3/s (**Figure 17**). The salinity at the sluice was generally high in 2014 and reached a maximum of approximately 17 ‰ in late August (**Figure 18**). The salinity was generally low during the winter and rose to a higher level again in spring 2015. The salinity at p.3000 was affected by the high salinity at the sluice in the last half of 2014 and reached a maximum of more than 10 ‰ (**Figure 18**). From the last months of 2014 the salinity generally was very low at this point. The oxygen level in the river was low when the sampling began in September 2014. The mean was 35 % but the lowest point measurement showed 12 % on the middle stretch. From September and forwards the oxygen level rose to a mean of about 80 % (**Figure 19**).

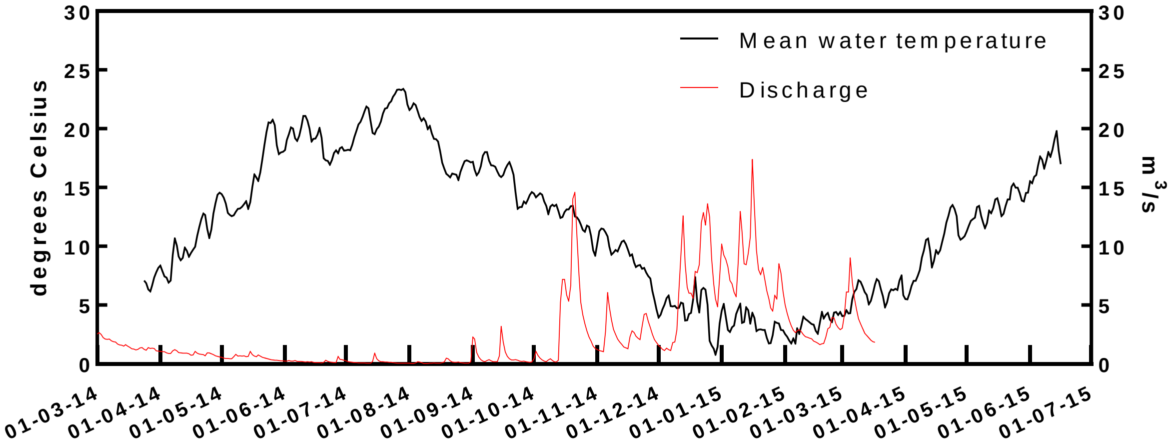


Figure 17: Mean water temperature and discharge in the river.

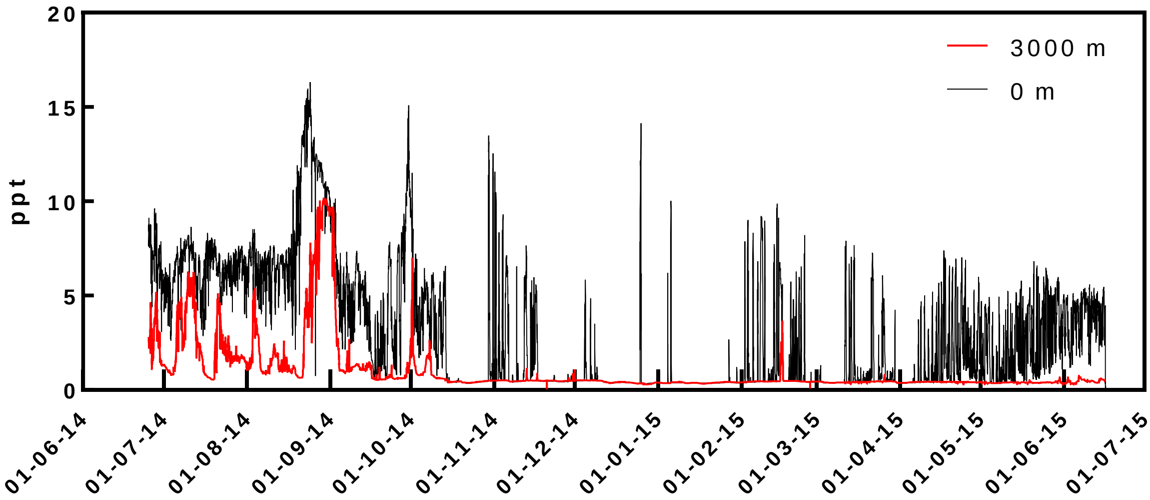


Figure 18: Salinity in the river at p.3000 and p.0.

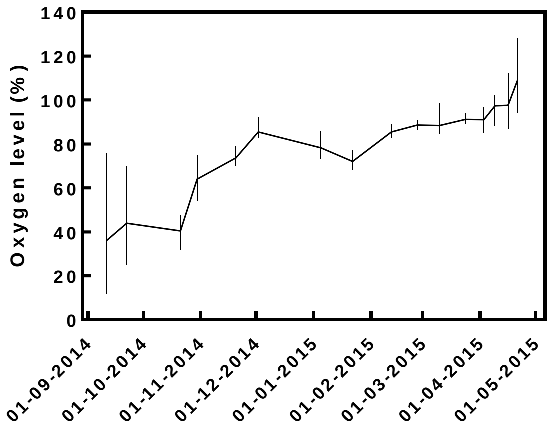


Figure 19: Mean oxygen level in the river from point measurements with min. and max.

Movements

The movements made during the study varied widely between individual pike (see Appendix A). Some pike were positioned in the same areas for longer periods (e.g. #121 & #129, see **Figure 22**) while others were more mobile and almost seemed hyperactive in their movements (e.g. #115 & #127, see **Figure 23**). Pike with a more intermediate movement level was also found (e.g. #126 & #130, see **Figure 24**) yet others were generally static but moved far distances in short time occasionally (e.g. #120 & #122, see **Figure 25**).

The mean daily activity for each individual pike that survived through the whole study showed a general activity between 143.6 and 748.1 m/day (mean = 352.8 m/day, **Table 7**). The distribution of the activity shows an even distribution between the thirty pike with #115 as a single outlier (**Figure 20**). The larger pike of more than 80 cm was located in the upper two-thirds of the distribution (the possible effect of length on movement is tested further down). The home range of the surviving pike were between 5526 and 12404 m (mean = 7382.6 m) corresponding to 44.6 - 100 % of the studied river stretch (**Figure 21**). Not all pike were found on every manual tracking event but a linear model showed no correlation between the number of times registered on a manual tracking event and the calculated activity per day (linear model, p = 0.48). This showed that the activity of the individual pike did not depend on how often it was tracked on the manual tracking events.

Table 7: Mean daily activity in m/day for the 21 pike that survived through the whole study.

Pike ID	Mean daily activity	Pike ID	Mean daily activity
115	748.1 m	**131**	297.0 m
117	348.0 m	**132**	151.8 m
120	265.2 m	**133**	510.7 m
121	171.9 m	**134**	360.2 m
122	183.2 m	**135**	213.1 m
123	497.6 m	**136**	186.7 m
126	465.4 m	**137**	264.9 m
127	534.2 m	**139**	545.0 m
129	143.6 m	**140**	263.9 m
130	347.9 m	**141**	472.7 m
		143	438.5 m

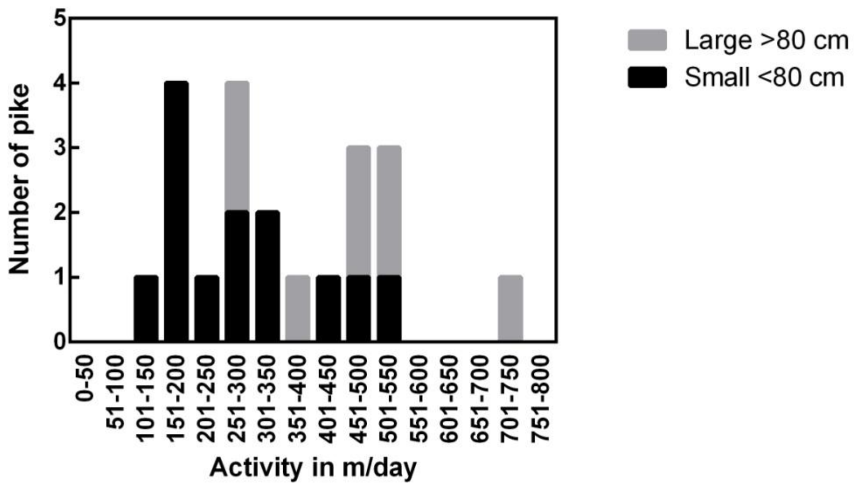


Figure 20: Distribution of the mean activity through study.

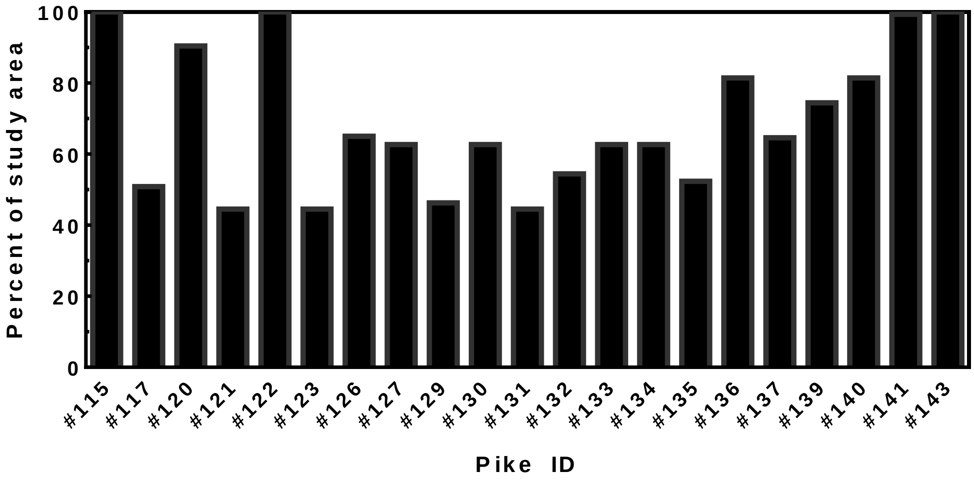


Figure 21: Home range in percent of study area for the 21 pike tracked during the whole study.

#121
Male
78.5 cm
3.76 kg.

#129
Male
76.1 cm
3.34 kg.

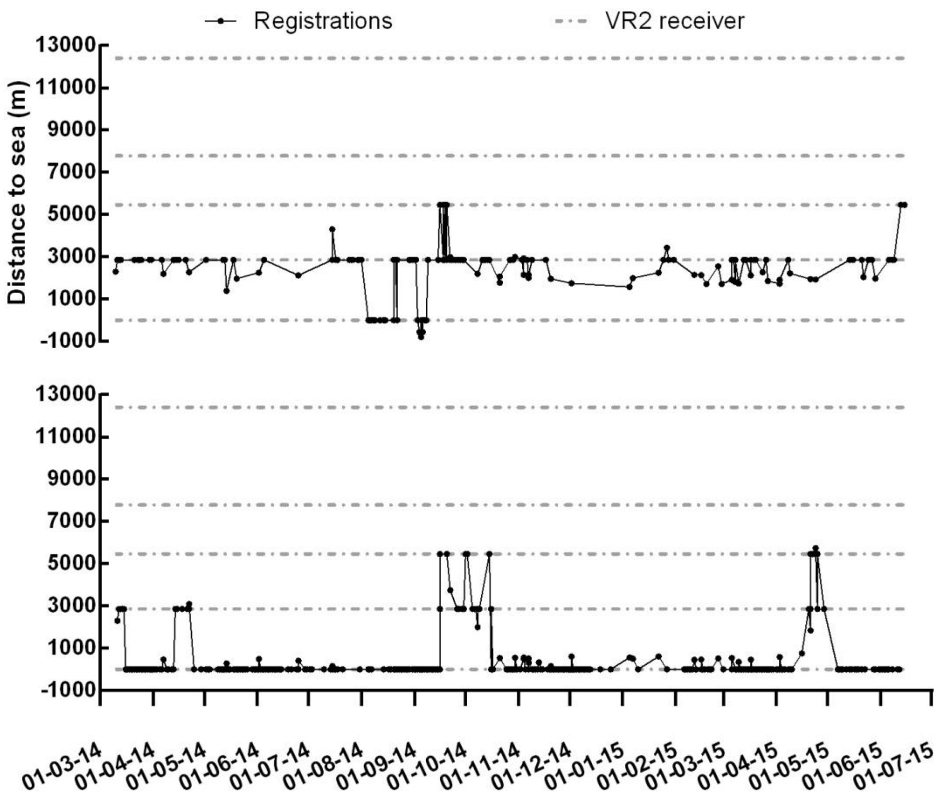


Figure 22: Position in the river for two mainly stationary pike.

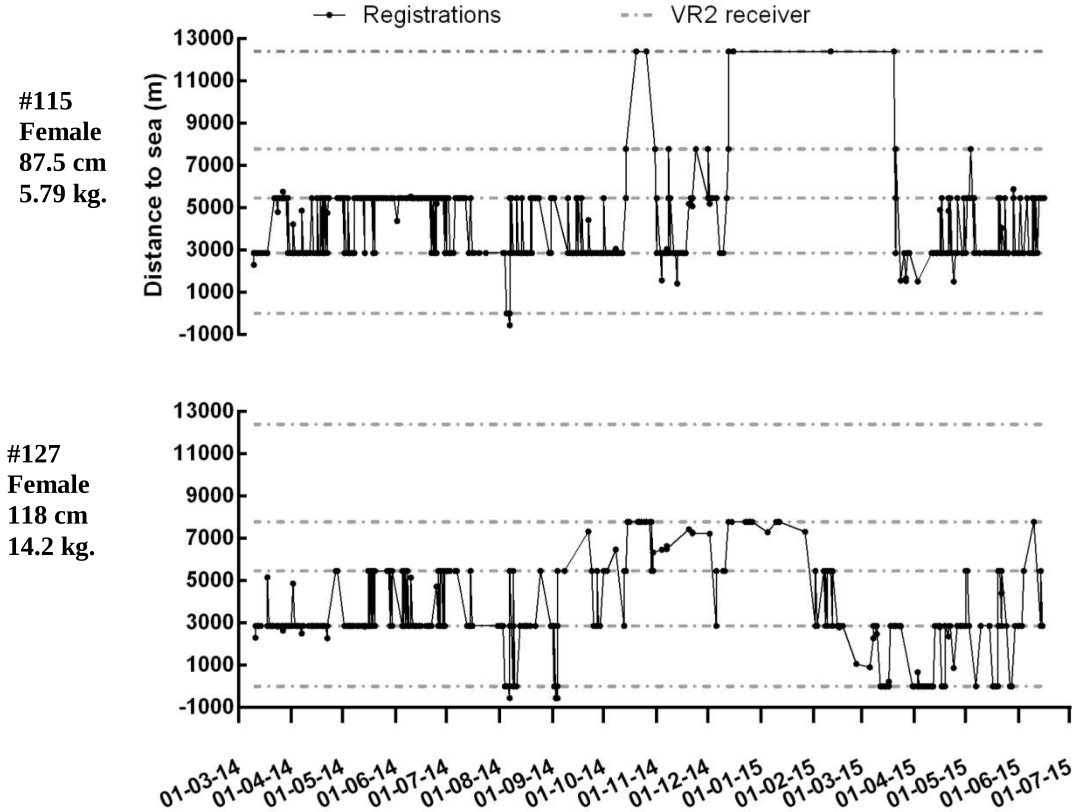


Figure 23: Position in the river for two mainly active pike.

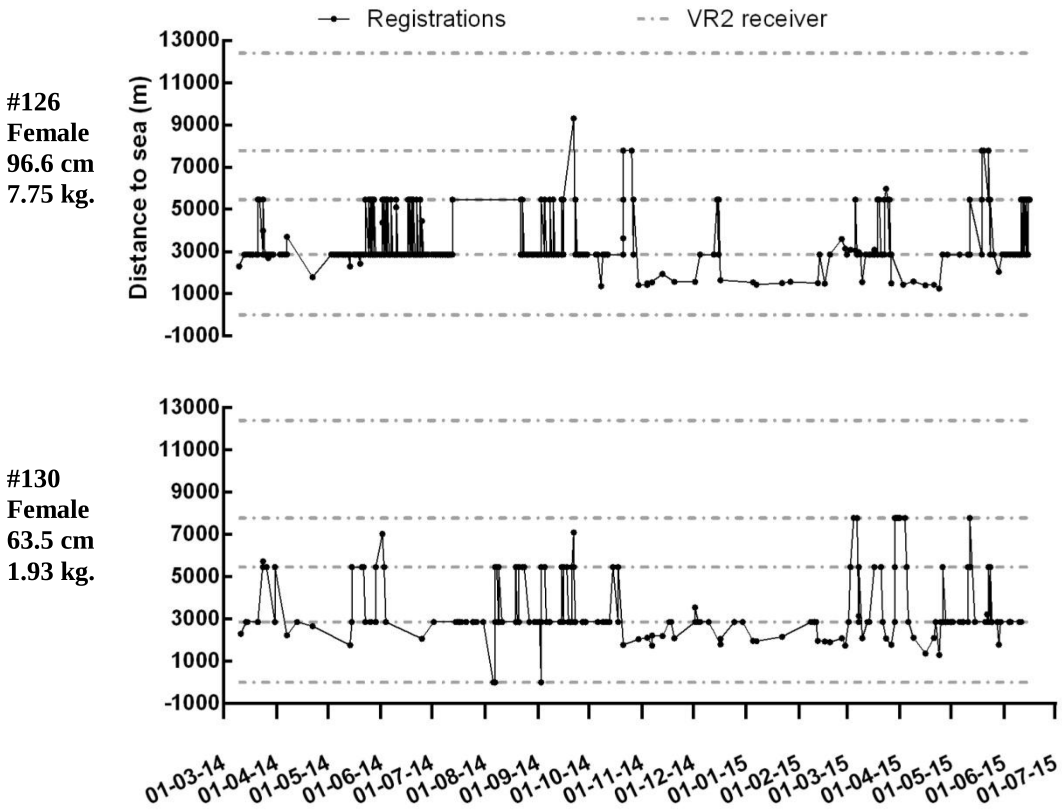


Figure 24: Position in the river of two pike with changing activity levels.

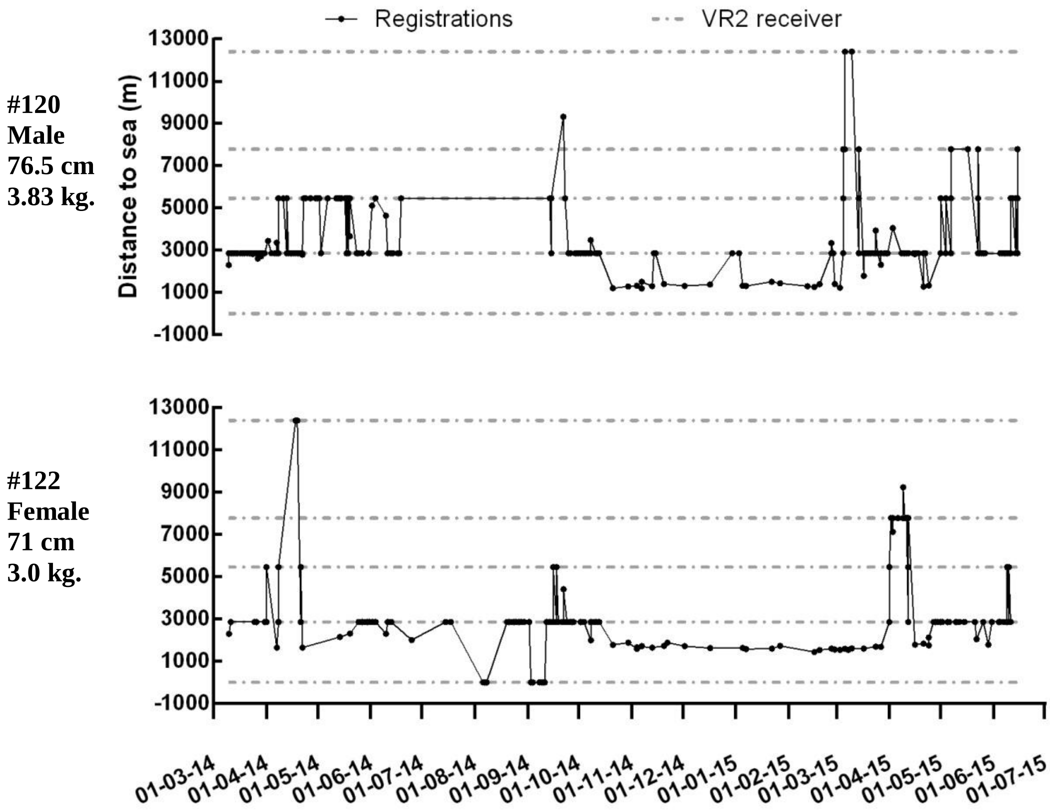


Figure 25: Position in the river of two mainly stationary pike which occasionally travels large distances.

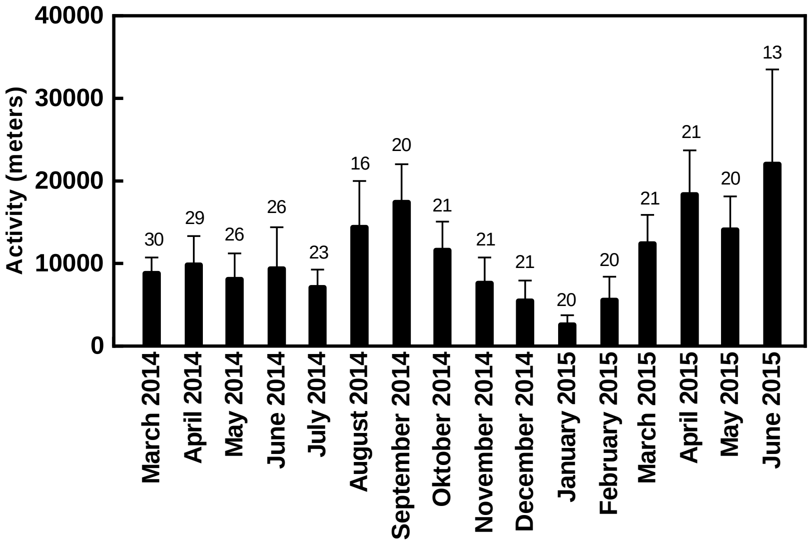


Figure 26: Mean activity in meters for each month through the study with 95 % CL. Number above bars equals sample size.

The mean activity through the study varied between months. Generally it seemed that the pike were more active with increasing temperature. However the activity in May - July 2014 was low which maybe was caused by a decrease in the activity when the temperature was too high (**Figure 26**). The manual tracking events varied between months e.g. due to the heavy vegetation cover during summer. A linear model showed that there was no correlation between the number of manual tracking events and the activity for each month (linear model, $p = 0.12$).

The first model used to investigate the possible time dependent effect of individual traits and physical parameters on the movement of pike showed that movement depended on max. temperature and max. temperature^2 (Max. temperature: estimate coefficient = 2886.92, $p = 0$; Max. temperature^2: estimate coefficient = -96.72, $p = 0$). The maximum of the second degree polynomial created by plotting movement against max. temperature^2 was found to be 16.76 ^{O}C which means that movements peaked at this temperature. This result was transferred to the second model which showed that the movement in the period where all physical parameters were measured depended on max. temperature, max. temperature^2, salinity at p.0 and salinity at p.3000 (Max. temperature: estimate coefficient = 2782.97, $p = 0$; Max. temperature^2: estimate coefficient = -116.1, $p = 0$; Salinity at p.0: estimate coefficient = 4338.9, $p = 0.0045$; Salinity at p.3000: estimate coefficient = -7469.9, $p = 0.032$, see Appendix B).

Diel movements

Data of the arrival and departure of a pike to a receiver was extracted and divided into different seasons (**Figure 27**). A diel pattern was seen for winter (December-February), April/May, June/July and October/November. In winter the registrations were most numerous at day time. The same was the case at April/May where a peak at dusk is apparent. Furthermore this period had many more registrations compared with the other three periods. At June/July the peak was found at late night and at sunset while the numbers of registrations were lowest at midday. At October/November there seemed to be a peak at dusk and dawn. It is worth to mention that all samples show some degree of nightly activity.

The two 24-hour samples for winter and spring respectively was pooled (2-way ANOVA; $p_{winter} = 0.46$, $p_{spring} = 0.19$). The activity during the periods in the diel trackings in winter and spring show movements in all periods (**Figure 28**). There are huge variations between individuals which causes the relative large standard deviations. There were no significant difference in the diel activity and time of day in neither of the samples (2-way ANOVA, Winter: $p = 0.26$, Spring: $p = 0.23$). Generally the diel movements show a considerable movement on a smaller scale by the pike (mean of 520 - 897 m/day). This is 4 and 3 times larger than the general activity found for the same pike in the same period (February: 130 m/day; March: 297 m/day).

Individual variation

A significant difference was found between the individuals in both 24-hour samples (2-way ANOVA, Winter: $p < 0.0001$, Spring: $p < 0.05$) indicating that the individual variation between pike is much larger than the timely variation. For both the 24-hour winter and spring measurement it was tested whether there was a correlation between the diel activity (found on 24-hour trackings) and the general activity (found with VR2 receivers and manual tracking) of the individual fish (**Figure 29**). This was done to find out if the activity of an individual pike found on a smaller scale were representative of the activity of the same pike found on a larger scale. The test showed no significant correlation between the diel and yearly activity (linear model, Winter: $p = 0.14$, Spring: $p = 0.84$). Thus, the distance moved during the diel tracking was not proportional with the general activity. In other words pike that were active during the diel tracking were not necessarily considered active on a yearly basis.

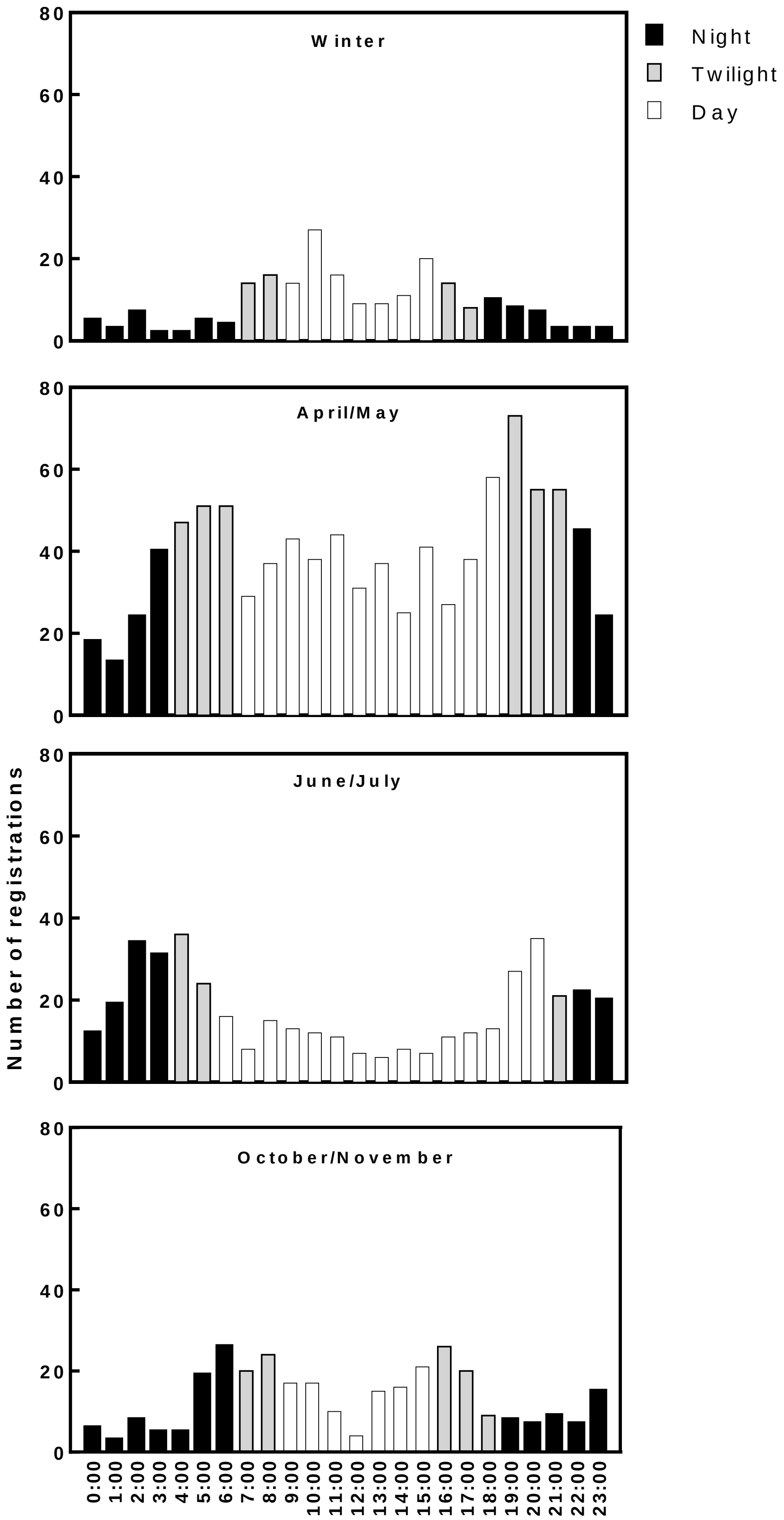


Figure 27: Number of registrations at an hourly interval in different seasons based on registrations from stationary VR2 receivers.

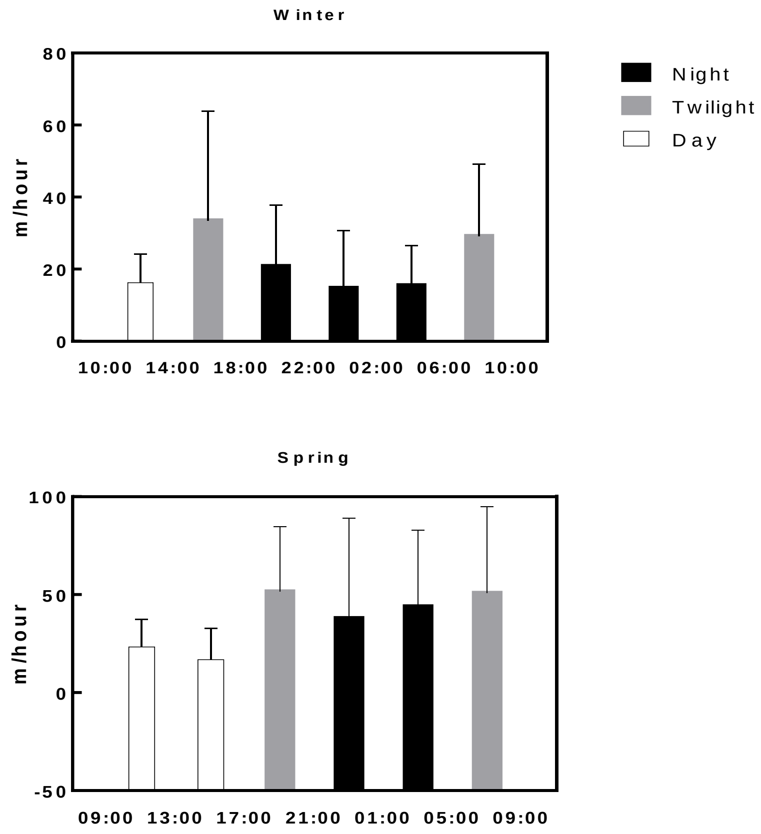


Figure 28: Diel activity measured on 24-hour trackings during winter and spring.

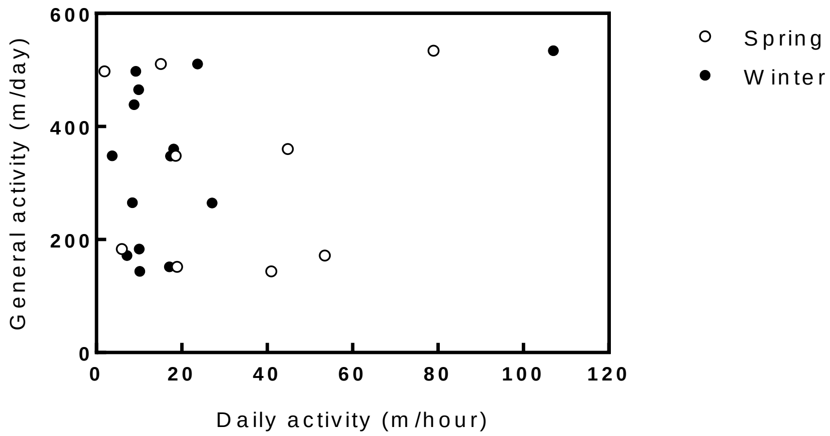


Figure 29: Correlation between general activity and daily activity found in winter and spring.

It was tested if any of the individual traits had an effect on the diel activity. In the winter sample it was found that the length had a significant positive effect on the diel activity (estimated coefficient = 1.4499, $p < 0.01$) indicating that larger pike were more active than smaller. For the spring sample it was found that both sex and length had a significant effect (Sex: estimated $coefficient_{male}$ = -74.799, $p_{male} < 0.01$, estimated $coefficient_{female}$ = -106.324, $p_{female} < 0.001$; Length: estimated coefficient = 1.5789, $p < 0.001$) again indicating an increasing activity with increasing length but also a difference between sexes where male pike moved more than female pike. This trend between sexes was assessed on a larger scale but the activity measured by the VR2 receivers and manual tracking events (1/3 -2015 - 30/4-2015) showed no effect of sex on spring activity ($p_{male} = 0.413$, $p_{female} = 0.107$).

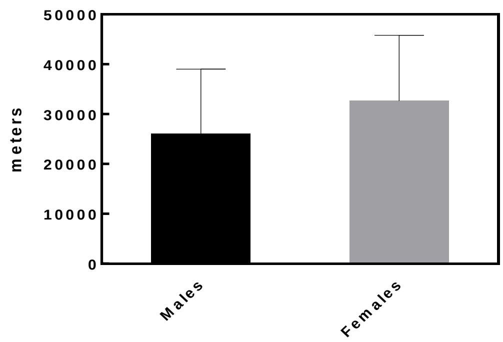


Figure 30: Spring activity (March 1st - April 30th - 2015) in meters moved for males and females.

Habitat choice

A variation in the occupancy of the different stretches was seen through the study (**Figure 31**). In late June - August eight pike are registered on a VR2 receiver for the last time and five of these are presumed dead (only one were found). The water temperature in the river is very high and the oxygen level is presumed very low. At this time very few of the pike are located on the middle stretch while several are found at the lower stretch towards the sea. This is followed by a period where almost no pike are located on this stretch. Later on when the water temperature drops it seems that several pike are gathered on the lower stretch. A large proportion of these were found on the same 500 meters of river week after week. This stretch stood out by being the only extended part of the river surrounded by trees on both sides. The pike on the lower stretch seems to move to the middle stretch of the river when the water temperature rises during spring. Furthermore it seems that the number of pike on the upper stretch increases during the warmer months. In general the pike primarily was found between p.0 and p.9000. Only in 2.5 % of the weekly positions the pike were found further upstream than p.9000.

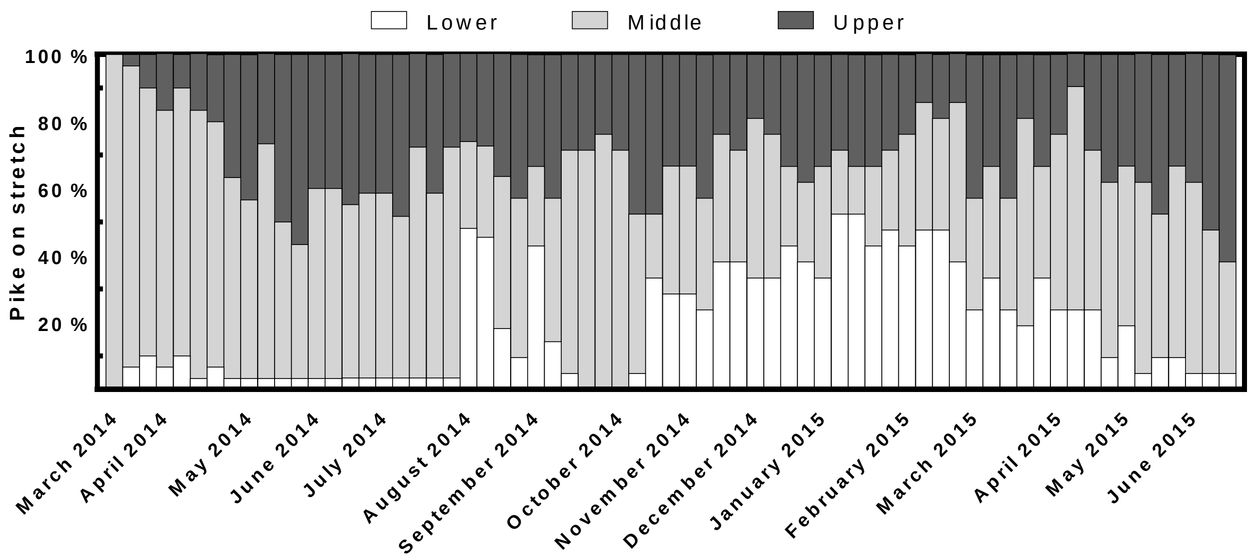


Figure 31: Frequency distribution of pike on the upper (> 5450 m from sea), middle (2000 - 5450 m from sea) and lower (< 2000 m from sea) stretch pr. week

The multinomial logistic regression showed a significant difference in the presence of pike on different stretches ($p = 0$). This justified making a model for each stretch separately.

For the lower stretch it was found that the presence of pike depended negatively on temperature and length (Temperature: estimate coefficient = -0.0997, $p < 0.001$; Length: estimate coefficient = -0.0272, $p < 0.001$, see Appendix B). This indicates that smaller pike are more likely to be found on the lower stretch and that the frequency of pike on the stretch increases with decreasing temperature (**Table 8**).

For the middle stretch a positive correlation of condition factor on presence were found (estimate coefficient = 527.18, $p < 0.001$). Furthermore a negative correlation of length and sex were found (Length: estimate coefficient = -0.0379, $p < 0.001$; Sex_{Male}: estimate coefficient = -0.7335, $p < 0.001$, see Appendix B). This indicated that smaller pike and pike with a higher condition factor were most likely to be found on this stretch. Furthermore it was more likely that the pike present on this stretch were male pike (**Table 8**).

A positive correlation of temperature, length and sex were found on the upper stretch (Temperature: estimate coefficient = 0.0690, $p < 0.001$; Length: estimate coefficient = 0.0634, $p < 0.001$; Sex_{Male}: estimate coefficient = 0.762, $p < 0.001$, see Appendix B) as well as a negative correlation of condition factor (estimate coefficient = -802.9, $p < 0.001$). This indicates that pike were more likely to be on this stretch when temperatures in the river were high. Furthermore larger pike were more likely to be on the stretch but generally with a lower condition factor. Female pike were more likely to be found on this stretch as well (**Table 8**).

In the models where salinity and discharge were included a positive correlation of discharge on the presence on the middle and upper stretch were found (Middle: estimate coefficient = -0.0611, $p < 0.05$; Upper: estimate coefficient = 0.07835, $p < 0.05$) indicating that pike moved from the middle to the upper stretch with increasing discharge.

Table 8: Correlation of different parameters on different stretches. * for p < 0.001 and * for p < 0.05. NS = Not significant.**

	Lower	Middle	Upper
Increasing temperature	**Negative*** **	NS	**Positive*** **
Increasing length	**Negative*** **	**Negative*** **	**Positive*** **
Sex (male)	NS	**Positive*** **	**Negative*** **
Sex (female)	NS	**Negative*** **	**Positive*** **
Increasing condition factor	NS	**Positive*** **	**Negative*** **
Increasing discharge	NS	**Negative***	**Positive***

Critical period in August

Seven pike were last registered by a VR2 receiver from June 29th to August 6th. Of these three disappeared and four were presumed dead. All of them were last registered by a VR2 receiver at about p.2800. The movement of the 29 pike that were alive in the time leading up to this period was investigated and a clear pattern was found. At the period with critical conditions on the middle stretch eight pike were located at the upper stretch and did not seem to be affected (#120, #126, #133, #136, #137, #139, #140 and #141). Pike #129 was registered at the lower stretch and seemed neither to be affected. The rest were located at the limit between the middle and upper stretch at p.4000 - p.6000. Of these remaining 20 pike thirteen moved downstream to the lower stretch and survived. Seven did not move downstream which resulted in the death of four and the disappearance of three (**Figure 32**). No difference in neither weight, length, age nor condition factor were found between the three groups (upstream (n=8), middle stretch surviving (n=13) and middle stretch presumed dead (n=4)). If the pike were pooled in groups of surviving (n=21) and dead (n=4) a significant difference in weight ($p = 0.0217$) and condition factor ($p = 0.002$) were found. This means that the 21 pike that survived the critical period in August were heavier and had a higher condition factor than the dead.

Pike in the bay

From March 2014 to December 2014 eight pike were registered in the bay (#115, #121, #123, #124, #127, #132, #135 and #143, **Figure 33**). The movements into the bay happened during two periods. First at August 7th were five pike moved to the bay and went back into the river the same day. Later from September 3rd to September 6th when four pike visited the bay. Pike #127 were the only one that visited the bay in both periods. The longest time a pike was in the bay was three days (#121). Data from the whole of 2015 were lost due to theft of the receivers but examination of the data from the receivers at the outlet showed that only one pike theoretically could have moved to the bay for nine hours in 2015.

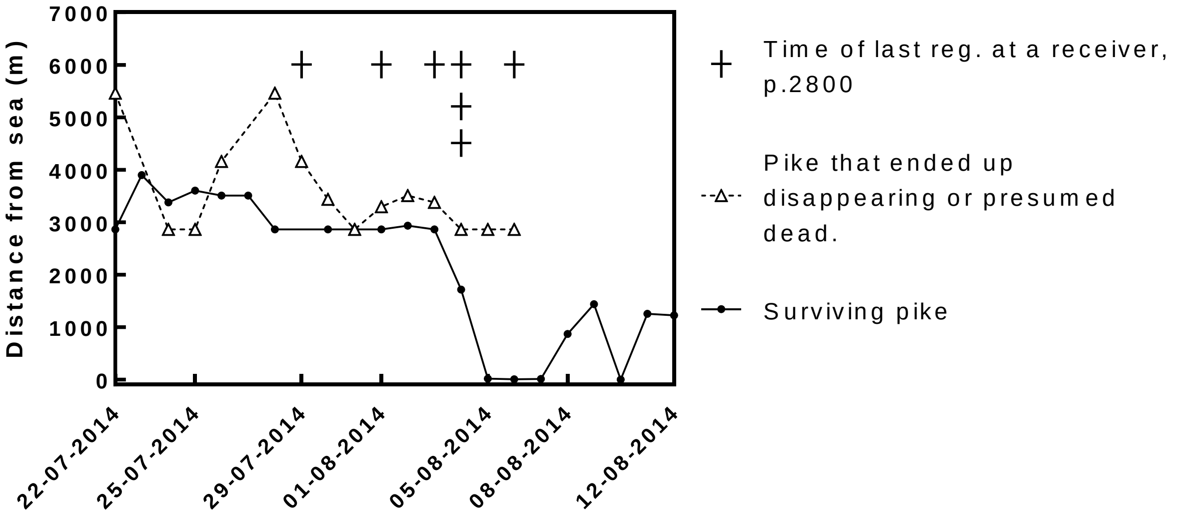


Figure 32: Movement pattern (mean position) of pike that survives and pike that end up disappearing or presumed dead. Crosses indicate the last time one of the dead or disappearing pike are registered on a VR2 receiver at p.2800 and only relates to the x-axis.

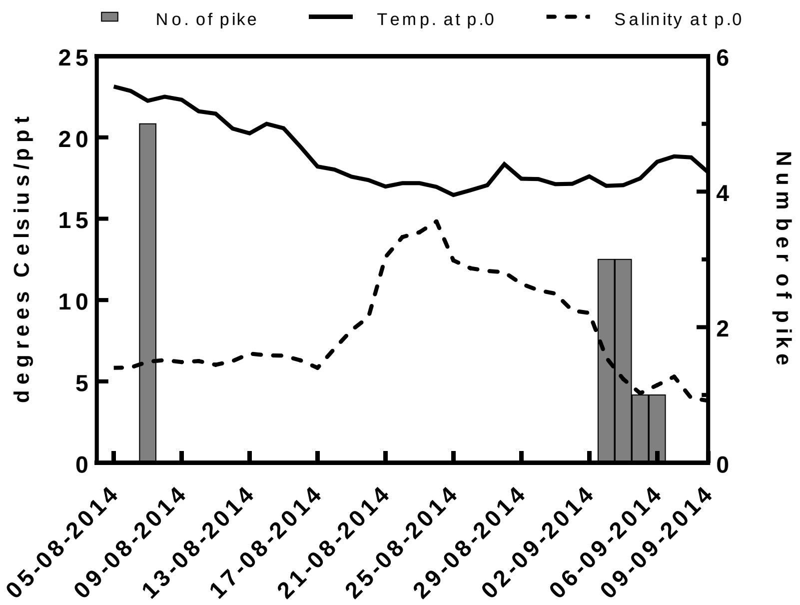


Figure 33: Number of pike in the bay + temperature and salinity.

Discussion

Movements

During spawning time movement rates of pike could be caused by the pike searching for conspecifics or suitable spawning areas (Koed et al 2006, Pauwels et al 2014). Outside spawning time movements are often considered as a result of feeding activity (Beaumont et al 2005, Kobler et al 2008, Baktoft et al 2012). However movements could also be caused by the pike avoiding or searching specific environmental conditions or avoiding conspecifics due to cannibalism and competition (Nilsson 2006b).

The difference in mean daily activity between the thirty pike in River Tryggevælde was found not to be caused by the variation in manual registrations for each pike. The mean daily activity found in this study is more than what was found by Koed et al (2006) in the Danish River Gudenå where the pike generally moved less than 100 meters per day during the study. The activity of the pike in River Tryggevælde is very similar to the results found in a Belgian river by Pauwels et al (2014) who generally found that the pike moved less than 500 meters per day with an average very similar to the one found in this study. It must be stressed that the activity found in this study as well as in the ones made by Pauwels et al (2014) and Koed et al (2006) is an expression of the minimum distance moved by the pike. The activity is measured from the registrations of the pike and therefore any movement in between two trackings (manual or stationary) will not contribute to the activity measure. A study in a Danish lake made by Baktoft et al (2012) used stationary receivers that covered the whole lake and thereby gave a more correct estimate of the activity. The activity found by Baktoft et al (2012) is 2 - 4 times greater than the activity found in this study. Since the estimate made in this study is on a much coarser scale it could indicate that the pike in River Tryggevælde are at least as moving as the one in the study made by Baktoft et al (2012). This is supported by the diel trackings which showed a considerable movement on a smaller scale by the pike which possibly would increase the general activity 3-4 times. The home range of the surviving pike was larger than the general home range found in other studies of river pike. These have typically found a home range of 500 - 3000 meters with the maximum being about 10000 m (Ovidio & Philippart 2003, Masters et al 2005, Koed et al 2006). It is interesting that each pike in River Tryggevælde seems to use such a large part of the river. This supports the theory that a large proportion of the river is to be considered as suitable habitat (see part 1).

The activity of the pike in this study shows an even distribution of both daily movement and home range between the thirty pike. This agrees with other findings (Ovidio & Philippart 2003, Masters et al 2005, Rasmussen 2007) which also showed that the pike could not clearly be divided into sedentary and mobile individuals but instead covered the whole activity scale. The pike showed no sign of spawning migrations and the movements during spawning did not stand out as particularly active months. Thus, it is likely that the movements made by the pike are caused by feeding activity, environmental factors and avoidance of conspecifics. The impacts on habitat choice of the two latter are discussed further below. If the pike in the river purely adapted a sit-and-wait strategy when hunting it would be expected that the pike generally was positioned at the same place in the river for longer periods. This would only be disturbed when the pike moved due to environmental factors, conspecifics or change of ambush site. However several of the pike show periods where they regularly moves several kilometers back and forth. It is likely that this behavior is caused by the pike following shoals of prey fish or actively hunting to increase the chance of encountering prey. It seems that the pike in the river, at least in some periods, choose to adapt a different and more active hunting strategy than the sit-and-wait strategy often related to pike (Craig 1996, Berg 2012). Indications of this have been found in other studies as well (Turesson & Brönmark 2004, Baktoft et al 2012) and show that the pike does not necessarily depends on the prey fish to enter the range of their ambush site. This active hunting strategy could be caused by a clustered distribution of the prey fish as well as the prey fish moving a lot. This would mean that no prey fish may be present at a chosen ambush site for a substantial amount of time. If it was possible somehow to follow the movements made by the large shoals of prey fish in the river it would be very interesting to see how it was correlated with the movements made by the pike.

Influence on environmental factors on movement

Pike movement depended on max. temperature and max. temperature^2. Movements peaked at 16.76 ^{O}C and decreased with temperatures higher or lower than this. This corresponds well with other studies which found that high temperatures inhibited pike activity (Vehanen et al 2006, Rasmussen 2007). The temperature for maximum activity found in this study agrees with the findings by Casselman (1978) who *in situ* found the highest activity (from CPUE) at 15-17 ^{O}C and a much lower activity when temperatures exceeded 19 ^{O}C . It is likely that the increasing movement with rising temperatures is caused by the food demand being greater which could make the pike switch from a sit-and-wait strategy to a more active hunting strategy. Furthermore it may be that the substantial vegetation cover in the river decreases the range for prey detection at an ambush site in a degree where it is more beneficial for the pike to hunt actively (Turesson & Brönmark 2007). The decrease in activity at temperatures above 16.76 ^{O}C could be linked to decreased food consumption which have been shown to occur at temperatures above 19 ^{O}C (Craig 1996). Moreover it should be noticed that large parts of the river seemed devoid of prey fish during the warmer months. It makes sense that the pike does not move as much if feeding activities decreases. Furthermore rising temperatures increases the pike's oxygen demand which may cause it to move less. It is even possible that the pike are capable of finding smaller areas with better environmental conditions such as cooler water which would decrease the metabolism (Headrick & Carline 1993). This too would result in the pike being less active. The decreasing movement with decreasing temperatures is similar to the result found by Casselman (1978) who showed that pike were significantly less active at temperatures below 6 ^{O}C than at temperatures greater than 9 ^{O}C. Likewise several studies have found a lower activity in winter compared with summer (Cook & Bergersen 1988, Ovidio & Philippart 2003, Vehanen et al 2006, Kobler et al 2008). Coupled with the fact that pike has a lower metabolism in cold water (Diana 1979) this corresponds well with the assumption that movements often are linked to feeding activity.

A positive effect on movement of salinity at p.0 indicated that the pike increased their activity when the salinity increased. This could be due to the pike moving away from high salinities but the model of habitat choice did neither show a negative or positive correlation with salinity and the frequency of pike on this stretch (see below). Therefore it is also likely that the increased activity is a response to changing conditions following the increasing salinity. A possible explanation could be that new prey fish entered the river from the bay when saline water was pushed into the river making the pike more active because of increased foraging. The negative correlation with salinity at p.3000 seems strange since the salinity levels are strongly correlated which their impact on movement should be too. It does not really make sense that a rising level of salinity at p.3000 should mean a lower activity of pike when the exact opposite is found a p.0. It is difficult to explain this but since the salinity range at p.3000 is much smaller compared with the salinity at p.0 it could just be a coincidence and not a real effect.

It must be stressed that the model used here can't include missing values and therefore assume that months with no detections equal no movement of that particular pike. This is a possible bias since months without detection often was caused by the pike being on a stretch of the river that was not accessible to track due to vegetation. Especially larger pike were located at the upper stretch and this could be the reason why no effect of size was found in this study.

Diel movements

The data of arrival and departure of pike to a receiver showed tendencies towards diel patterns according to season. Because data consists of counts of registrations it is not possible to test the significance of the patterns found. If the movements does not depend on the time of day it would be expected that the counts were evenly spread out through the day. Thus, the patterns found may not be possible to test but still gives insight to the possible diel activity patterns displayed by the pike. A similar analysis has been carried out on data from PIT-stations in Sweden (Engstedt 2011). The registration at winter (**Figure 27**) showed almost no nightly activity which could be due to the water being coldest at this time. Instead most of the registrations were spread out during the day with peaks a couple of hours after sunrise and a couple of hours before sunset. This supports the findings by Cook and Bergersen (1988) and corresponds well with the angling records at the river which often showed bite times in winter at these times of day. The registration of April and May (**Figure 27**) show a large increase in nightly registrations which could be due to the higher nightly temperatures at these months compared with winter. A small peak is seen around dawn and at late morning and a large peak is seen at dusk. This is very likely to be caused by the change in light intensity which has been found to affect the activity of pike (Cook & Bergersen 1988, Baktoft et al 2012). The number of registrations in April/May is much larger than the other three periods but this is mainly caused by the fact that data for both 2014 and 2015 were available for these two months. In June and July (**Figure 27**) the diel pattern is turned around with few registrations during day maybe caused by the water being at its warmest here. Again a peak around dusk is seen but interesting a large peak before and at dawn is also seen. This again could be related to the change in light intensity at these periods. At October and November (**Figure 27**) it seems that the nightly activity starts to decrease again. There are obvious peaks at both dusk and dawn while the number of registrations reaches a minimum at midday. Nights at October and November are cold and therefore it is interesting that a peak is found at both dusk and dawn. This indicates that it is most likely light that affects the pike. If the pike's diel activity also were heavily affected by temperature it would be expected that there would only be a peak at dusk where the water is at its warmest. Generally these data agrees with other studies which found a change in diel patterns between seasons and that pike had activity peaks at dusk and dawn probably caused by optimal hunting conditions when light intensities were low (Beaumont et al 2005, Kobler et al 2008, Baktoft et al 2012).

The indications of a diel activity pattern could not be shown during the diel trackings. These did not find a significant difference in the activity of pike and time of day. Instead a significant difference between individual pike was found which meant that the individual variation was much larger than the timely variation. The result could be due to a small sample size of two periods or the timely scale being too large (four hour intervals). With four hours between each tracking it was possible for the pike to move from a resting site and being active on a smaller scale before settling on the same resting site without being noticed. However it was not possible to track on a smaller scale since every manual tracking event lasted two hours and there needed to be time for resting too.

The two ways of showing a possible diel activity pattern is very different. The analysis of registrations is based on data from the whole study period which makes it possible to show the more general patterns that are displayed on a larger scale. However this may only tell something about the more active pike since pike that only moves smaller distances have a great chance of not being included at all. This could mean that the activity patterns found by this analysis only applies to the more active pike. The 24-hour analysis is on a much smaller timely scale but is more detailed and standardized since the position of every pike is tracked on a regular basis. However this also causes a large variation between individual pike and may include pike which are not active at any point during the trackings. This may blur the general pattern so no effect of time is shown.

Individual variation

No correlation was found between the individual pike's diel activity from the 24-hour trackings and the general activity measured from the VR2 receivers and manual trackings which could have several explanations: Either the pike have a variable activity pattern which means that one pike can vary a lot in its movements from day to day and does not exhibit a steady movement pattern. This was found by Rasmussen (2007) in a Danish lake. It could also be caused by the movements on a smaller scale contributing with a large and important part of the total activity so the yearly activity found on a larger scale is not fully representative for the activity of the individual pike. Estimations showed that the small scale movements possibly would increase the general activity 3-4 times. This is of course some but at the same time not surprising with the coarse scale of this study's design in mind. Furthermore this would only be an important bias if the level of underestimation varies between pike.

No effect of individual traits was found on a larger scale but in both of the diel trackings an effect of length on the activity was found. A tendency towards this was also apparent when dividing the general activity into pike of more and less than 80 cm. Here it seemed that the larger pike generally moved more than the smaller. This is similar to the results found in other studies (Masters et al 2005, Vehanen et al 2006, Kobler et al 2008) and is often explained as a consequence of the larger fish being less in risk of predation which means they can move around more freely. The possible reason to why this was not found on a larger scale is discussed earlier. The results from the diel trackings show that there possibly is a correlation between the movement and size of a pike where larger pike tends to move more. This could explain the increase in condition factor with increasing length found in part 1: If large pike can move around more freely they only have to focus on feeding and are able to exploit the feeding opportunities better. Furthermore as a large sized top predator they are capable of eating almost anything they come across in the river.

The diel measurements in spring showed an effect of sex on the movement of pike where male pike moved more than female pike. This effect was not apparent on a larger scale and since the sample size of males in the diel measurements was small (n = 2) it is likely that this result is not representative for the population as a whole.

Habitat choice

The pike were more often found on the lower stretch when the water was cold while they were more likely to be found on the upper stretch when the water was warm. This could be caused by differences in the physical parameters. In summer the water is generally colder further upstream and it would be expected that the pike would seek colder water when the water temperature exceeds 20 ^{O}C (Headrick & Carline 1993). Furthermore the velocity in the river is larger at the upper stretch creating a higher turbulence and thereby higher oxygen levels. At the same time it is worth noticing that the lower and middle stretch are heavily covered in decaying weed and duck weed during summer and that this most likely will cause very poor oxygen levels. However observations during electro fishing indicated that only few prey fish were present at the upper stretch during summer. It is possible that the pike prefer the more favorable conditions in terms of environmental factors over the availability of prey fish when the water in the river is very warm. The increasing likelihood of pike on the lower stretch as the water temperature decreases could be explained by the large shoals of smaller prey fish which are often observed at this stretch during winter.

Larger pike were more frequent on the upper stretch while smaller pike were more frequent on the middle and lower stretch. This could purely be a result of the larger pike preferring the upper stretch and thereby forcing the smaller pike to be on the other stretches. This supports the hypothesis made by Nilsson (2006b) who expected that smaller pike would avoid larger pike due to the risk of cannibalism as well as the larger pike being competitively superior. Beside the risk of cannibalism which probably is small for the pike in this study it is possible that aggressive behavior can occur between pike. Frost and Kipling (1967) showed that aggressive behavior and threats was demonstrated by pike fry kept in tanks. It is likely that this behavior also can be displayed by adult pike. It was noticed that large shoals of large ide frequented the upper stretches for longer periods. This could be a reason for the larger pike to be there while the prey size (> 1 kg) probably is too large for the smaller pike. Thus, the larger frequency of larger pike on the upper stretch could also be due to different preferences in prey. This was supported by the fact that one of the largest pike (#139) often was found with one of the two other large pike in the study (#127 & #140). This could be due to the large pike having the same prey preferences but at the same time two large pike in the same area may also be increasingly intimidating for the smaller pike and thereby explain the first theory. The difference between sexes where males were more likely to be on the middle stretch and females more likely to be on the upper stretch could possibly just be a result of the difference in size since female pike in this study were significantly larger than male pike.

It was found that pike with a high condition factor were more likely to be found on the middle stretch while pike with a low condition factor were more likely to be found on the upper stretch. This could be a tradeoff between condition factor and risk of death. All five pike that died during this study presumably died on the lower and middle stretch which means that choosing to be on the upper stretch equals a decreased risk of death. The general impression through observations and electro fishing were that the largest concentrations of prey fish were at the lower stretch and decreased with increasing distance from the outlet especially during summer. Thus, it makes sense that pike that chooses to be on the upper stretch have a lower condition factor due to less food. Apparently the large pike on the upper stretch prefer to be at a safe place instead of gaining a high condition factor.

Lastly pike were less frequent on the middle stretch when the discharge was high while they were more frequent on the upper stretch. This is interesting since the river is wider at the middle stretch than on the upper and the velocity thereby will be more favorable for the pike on the middle stretch. Somehow it seems that the pike's response to an increasing discharge is to swim further upstream. The reason for this is difficult to interpret but could possibly be due to a response from the prey fish on the increasing discharge where the pike follow these and thereby are not directly affected by the discharge. This finding contrasts with the results in Pauwels et al (2014) who found that the movement rate decreased with increasing flow.

An interesting aim of a future study of the pike's habitat choice would be a more detailed observation of the habitats utilized by river pike. This would require more accurate receivers than what was used in this study and could focus on describing exactly where in the river the pike was found according to parameters such as visibility, depth, vegetation cover, width of the river and position in the river. As mentioned before some kind of quantification of the prey fish at the habitats would be valuable knowledge since it must be expected that these have a great impact on where the pike are located.

Critical period in August

Data for the weeks where four pike died and three pike disappeared showed an interesting result. The eight pike placed on the upper stretch and the one pike placed at the sluice all seemed to be unaffected by the poor conditions in the river. Of the remaining 20 pike thirteen moved downstream to the sluice from August 4th - 6th and survived. Seven pike did not move downstream and either disappeared or were presumed dead. The reason for presuming them dead at this time was the fact that they had their last registration on a VR2 receiver here and thereafter was found on the exact same spot with the manual receiver for the rest of the study. The pike that disappeared could possibly also have died during this period. However it is difficult to say since their signal disappeared while the four other signals kept on being transmitted. #125 which disappeared completely in the beginning of August could also have been caught by an angler or a predator (e.g. a mink) or the transmitter could be defect. For the two other pike the same could have happened but it is worth noticing that they were found on manual trackings in the fall before disappearing completely. This could indicate that the pike were dead and that the signal kept transmitting until it got buried in mud. However why this did not happen to the remaining four is hard to say but it could just be a matter of coincidence.

For the four pike that were presumed dead there are two possible scenarios: Even they died because they did not move downstream or else they were dead and therefore did not move downstream. If the pike died because they did not move it show that it is crucial for the pike to make the right decisions according to where to place themselves in the river. If the pike did not move because they were dead it show that the pike that survived were capable of tolerating poorer conditions than the pike that died. If this was the case the lethal period acted selectively towards the hardiest pike. The choice of position in the river during the critical period was not correlated with any individual traits and the mortality could not be linked with the movements made before the lethal period. However if the pike were pooled in two groups a significant difference in weight and condition factor were found. This show that pike in good condition and with a large weight were more capable of surviving the conditions experienced in the lethal period. Thus, which pike dies and which pike survives seems partly to be determined by the movements made by the pike in the few critical days but also by the weight and condition factor of the pike where heavier and fitter pike are more likely to survive.

The critical period showed that conditions are not always perfect in the river and it is likely that periods with poor conditions occur regularly. The period explains the decrease in condition factor found in part 1. This was probably caused by decreased feeding activity in a substantial period during summer but also by the reduction in prey fish which occurred in late summer. The negative effect on movements by very high temperatures in the river was also visible in the mean monthly activity for all pike which were much lower in June 2014 than in June 2015.

Pike in the bay

Eight of the original thirty pike visited the bay during the study. The time where pike was in the bay only counted a little more than 1 % of the total study period. Thus, it is very unlikely that the time spent in the bay have any influence on the condition factor and growth rate of these pike. However it is interesting that the pike are capable of utilizing the bay and this opens a possibility of the pike's options for migration. The salinity at the time when pike was found in the bay was below 10 ‰ in both instances and thus it can't be rejected that pike will not enter the bay at higher salinities. It is interesting that the first time pike entered the bay was around the same time when four of the pike with a transmitter died and further three disappeared. At around this time the conditions in the river seemed very poor. This could indicate the importance of the pike having free access to the bay in such circumstances which is not a given with the sluice placed at the outlet. It was expected that the pike would use the bay more often. Especially since this study showed how saline water in periods were pushed far upstream which means the pike in the river are familiar with brackish water. The utilization of the bay in summer is similar to the results found by Koed et al (2006) in River Gudenå. Here two of ten pike studied moved into the fjord during the summer months. However the pike in this study were in the fjord for longer time. One of these also swam back and forth into the fjord during the late fall and winter. Despite of these findings it is still possible that the bay has a large influence on the ecology of the pike. Observations at the sluice indicated that large amounts of prey fish swam back and forth between the river and the bay. The bay first of all allows a larger production of prey fish which can feed in the productive environment. Second of all it provides the prey fish with more space and better environmental factors in warm months where the river is low and conditions may be poor in terms of high temperatures and low oxygen levels.

Evaluation of methods

In this study the receivers in the river were placed pair wise as to determine the directions swam by the pike. This information was fine in periods where a pike could not be found since it made it possible to determine where in the river the pike was likely to be. However if it was chosen to place the receivers in singles instead it would mean that twice as large an area of the river would be covered. This would make it possible to divide the river into more stretches as well as give a greater chance of registering movements on a smaller scale. At the same time since there would be shorter distances between receivers it would still be possible to determine approximately where in the river a missing pike was located. This is a trade off that should be considered carefully in future studies of this kind.

An issue of importance when making an acoustic telemetry study is to make sure that the fish with a transmitter represents the population. The thirty pike with a transmitter fitted the model of W/L-relationship made for pike in River Tryggevælde and covered almost the whole range of length. Furthermore an un-paired t-test showed that there was no difference in neither weight nor length between the pike with a transmitter and the rest of the population. Thereby it is concluded that the thirty pike, when it comes to size, represents the population in a satisfactory way.

It is important that the transmitter inserted does not affect the pike (Jepsen & Aarestrup 1999, Jepsen et al 2002). If this was the case it possibly would have been apparent in a change in condition factor. The test of the change in condition factor between pike with and without a transmitter showed that there was no difference and therefore it is concluded that the transmitters did not affect the pike negatively. Pike with a transmitter caught one year after the operation showed a healed wound and all of them had grown with a mean of 5.38 cm (see part 1).

The VR60 performed most optimal when sailing at low speed with an electrical engine. It was possible to determine how close a pike were by listening to how loud the signal was. An accuracy of about 13 meters was found which is acceptable in this study. There is no doubt that a better accuracy would be preferable - especially during the diel measurements or if more specific habitat requirements was investigated. But due to the fact that the river in periods had saline water even far upstream and that the pike's possible movements to the bay was investigated it was not an option to use radio transmitters. The range of the VR2 receivers was satisfactory and even the one placed just before the PIT-station where the river is very shallow and narrow seemed to register every pike that swam near it. The PIT-station was placed to create an upper limit where it was certain that every pike that swam further upstream this point was registered. Unfortunately there were several occasions where the PIT-station was destroyed by the discharge and thus did not register properly for longer periods. Fortunately there were only few occasions of pike at this position and the VR2 placed just before the PIT-station seemed to register every pike that swam to this point. It is of course impossible to say if there have been occasions of pike at the position which have not been registered but it is safe to say that no pike have disappeared upstream in the periods where the PIT-station has been out of function.

Conclusion - Part 2

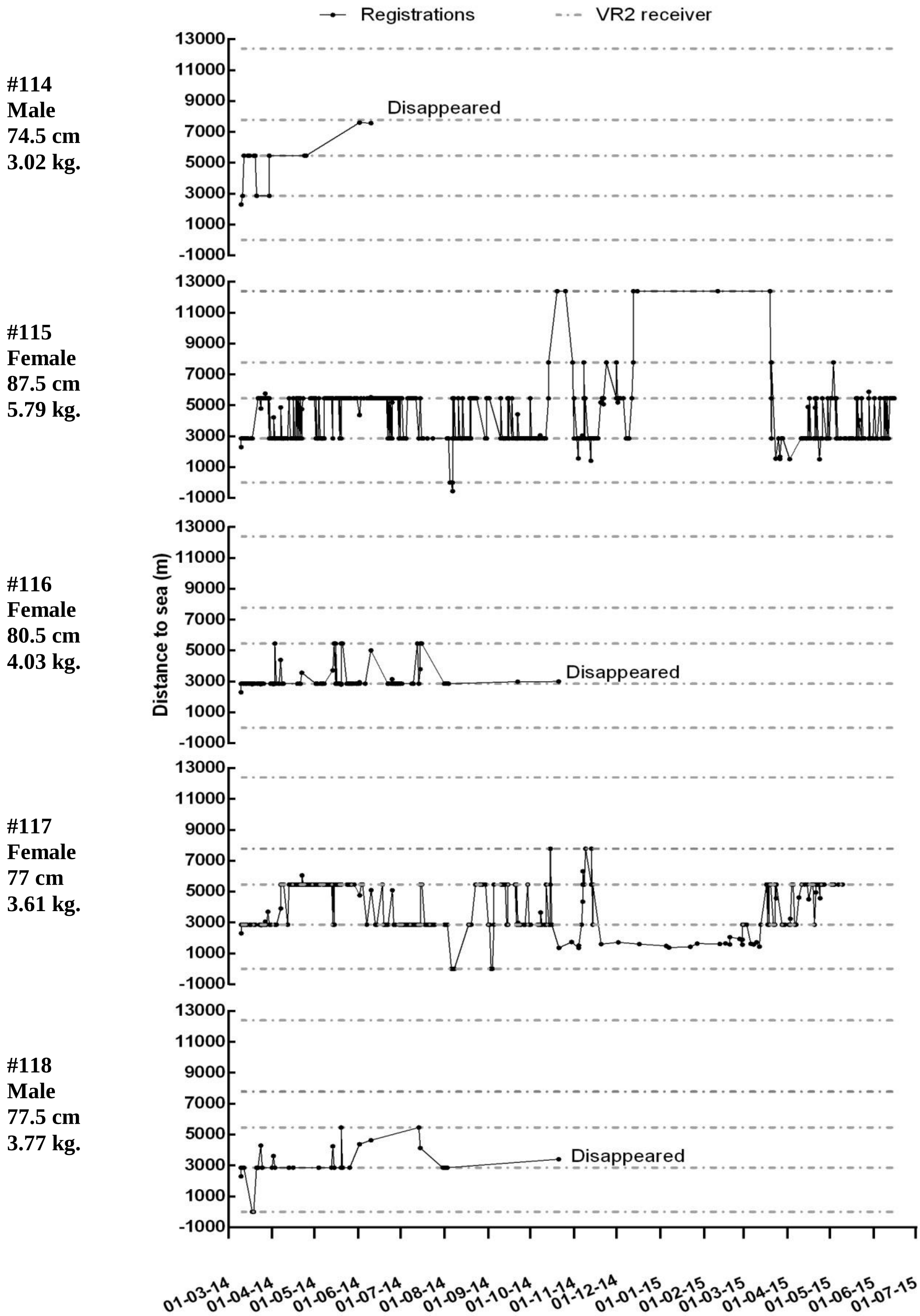
Movements in this study were mainly considered as a result of pike feeding activity. The pike were generally not static and all thirty pike with a transmitter utilized a large proportion of the river. The distribution of activity levels between pike agrees with other findings that pike cannot be separated into sedentary and mobile individuals (Ovidio & Philippart 2003, Masters et al 2005, Rasmussen 2007). There was no correlation between the activity measured on a small daily scale and a large yearly scale which could indicate a varying movement pattern of the individual pike. The general movements of pike may reflect a change between active and static hunting strategies through the year. Movements peaked at about 17 ^{O}C which corresponds well with optimal foraging being at this temperature. A positive effect on movement of salinity at the outlet could possibly be explained by new prey fish entering the river causing the pike to be more active. Indication of a diel activity pattern was found on a larger and coarser scale but not on the standardized small-scale 24-hour trackings. The first mentioned indicates that the diel activity may change according to seasons with a daily peak in winter and crepuscular peaks in April/May, June/July and October/November probably caused by light intensity. Generally the pike showed large individual variations. The 24-hour trackings indicated an effect of size on movement which could not be confirmed on a larger scale. Habitat choice varied between individual traits (sex, condition factor and length) and depended on temperature and discharge. Habitat choice may be largely affected by the distribution of prey fish all though it seemed that some pike preferred the safety of the upper stretch over the availability of prey fish. The movements of prey fish and a more detailed insight to the habitat choice of pike according to visibility, depth, vegetation cover, width of the river and position in the river could be an interesting aim of a future study which would clarify the more specific habitat requirements of pike. A critical period in August showed that the individual choices of movement and position in the river were very important. Furthermore it seemed that heavier pike with a higher condition factor had a better chance of surviving lethal river conditions. Pike did visit the bay but only for a short amount of time. It was possible that pike moved to the bay to avoid poor conditions in the river and the bay may also play an important role with regards to the large amount of prey fish.

Joint conclusions

The study of pike in River Tryggevælde supported the hypothesis of the river holding many pike with a high growth rate and condition factor. Based on the population analysis it was concluded that the thirty pike with a transmitter represented the whole pike population in the river. The large density and biomass of pike in the river suggested that a large proportion of the river could be considered as suitable habitat. This was supported by the home ranges found in this study which showed that each pike utilized a large part of the river. Generally the pike were mobile and the population could not be divided into sedentary and mobile pike. The high growth rate was not caused by the pike foraging in the bay but could be a result of good conditions in the river in terms of food and suitable habitat. Regarding the former it is possible that cyprinids feed in the bay and bring the production into the river. These "pulses" of new prey fish from the bay could possibly compensate for the fact that the river seems devoid of prey fish in periods. The seasonal activity and habitat choices suggested that movement mainly was a result of feeding activity which especially depended on temperature and light intensity. Furthermore there were indications that the pike adapted both active and static hunting strategies through the year. Pike activity peaked at about 17 ^{O}C and decreasing activity caused by temperatures higher or lower than this could be explained by a decrease in feeding activity. The peak in activity at the outlet could also be caused by an increased feeding activity when new prey fish entered the river from the bay. Decreasing movements at high temperatures could also indicate that pike sought local areas with colder water. This was further supported by modeling the habitat choice of pike. 24-hour trackings showed a tendency towards larger pike moving more than smaller. This pattern was supported by the distribution of general activity between pike of more and less than 80 cm but it was not apparent on a larger scale. This may be explained by a bias in the model which assumed that months with no detections equaled no movement of that particular pike. Months without detection were often caused by the pike being on a stretch of the river that was not accessible to track due to vegetation and especially larger pike were located at the upper stretch. This could be the reason why no effect of size was found in this study. The tendencies towards larger pike moving more could explain the higher condition factor possessed by larger pike which possibly moves more freely and are capable of exploiting the available food in the river better. The study of movements indicated very poor conditions in the river during summer where some pike died and others sought refuge on the lower stretch and in the bay. This most likely caused the decreasing condition factor experienced by the pike from 2014 to 2015. In general the population in River Tryggevælde seems to be healthy and in good condition and it is likely that the population is close to the maximum capacity of the river. To preserve this status it seems important that the pike are able to use as much of the river as possible including the bay. Different areas are important for feeding and refuge in different seasons. Based on this study it is concluded that the pike population in the river does not contribute to the Danish coastal pike population in any significant degree. Hence they should not be implemented in future actions towards improving these. However the bay seems to be important for the pike since it offers refuge in periods with critical conditions in the river and allows for a larger production of prey fish. Future studies could focus on gaining knowledge about the young pike in the river aged 0 and 1 year. Especially the number and condition of these could be addressed as well as insight to the factors affecting them. A more detailed study of the habitats of adult pike with respect to visibility, depth, vegetation cover, width of the river and position in the river could be carried out with radio telemetry and would clarify more specific requirements. Furthermore an insight into the movements of the prey fish in the river might be able to explain a large degree of the movements displayed by pike in the river.

Appendix A

Mean position in the river of thirty pike.



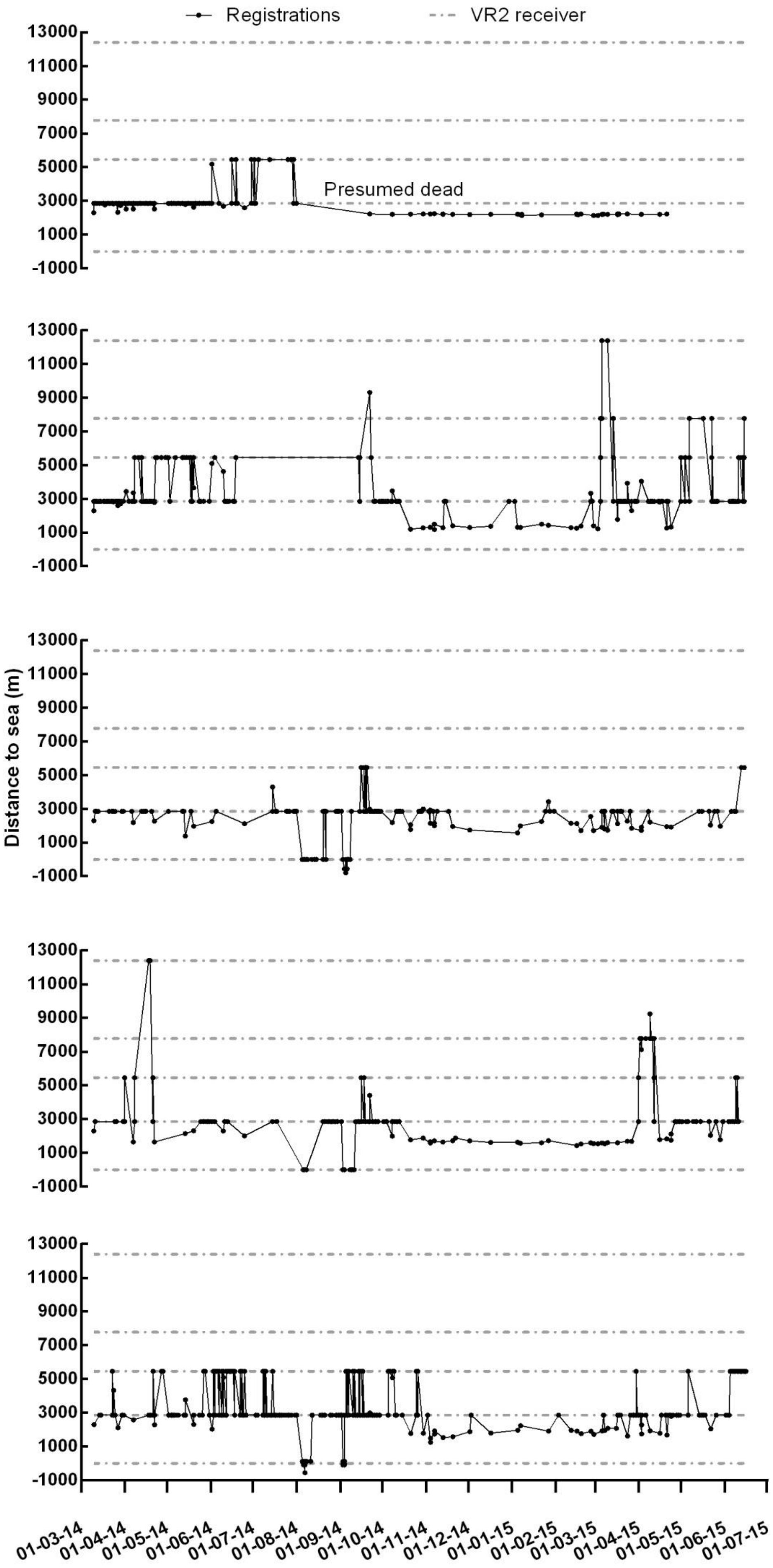
#119
Male
72 cm
2.83 kg.

#120
Male
76.5 cm
3.83 kg.

#121
Male
78.5 cm
3.76 kg.

#122
Female
71 cm
3.0 kg.

#123
Female
75 cm
3.82 kg.



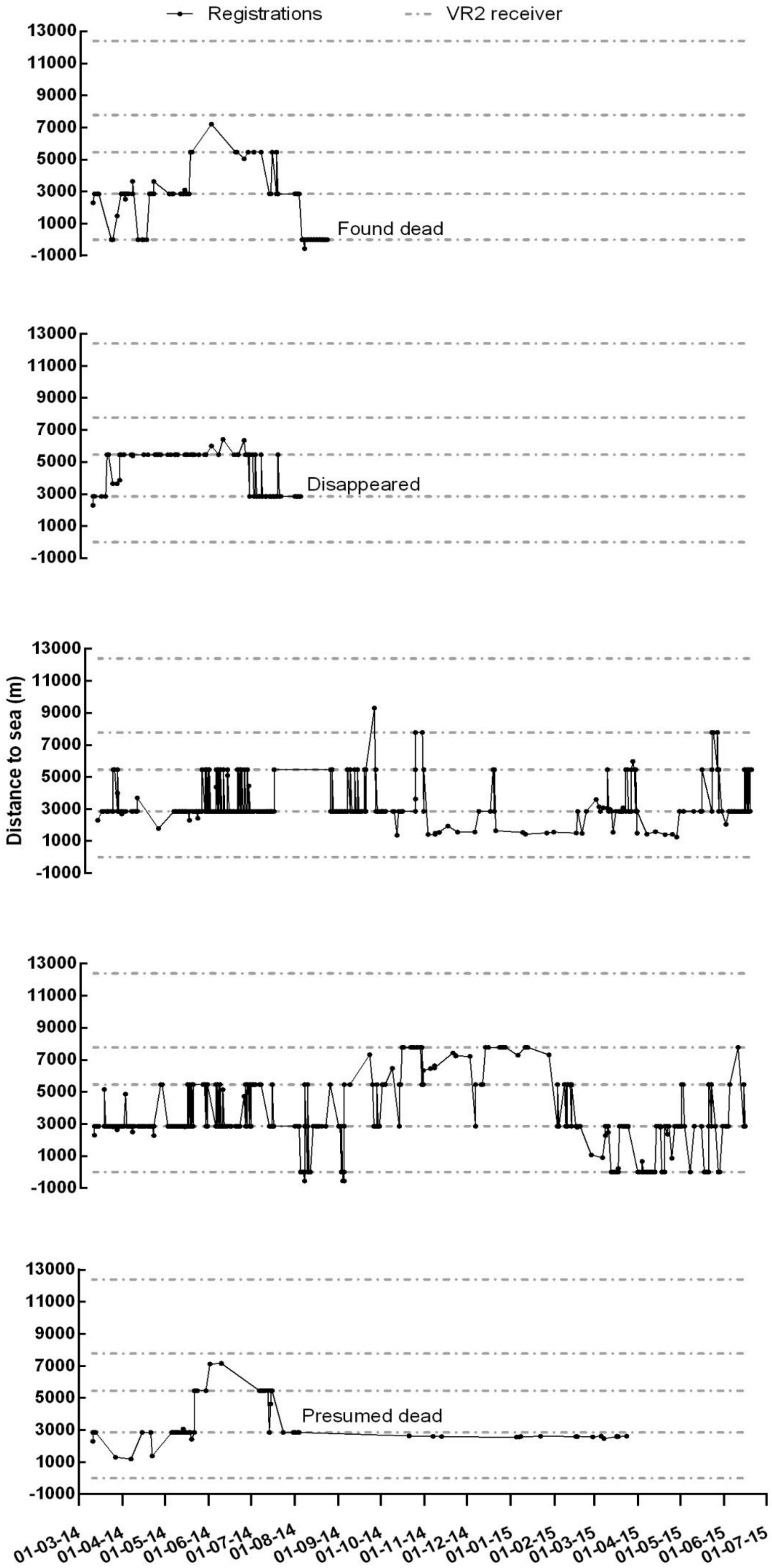
#124
Female
92 cm
7.4 kg.

#125
Female
77.8 cm
3.58 kg.

#126
Female
96.6 cm
7.75 kg.

#127
Female
118 cm
14.2 kg.

#128
Male
82.6 cm
4.09 kg.



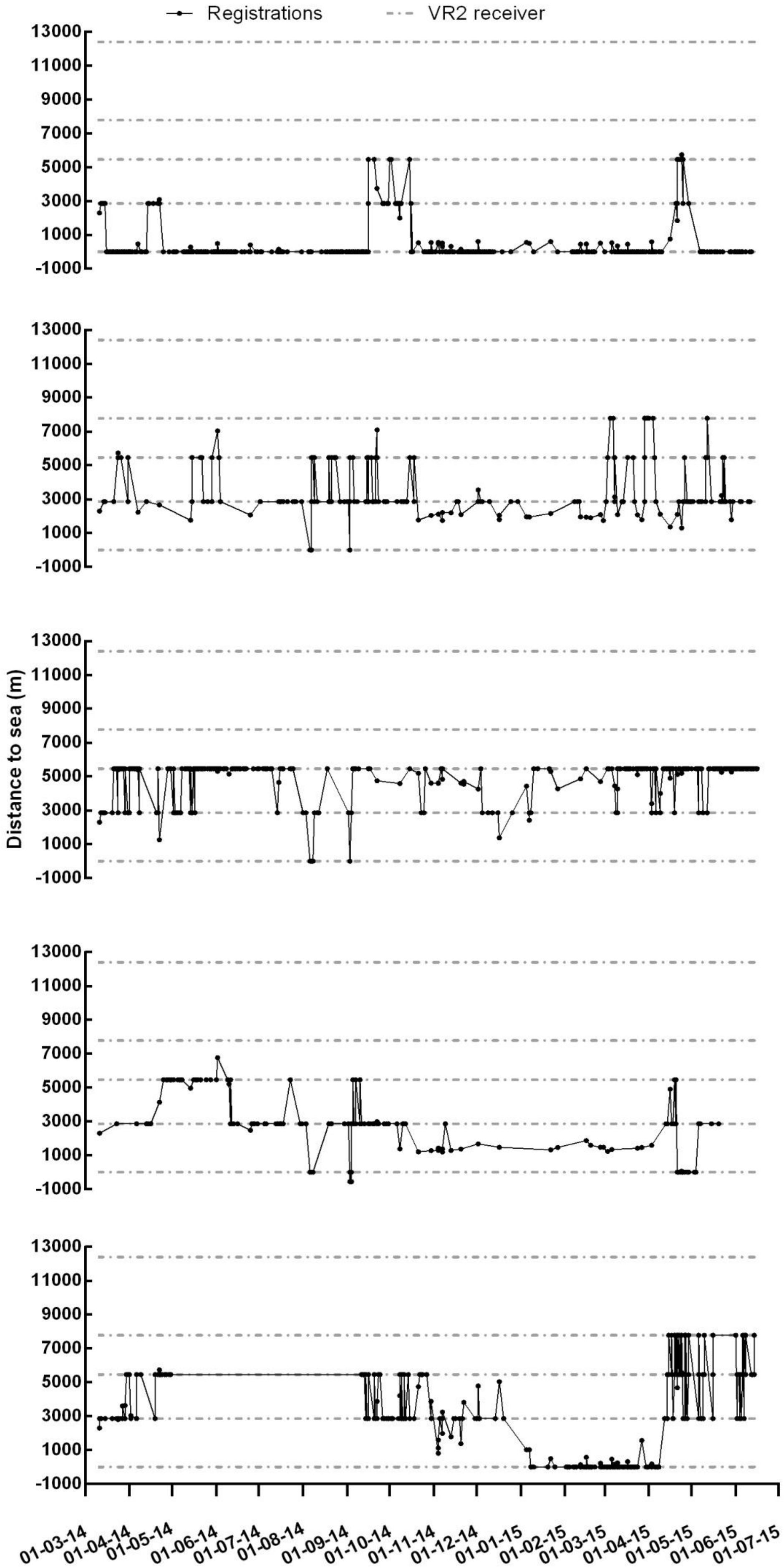
#129
Male
76.1 cm
3.34 kg.

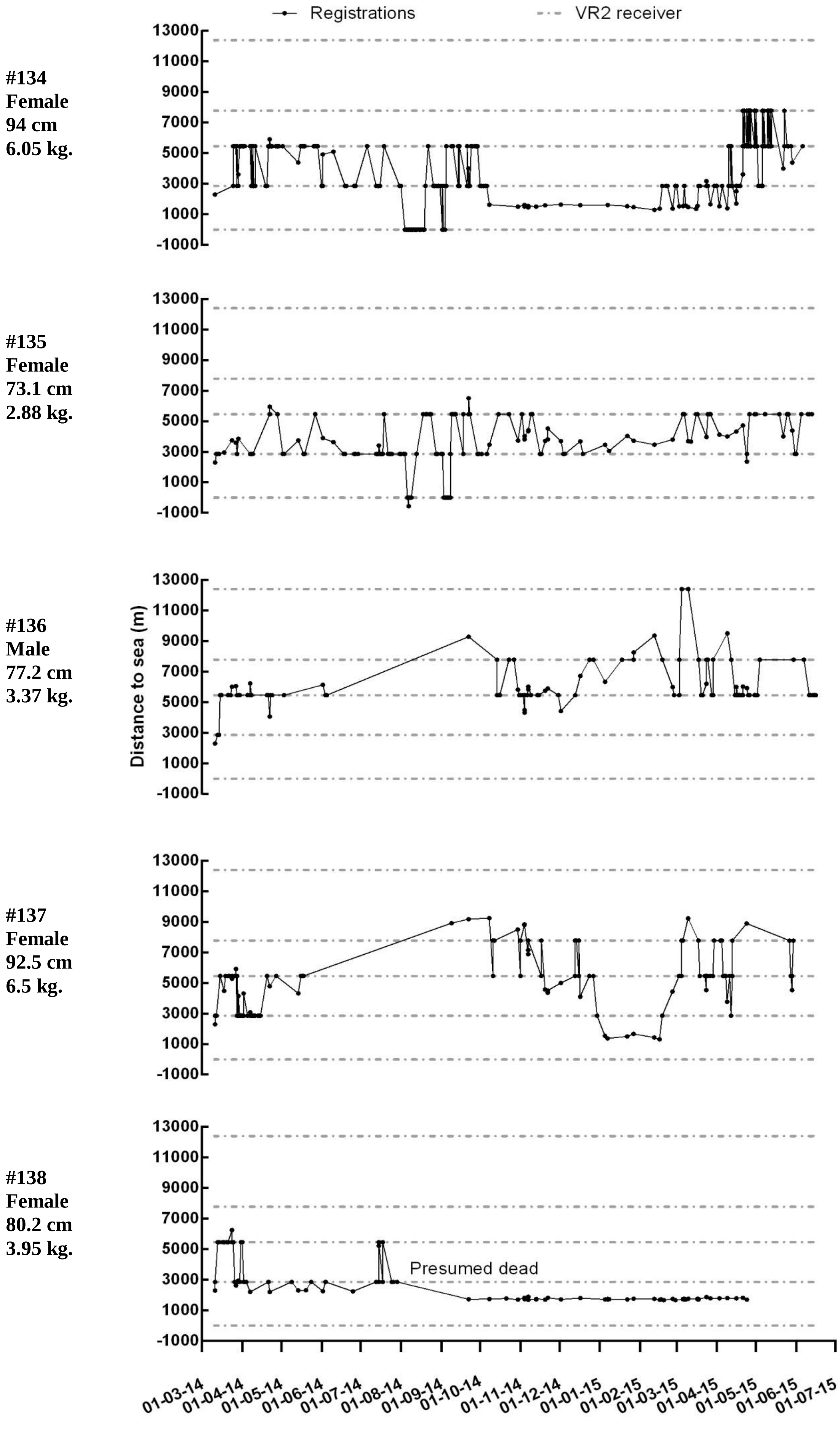
#130
Female
63.5 cm
1.93 kg.

#131
Male
66.1 cm
2.2 kg.

#132
Female
73.9 cm
3.33 kg.

#133
Female
79.2 cm
3.59 kg.




Registrations
VR2 receiver
#134
Female
94 cm
6.05 kg.
#135
Female
73.1 cm
2.88 kg.
#136
Male
77.2 cm
3.37 kg.
#137
Female
92.5 cm
6.5 kg.
#138
Female
80.2 cm
3.95 kg.
Presumed dead
Distance to sea (m)
13000
11000
9000
7000
5000
3000
1000
-1000
01-03-14
01-04-14
01-05-14
01-06-14
01-07-14
01-08-14
01-09-14
01-10-14
01-11-14
01-12-14
01-01-15
01-02-15
01-03-15
01-04-15
01-05-15
01-06-15
01-07-15

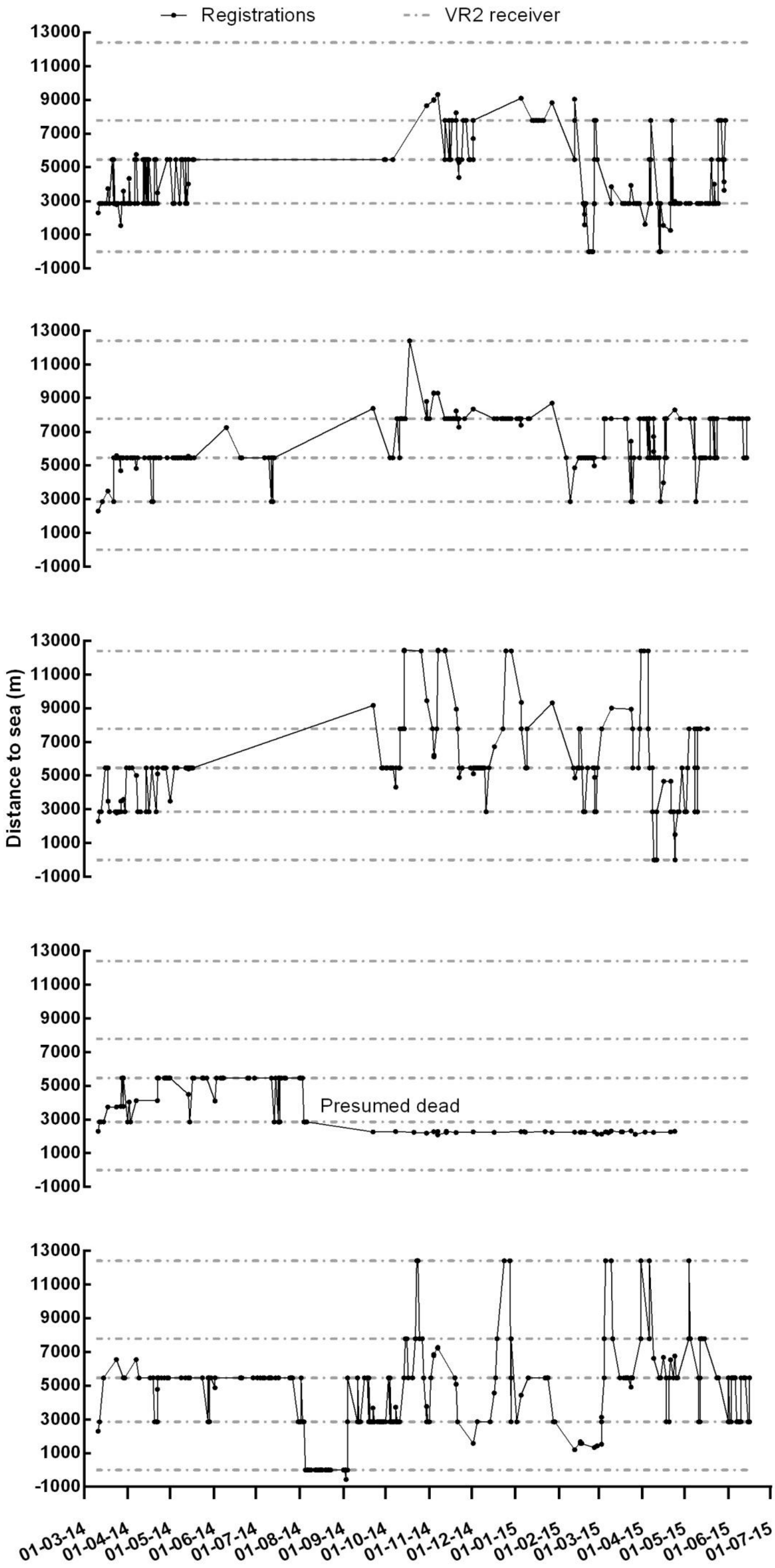
#139
Female
115.5 cm
14.1 kg.

#140
Female
110 cm
11.31 kg.

#141
Female
102.3 cm
7.61 kg.

#142
Male
79.5 cm
3.65 kg.

#143
Male
77.9 cm
3.63 kg.



Appendix B

Model outputs from the statistical analysis.

Model of factors affecting movement:

```
Linear mixed-effects model fit by maximum likelihood

Data: pikelmefull

       AIC      BIC   logLik
  4401.059 4431.183 -2191.53

Random effects:
 Formula: ~1 | ID

        (Intercept)    Residual
StdDev:    3124.593    8453.839

Correlation Structure: Gaussian spatial correlation
 Formula: ~month | ID

Parameter estimate(s):
    range      nugget
1.0340942      0.1590967

Fixed effects: movement ~ max_temp + max_temp2 + sal_0 + sal_3000

                Value Std.Error  DF   t-value p-value
(Intercept) -7341.401  3647.026 185 -2.012983  0.0456
max_temp     2782.969   608.706 185  4.571940  0.0000
max_temp2    -116.097    24.051 185 -4.827023  0.0000
sal_0        4338.900  1508.586 185  2.876138  0.0045
sal_3000    -7469.864  3451.268 185 -2.164383  0.0317

Correlation:
          (Intr) mx_tmp mx_tm2 sal_0
max_temp  -0.929
max_temp2  0.834 -0.929
sal_0      0.106 -0.100 -0.111
sal_3000  -0.198  0.184 -0.081 -0.926

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.6671271 -0.6368087 -0.2000199  0.3455114  4.9412308

Number of Observations: 210
Number of Groups: 21
```

Model of factors affecting the presence on the lower stretch:

```
Call:

glm(formula = present ~ temp + length + week, family = "binomial",data =
habitatL)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.2257  -0.7018  -0.5093  -0.3130   2.7303

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.527803   0.498280   3.066  0.00217 **
temp        -0.099677   0.013345  -7.469 8.07e-14 ***
length      -0.027179   0.005216  -5.210 1.88e-07 ***
week         0.011141   0.004221   2.639  0.00831 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1363.3  on 1364  degrees of freedom
Residual deviance: 1239.4  on 1361  degrees of freedom
AIC: 1247.4

Number of Fisher Scoring iterations: 5
```

Model of factors affecting the presence on the middle stretch:

```
Call:

glm(formula = present ~ length + week + sex + fitness, family = "binomial",
    data = habitatM)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.7193  -1.0478  -0.7567   1.1481   1.8244

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  -0.432504   0.804347  -0.538    0.591
length       -0.037688   0.004332  -8.699  < 2e-16 ***
week         -0.015227   0.003054  -4.985 6.19e-07 ***
sexM         -0.733498   0.137075  -5.351 8.74e-08 ***
fitness     527.182681 104.148270   5.062 4.15e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1886.0  on 1364  degrees of freedom
Residual deviance: 1763.7  on 1360  degrees of freedom
AIC: 1773.7

Number of Fisher Scoring iterations: 4
```

Model of factors affecting the presence on the upper stretch:

```
Call:

glm(formula = present ~ length + week + temp + sex + fitness,
    family = "binomial", data = habitatU)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.7646  -0.8419  -0.5632   1.0696   2.3152

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.082e+00  8.909e-01  -1.215   0.2245
length       6.341e-02  5.102e-03  12.430  < 2e-16 ***
week         8.779e-03  3.606e-03   2.435   0.0149 *
temp         6.895e-02  1.231e-02   5.603 2.11e-08 ***
sexM         7.622e-01  1.550e-01   4.918 8.74e-07 ***
fitness     -8.029e+02  1.169e+02  -6.867 6.54e-12 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1740.4  on 1364  degrees of freedom
Residual deviance: 1522.3  on 1359  degrees of freedom
AIC: 1534.3

Number of Fisher Scoring iterations: 4
```

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