



## **DEDICATION**

I want to dedicate this dissertation first and foremost to God Almighty for His divine Love and Faithfulness to me throughout my study period.

I also want to dedicate this study to the most important woman in my life, my mum, Madam Judith Mawusi Akoto. Thank you for your love. Thank you for everything. I would not have been where I am now if not for your love and discipline. You believed so much in me when no one else did. You are the best thing that has ever happened to me. I LOVE you so much mum.

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## **Abstract**

Fish have a wide variety of feeding habitats and feeding patterns, making them a good experimental model for the study of feeding behaviour. Recent studies show that fish forage actively when perceived risk is low, but decrease foraging and increase vigilance when perceived risk is high. Several studies also show that fish feed more as group size increases and as perceived risk decreases. Feeding of trout in freshwater has been well described but there is insufficient knowledge about their feeding behaviour when at sea. The Acoustic telemetry was applied to explore the movements and habitat use of sea trout (*Salmo trutta* L.) in the Oslo fjord in Norway. Specifically, what habitat type sea trout prefer and the aspect of area use that relates to both individual as well as season specific characteristics were explored. Furthermore, the study investigated whether sea trout are selective in their habitat use, and the effect of season, water temperature and salinity on the utilization of sea depth by sea trout. In all, nine (9) trout were tagged with VEMCO and THLEMA identification tags. The average (mean  $\pm$  SE) length of the studied trout was  $44 \pm 5.87$ cm. All fishes were monitored with stationary hydrophones in addition to manual tracking over the entire study period. Concerning area use, sea trout explored larger area as they moved out of the study area (how big was the study area?). However, there was no significant difference in size relating to area use, but evidence of growth-compensating habitat use, where larger sea trout using relatively small habitat area was found. Concerning temperature use, sea trout appears to be selective in their temperature use. The preferred temperature range was 6-7 °C. The evidence of growth-compensating habitat use suggest the need for more study on how to prevent slow growers from being attacked by predators or caught by fishermen after being chased away by more dominant and larger individuals. This will also lead to a better foundation for understanding the dynamics of large activity area used by sea trout.

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# 1 INTRODUCTION

One of the key factors in conservation and management of fish species is their spatial ecology in their natural habitat (Cooke 2008). There are close associations between how individuals and populations exploit, compete for and share habitats and food resources in time and space, and their ability to survive and reproduce (Kramer et al. 1997). For instance, individuals exploiting rich habitats can grow larger and compete better and give birth to more offspring than conspecifics, exploiting poorer and more hostile environment (Jonsson & Jonsson 2011).

However, behavioural traits are not affected by environmental factors only. Some behavioural characteristics of animals are genetically influenced. But this genetically influenced traits are underrepresented, due to the assumption that behaviour is too subjective to measure, to susceptible to environmental influences, to plastic and not repeatable (Carin et al. 2008).

It is usually more difficult to accept that something as complicated and openly defined as behaviour can have genetic basis (Barlow 1993). Behaviours can be inherited, with estimates of behavioural heritability generally compared to other kinds of traits (Meffert et al. 2002; Stirling et al. 2002), and they show adaptive, heritable geographic variation. Fishes show particularly good examples of geographic variation in behaviour.

Understanding genetics behaviour is important for ecologists (Ruber et al. 2004), as well as those trying to predict how animals respond to a changing environment including anthropogenic-induced changes (Schlaepfer et al. 2002).

It can be debated that the adaptive nature of most characteristics of animals, including behaviour is evidence that natural selection has affected those characteristics to the particular features of the animal's habitat (Barlow 1993).

Salinity has long been recognised as a primary factor influencing the use, movement and community composition of fish in the marine ecosystem while water temperature has been found to control, key physiological, biochemical and life-history processes (Harrison & Whitfield 2006; Selleslagh & Amara 2008). There are positive correlations between sea temperature and activity of fish to feed and avoid predators (Domenici et al. 2007; Linehan et al. 2001). Biotic factors including the distribution and behaviour of predator or prey species also influence the movement of fish (Marshall & Elliott 1998). This is not unusual as the activity of patterns of fish have been often found to follow the cycle of day and night

(Broadhurst et al. 2012). The rising and setting of sun imposes a predictable set of controls on the behaviour of fishes (Broadhurst et al. 2012) Many freshwater species exhibit a consistent diel activity pattern (Bourke et al. 1996; Vokoun & Rabeni 2006).

Many estuarine-resident, including estuarine dependent fishes have well-defined home ranges for most of their routine activities before migrating to distant discrete spawning areas (Crook et al. 2010; Pittman & McAlpine 2003; Walsh et al. 2012). Salmonids are well known to accomplish trans-oceanic navigation and return to their natal rivers for spawning (Dittman & Quinn 1996). Long-distance migration of fish makes it difficult to observe homing behaviours in the sea (Mitamura et al. 2012). In contrast to fish that show long-distance migration some fish with a restricted area use exhibit short-range homing to a specific location such as a shelter hole, burrow or nest (Dodson 1988; Kaunda-Arara & Rose 2004; Reese 1989). Homing can occur regularly in natural environments as fish move away from their habitat when searching for new feeding sites or habitats and then subsequently return to their original location (Matthews 1990a; Matthews 1990b; Reese 1989).

Studies on feeding ecology are very important so as to understand the ecological dynamics of species and their role in natural ecosystem, since is a basic tool for the conservation and assessment of fish stocks, as well as the analysis of the ecosystem as a whole (Power 1997; Wootton 1990). The identification of food resources can provide information on population dynamics and environmental adaptation features (Wootton 1990) and supply information on the co-existence mechanisms and resource exploration by species in an ecosystem(Braga et al. 2012)

Fish have a wide variety of feeding habitats and feeding patterns making them good experimental models for the study of feeding behaviour (Volkoff & Peter 2006). Feeding behaviour comprises complex behaviour that is closely related to food intake (Volkoff & Peter 2006). Feeding behaviour involves several categories of behaviour and, but usually refers to the major period of foraging including movement between foraging areas and other sites (Helfman 1986). In the wild, most of the fish's day appears to be spent either pursuing food or avoiding predation; many fish appears to separate the day into an active, food gathering phase and a relatively inactive resting phase that is intimately linked with predator avoidance (Helfman 1986). Recent studies show that fish forage actively when perceived risk is low, but decreases foraging and increase vigilance when perceived risk is high (Ryer &



Olla 1991). Again, several studies also shows that fish feed more as group size increases and as perceived risk decreases (Morgan 1988).

Locomotor abilities of fish or accessibility and anti-predator behaviour of prey play an important role in feeding behaviour (Sanchez-Hernandez et al. 2011).

In general, brown trout (*Salmo trutta*, “trout” hereafter) are predators and whilst feeding, they take a wide variety of prey categories, including both aquatic animals and terrestrial casualties both at and below the water surface. In general they are opportunistic feeders and may feed either by active foraging or by intercepting prey that drift close to a selected feeding territory (Crips 2005). Feeding of trout in fresh water has been well described (Ogrady 1983; Vøllestad & Andersen 1985), whereas less is known about the anadromous form of trout, sea trout, feeding while at sea (Lyse et al. 1998; Pemberton 1976a). Sea trout feed on a variety of prey items at sea, and the diet changes with season and habitat (Knutsen et al. 2001). In southern Norway and around Scotland, the marine food of sea trout varies with habitat, season, fish size, fish age (Knutsen et al. 2001; Pemberton 1976a). Most preys are often taken at shallow and brackish water (Knutsen et al. 2004; Pemberton 1976a). For southern Norway, Knutsen et al. (2001) discovered that the important prey categories were fish, crustaceans, surface insects, polychaetes and sprat (*Sprattus sprattus*) (Crips 2005). These correspond to the findings of Knutsen et al. (2011), who also discovered that, the diet of sea trout is mostly made up of small-sized fishes (sand-eel, gadoids or herring), crustaceans (benthic amphipods) and insects (adults and larvae).

Significant variation in feeding among seasons was found both in terms of frequency of occurrence and number of items consumed for all age groups of prey (Knutsen et al. 2001). Sea trout feed heavily during winter. This may be due to strong need for food as most of them do return to sea after having used about half of their total energy for reproduction (Knutsen et al. 2001). Polychaetes were mainly eaten during winter by all length groups of fish (Knutsen et al. 2001). Fish prey became gradually more important from spring to autumn. Insects dominated numerically in all seasons, but were mainly found in autumn in terms of frequency of occurrence (Knutsen et al. 2004). Crustaceans were important numerical part of the diet in spring.

In the study by Knutsen et al. (2001), they also discovered that, the sea trout feed most intensively in spring and early summers. Berg and Jonsson (1990) also found that most of the

seasonal growth occurred during the first month in spring. These seasonal variation in diet supports the concept that sea trout are opportunistic feeders (Knutsen et al. 2001)

Numerically, significant variation in feeding was found among different age groups of sea trout. Both polychaetes and crustaceans were mainly eaten by 3 and 4 year sea trout. Insects dominated numerically for all age groups except for the oldest (5-7 years). In 1- to 2-year sea trout, the percentage of fish with food was highest, whereas 3-year fish had the highest number prey items per stomach (Knutsen et al. 2001). During mid-winter, Clupeids are particularly important prey item for larger fish (>370mm), while absent from the stomachs of all smaller fish (170-260mm) which took gobiids and amphipods (Knutsen et al. 2004). Large sea trout feed on large prey such as clupeids and the remains of these may be present in the stomach for a longer time than many amphipods and gobiids eaten by smaller fish, especially at low temperatures when the rate of gastric evacuation is low (Elliott 1975b).

In a field study carried out by Wennhage and Pihl (2002), sea trout was found to have a low similarity in food composition with other species. Sea trout feeds on materials that are not common to other fish species. The major prey of sea trout in this experiment was teleost and these teleost were found in higher frequencies in the soft bottom habitat. This may mean that sea trout feed also in soft bottom habitat. In the field study carried out by Knutsen et al. (2001), it was discovered that, sea trout caught in estuarine habitats fed mostly on insects and polychaetes. When insects were excluded from their data, it was discovered that crustaceans and fishes were the most fed-on preys by sea trout in all habitats. However, aquatic life is continuously affected by a changing environment. Habitat and food preference change as the fish grow. Furthermore, to ensure growth and survival, animals need to respond (often rapidly) (Jonsson & Jonsson 2011) to changing environmental conditions such as those caused by variable climate. Fishes exhibit diel changes in feeding behaviour and habitat use and seek shelter or move to a more favourable habitat under hostile conditions (Jonsson & Jonsson 2011). Strong relationships exist between the distributions of fish and such changes in the marine environment (Blaber & Blaber 1980; Marshall & Elliott 1998).

Knowledge on the spatio-temporal distribution and movement of species forms fundamental and important knowledge in biology and is very useful when formulating sustainable management strategies for the species in question. Most importantly, knowledge on abiotic and biotic factors that determine spatio-temporal movement and distribution enable formulation of predictive models that shed more light on ecological theories.

In this study, I explore spatio-temporal aspects of habitat use in sea trout in the inner parts of Oslofjord. I do so by using acoustic telemetry where I follow a number of sea trout individuals for a period lasting up to a year. In particular, I explore what habitat type that sea trout prefer and aspects of area use that relate to both individual- as well as season-specific characteristics. Also, I test if sea trout are selective in their habitat use and if season and water temperature affect how sea trout utilize sea depth.

## 2 MATERIALS AND METHODS

### 2.1 THE STUDY AREA

The core study area was in the inner Oslo Fjord, in the Bærum basin and comprised 2,200 ha of surface area (fig1). The Oslo Fjord is 107 km long with a mean annual surface temperature of 7.5°C. The Bærum basin has an average depth of 30 m and a threshold depth of 16 m. Three medium-sized rivers (Sandvikselva, Askerelva and Lysakerelva with a median discharge of 3.0, 0.4 and 1.6m<sup>3</sup>/s respectively) and numerous smaller rivers empty into the Bærum basin (Baalsrud & Magnusson 2002)

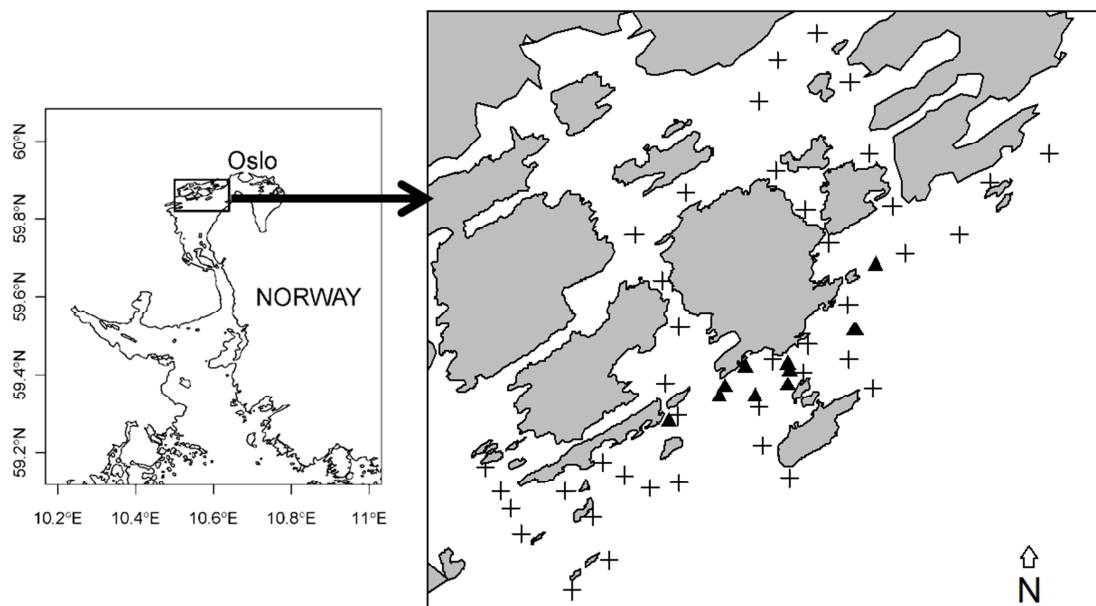


Figure 1: Location of the study area in the Oslofjord (left). Close-up of the core study area. Triangles represent VR2Ws and crosses represent CTD/manual tracking positions.

## 2.2 The study species



Figure 2: Sea trout (*Salmo trutta*).

The sea trout is a migratory form of the familiar brown trout. This is a muscular, rounded fish, with silvery colour and a variable amount of dark blotches on the upper body, which can extend below the lateral line (Chis 2010). In general, the sea trout is stouter than the salmon (*Salmo salar*), and broader at the neck of the tail (it is said that when held by a tail, a sea trout will slip through the fingers, while salmon will hold steady). The “fatty” adipose fin characteristic of salmonids is present between the dorsal and caudal fins and the relatively indistinct lateral line is straight. The breeding male is darker, with increased spottiness and distinct curvature to the lower jaw (Chis 2010).

Sea trout is an anadromous fish species distributed from the white sea in the North-East to the border between Spain and Portugal to the South (Jonsson 1989). The species is iteroparous and spawning takes place in running waters during the fall (Jonsson 1989). Sea trout migrate from the sea to rivers to spawn between July and November; females lay about 10,000 eggs, but this number depends heavily on size.

While in freshwater as juveniles, sea trout seem to prefer habitats containing physical structures and population density often increases with structure complexity. In addition to protection from predators and aggressive competitors, presence of physical structures reduces territory size, aggression levels and resource monopolization by dominants (Jonsson & Jonsson 2011).

Breeding mortality is low and after spawning trout returns to the sea (Chis 2010). The eggs are buried in redds in the gravel and in the southern part of Norway they hatch between April and May (Jonsson 1989). During the alevin stage, the fish lives in red, feeding solely on the

yolk sac. When this sac is depleted the fry emerge from the gravel and start dispersion and feeding (Elliott 1993). The young (juveniles) develop in freshwater, feeding principally on insects until reaching a length of 15-25cm, when they migrate to the sea (Chis 2010). In order to prepare for the seawater habitat the fish undergoes a physiological and morphological transformation- which is termed smoltification. A common smolt age is 2 years in the Southern part of Norway, but varies between 1 and 7 years (Gibson 1993). Smolt age and body length at smoltification increases with latitude. Habitat preference and use during the freshwater stage vary with both fish size and physical factors in the marine ecosystem (Jonsson & L'Abée-Lund 1993; L'Abée-Lund et al. 1989). Depth conditions are of major importance for habitat choice, and there is a correlation between fish size and water depth (size structured habitat selection) (Bohlin 1977; Heggenes et al. 1999; Hermansen & Krog 1984). Sea trout is a very wary fish species and cover such as vegetation, turbulence, undercut banks and larger rocks, are therefore important for the choice of habitat (Fausch & White 1981; Lewis 1969).

While at sea, sea trout tend to remain close to the coast, particularly favouring estuaries or other areas where freshwater enters the sea (Chis 2010).

### **2.3 TAGGING PROCEDURE**

The fish used in the study were sampled by angling. The total number of sea trout sampled was 9. Sea trout were caught by casting from land or boat, with the help of a Rapala Original 13cm wobbler with the barbs removed from the treble hooks so as to reduce injury cause to the fish. One individual was caught using flyfishing.. As soon as the fish is hooked, it is retrieved as quickly as possible to minimize the struggling and reduce loss of energy and accumulation of lactic acid that can have serious harmful effect on the fish.. Each fish was landed by pulling them gently out of the water and placing them gently and quietly and directly into an 80 litter (L) tank containing water where the fish remained until tagging. The tanks are made of hard, black plastic and were covered with a towel to provide darkness. The black, hard nature of the tank and the darkness provided by the towel was found in earlier fieldwork (by Colman and Haugen) to be very important for sea bass. Lighter (white) tank/bucket/plastic nature and sunlight stress fish and caused mortality in an earlier study.

New water was added to the tanks by buckets every 5 mins. Not more than 5 fish were in a tank at the same time. Handling of the fish was done using a wet towel.

Tagging was done in three (3) different time frame, (that is on the 16th of March, on the 12th of April 2012 and 11<sup>th</sup> and 19<sup>th</sup> of August) and one was carried out outside the main periods (that is on the 20th of September 2012). Seven (7) sea trout were tagged on the 12th of April 2012, one sea trout was tagged on the 16th of March 2012 and the other one was tagged outside the tagging period (that is on the 20th of September). One sea trout was attacked by crab, but was looking good after 1 and half hours in the tank. One female trout at stage 7 was also caught. One male trout was also caught. Individual lengths were  $44\pm 5.87$ cm ( $\pm$ SD) for sea trout. Following the implantation protocol recommended by Mulcahy (2003) each fish was tagged with acoustic transmitters (AD-MP13, Thema AS), measuring 7x37 mm and weighing 11 g in air and 6 g in water. The transmitter contained a pressure sensor that enable depth censoring at a precision of 0.2 m, with a maximum depth of 100 m (that is, in cases where the individuals dwelled at depth greater than 100 m the tag will provide information of 100m). The main idea behind using maximum depth of 100m was that the deepest point in Bærum basin is less than 100m (approximately 80m). VEMCO transmitters were also used (V9TP – characteristics: 9x47 mm, 6.4 g) sending one code burst with random delays between 90 and 180 seconds at 69 kHz frequency)..

For sedation, each fish was placed in a 50L black bucket with seawater and AQUI-S® (concentration of 2 mL per 5 L seawater) (Mylonas et. al 2005). Once anesthetized (after 1-2 min), the fish were placed in a V- shaped polystyrene cradle with stomach pointing upwards and the length of the fish was determined (Figure 2A-C). Water was constantly poured over the gill by using a cup to fetch the sea water or with silicon hose attached to an aquarium pump. The surgical area was carefully cleaned with Chlorhexidine (0.5mg/ml) before a small incision was made (as small as 12-15mm) into the peritoneal cavity (Cote et al., 2002, Fabrizio and Pessutti, 2007). The ethanol-sterilized transmitter was rinsed in sterile physiological salt water before being implanted into the peritoneum of the fish. Using monofilament suture (RESOLON®, DS24, 4/0 USP), 1-3 stitches (one for the VEMCO tags and 2-3 for the Thelma tags) sealed the incision using surgical sewing equipment. All the surgery was carried out by Professor Thrond Haugen ( Norwegian University of Life Sciences) and the implantation protocol was approved by the National Animal Research Authority (Forsøksdyrutvalget Licence number 11/180321) before the implantation was initiated

After the surgery, the total length ( $\pm 0.1$  cm), sex (if possible) and the identification number of each fish was noted. In addition, a sample of 5-8 scales were removed from just above the lateral line at the anterior part of the caudal peduncle before the fish were transferred back into the water by putting them at the edge of the sea for them to recover and swim away by themselves. The full surgery procedure from the moment a fish was removed from its keep tank to the time it was released into the water was less than 3 mins per fish. Each fish was released into the study area at their respective captured locations.

The scale samples were used for aging the fish and for back-calculating their individual growth histories. The back-calculation data (length at age:  $L_t$ ) were obtained from annuli radii ( $R_t$ ) measured using a microfilm reader. The method used was the Lea-Dahl method (e.g., (Bagenal & Tesch 1978)– assuming proportional growth of scale radius ( $R_{tot}$ ) and body length ( $L_{tot}$ ):

$$L_t = \frac{R_t}{R_{tot}} L_{tot}$$



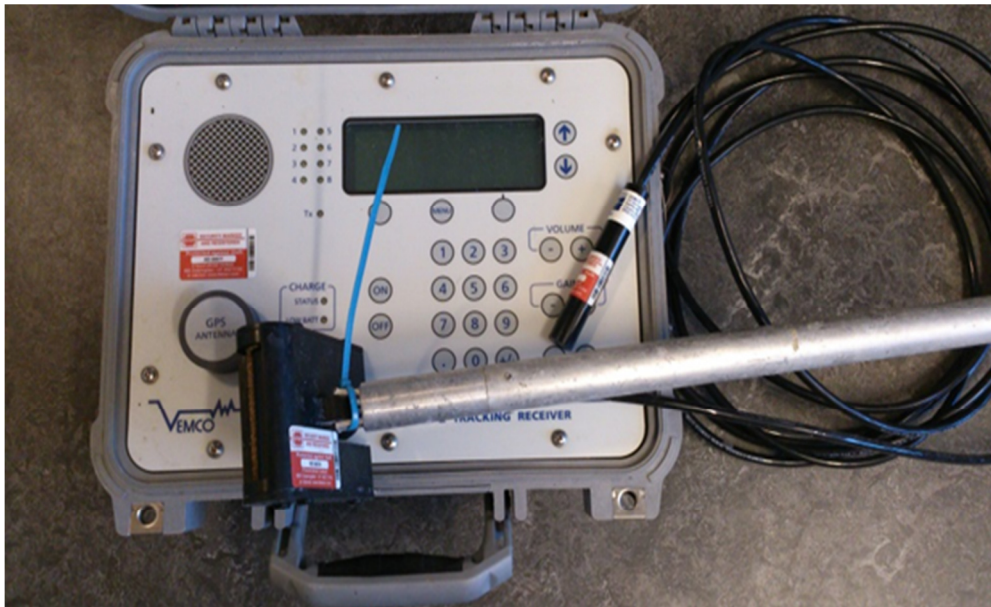
**Figure 3:** The fish been sedated before the implantation of the acoustic transmitter and is provided a maintenance dose during the implantation procedure. Here we see application of two stiches to a sea trout individual following implantation of the transmitter

## **2.4 TRACKING PROCEDURE**

Tracking data were obtained using two methods; manual tracking and stationary tracking (logging). Daytime manual tracking was conducted from April 2012 to March 2013, and stationary VR2 w receivers operated from May 2012. Tracking began the same day as released using THELMA AR-MANUAL portable receiver. Two types of hydrophones were used; omnidirectional (VH 165 receiver) hydrophone was used to detect individuals in the detection range and the directional hydrophone (VH110) was used for cross-tracking to obtain a position estimate for the detected individual (Figure 4a). Each position was obtained where the signal (RSSI) was strongest, that is the highest position of resolution



The tracking signals (ID and depth information) were stored directly in the VR100 receiver along with GPS position.. The transmitters were programmed to ping at 69KHz frequency with random intervals at every 30120 seconds. The estimated longevity of the acoustic transmitter was 12 months (guaranteed to be longer than 7 months). Tracking covered 50 stations based on a grid of 500x500m within the study area (fig 1). Water temperature (accuracy:  $\pm 0.01^{\circ}\text{C}$ ), salinity ( $\pm 0.02$  ppt), dissolved oxygen ( $\pm 0.2$  mg/L) and depth ( $\pm 0.01\%$ ) were measured at each station using a conductivity-temperature-depth logger (CTD, SAIV-SD 204) with the resolution of 0.001 $^{\circ}\text{C}$ , 0.01ppt, 0.01mgL and 0.2m respectively At each station tracking was conducted for 3 min (180 secs). At each station where fish were detected, the depth of the fish was recorded with a resolution of 0.2 m





**Figure 4** a. The manual tracking logger (VR100) and omnidirectional (thin cylinder) as well as directional (attached to metal rod) hydrophones. b) The Vemco acoustic transmitter

Table 1 Tagging data. This table shows the different tag typed used and length of the fish. Form the table, one will observed that one of the individual specie was attack by crab.

Tagging			Length			
date	Tag type	Tag ID	Gear	(cm)	Release site	Comment
12.04.2012	Thelma	19	Flie	44	Ostøyasundet	
20.09.2012	Vemco	7525	Flie	39	Ostøya	
19.10.2012	Vemco	7533	Wobbler	44	Ostøya(Einar)	
19.10.2012	Vemco	7535	Wobbler	54	Ostøya(Einar)	Female
19.10.2012	Vemco	7802	Wobbler	46	Ostøya(Einar)	
11.10.2012	Vemco	7808	Wobbler	36	Ostøya(Einar)	Crab attack
11.10.2012	Vemco	7812	Wobbler	37	Ostøya(Einar)	
11.10.2012	Vemco	7814	Wobbler	47	Ostøya(Einar)	
11.10.2012	Vemco	7818	Wobbler	49	Ostøya(Einar)	Male

In addition to the manual tracking system, seven stationary underwater, omni-directional loggers (Vemco, VR2W) were placed within the study area. With a range extending up to 1km, identification number and depth of the detected fish were recorded and stored on flash memory devices. The data were transferred to ordinary laptop computers via bluetooth connection. The seven receivers were moored within the study area. The receivers were attached to the mooring rope at about 5m depth, with the hydrophone pointing downwards. The buoys were located ca 3 meters sub surface in order to prevent destruction by locals and also conflict with ice. The VR2W were emptied at three occasions: November 2012, Jan/Feb 2013, and March 2013. This was carried out in situ via a bluetooth connection.

## **2.5 TRIANGULATION**

Triangulation is a method often used in long term studies where animals are located at different positions at regular time interval (Simpfendorfer et al. 2002). Tracking the movement of fish and other aquatic species has most been obtain by active tracking in which an acoustic transmitter is inserted in an individual species, and this individual is followed as long as it stay alive and its position is measured at regular time interval (Nelson 1990). Radiotelemetry method is use to track the movement and habitat utilization of fish and other biota in water bodies on a scale ranging from meters (Jellyman & Sykes 2003; Khan et al. 2004) to hundreds of kilometres (Karppinen et al. 2004; Zurstadt & Stephan 2004). Radio telemetry has been especially useful in revealing large scale movement including migration (Broadhurst & Ebner 2007). Recent advances in acoustic receiver technology have made automated submerged data-logging instruments available that permit automated collection of long term data. All of these units employ omnidirectional hydrophones but have differing abilities to estimate position of animals carrying acoustic transmitter. The advanced linked receivers provide accurate position data. The location estimates are mostly limited to areas between three or more receivers (Klimley et al. 2001; Voegeli et al. 2001). If animals swim outside the range of one of the linked receivers, triangulation is impossible. The ability to estimate an animal's location within an array more accurately than simple presence or absence at a given receiver would enhance the information gathered from independent style receivers. It would also allow for more detailed analysis of animal movement patterns, which to date have been restricted to changes in broad spatial patterns. In this study, triangulation positioning was performed at 30 minutes time intervals (allowing for up to 10 detections per

individuals for tags that on average pinged every three minutes) using the method described in Simpfendorfer et al. (2002)

## 2.6 DATA ANALYSIS

The detection range of the receivers was estimated using different approaches for the two type of receivers. For the VR100, generalized additive models (GAM), (Hastie & Tibshirani 1990) were fitted the signal strength data (response) using distance to boat (and tag) as predictor along with tag type. The maximum number of smoothing knots ( $k$ ) was set at 4 to avoid unrealistically complex curvature of the response line. Model selection was based on AIC (Akaike 1974). For the VR2W receivers, information about signal strength is not provided, a generalized linear model (McCullagh & Nelder 1989) approach was therefore used where detection probability was modelled as a binomial process (i.e., detection/no detection) using a logit link function and distance to tag and tag type as predictors. Again, AIC was used for model selection. The R packages `mgcv` and `glm` were used for fitting the GAM and GLM models (R Development Core 2012).

Individual-based activity areas (AA) were estimated using the R package `adehabitatHR` (R Development Core 2012). The AAs were based on daily mean positions estimated from a combination of VR2W triangulation data and VR100 positioning data. The AAs comprised 100% areas and were estimated using the minimum convex polygon method. I separated the AAs into spring (i.e., January to May) and fall (i.e., August to December) AAs and differences in season AAs were tested using one-way anova, using the `lm` function in R. Effects from individual growth and size characters on AAs were estimated using linear regressions (`lm` function).

In order to estimate temperature selection ratios (i.e., habitat selection) the R package `adehabitatHS` was applied (R Development Core 2012). Habitat selection ratio ( $w_i$ ) is simply the ratio between time used ( $U_i$ ) in a specific habitat ( $i$ ), in this case a given temperature, on the availability ( $A_i$ ) of this particular habitat. Hence, the interpretation will be that  $w_i > 1$  indicates positive habitat selection (preference) and a  $w_i < 1$  indicates avoidance.  $w_i = 1$  indicates that the habitat is used according to its availability. The availability data was estimated from compiled temperature-use data from both tagged cod and sea trout located within the core study area. From these data mean daily depth-specific (resolution 0.5 m) temperatures were estimated producing more or less complete daily temperature profiles for the study area. A spatiotemporal model was fitted these data, using the `Tps` function in

package fields, producing temperature at depth and time availability data. Combining these availability data with individual-wise daily mean temperature use data (from both Vr100 and VR2W data) enable estimating wi ratios. I used the average wi estimates over all individuals at week level using the widesI method. Significance of the wis were assessed based on non-overlap of the wi's 95% confidence interval with 1.

### 3 RESULTS

#### 3.1 GROWTH TRAJECTORIES

Due to poor scale quality (replacement scales) freshwater growth pattern was not possible to read properly for most individuals. Sea-stage growth, including size at smolt, was possible to read for 7 individuals. Maximum sea age was four winters and minimum one winter. There was large inter-individual variation in the back-calculated growth pattern (Figure 5) Back-calculated size-at-smolt varied between 11.3 cm and 16.6 cm (mean $\pm$ SD: 13.13 $\pm$ 1.82 cm). Back-calculated size at sea-age 1 varied between 18.8 and 30.4 cm (24.52 $\pm$ 4.51 cm) and for sea-age 2 between 26.9 and 43.9 (35.81 $\pm$ 6.85 cm).

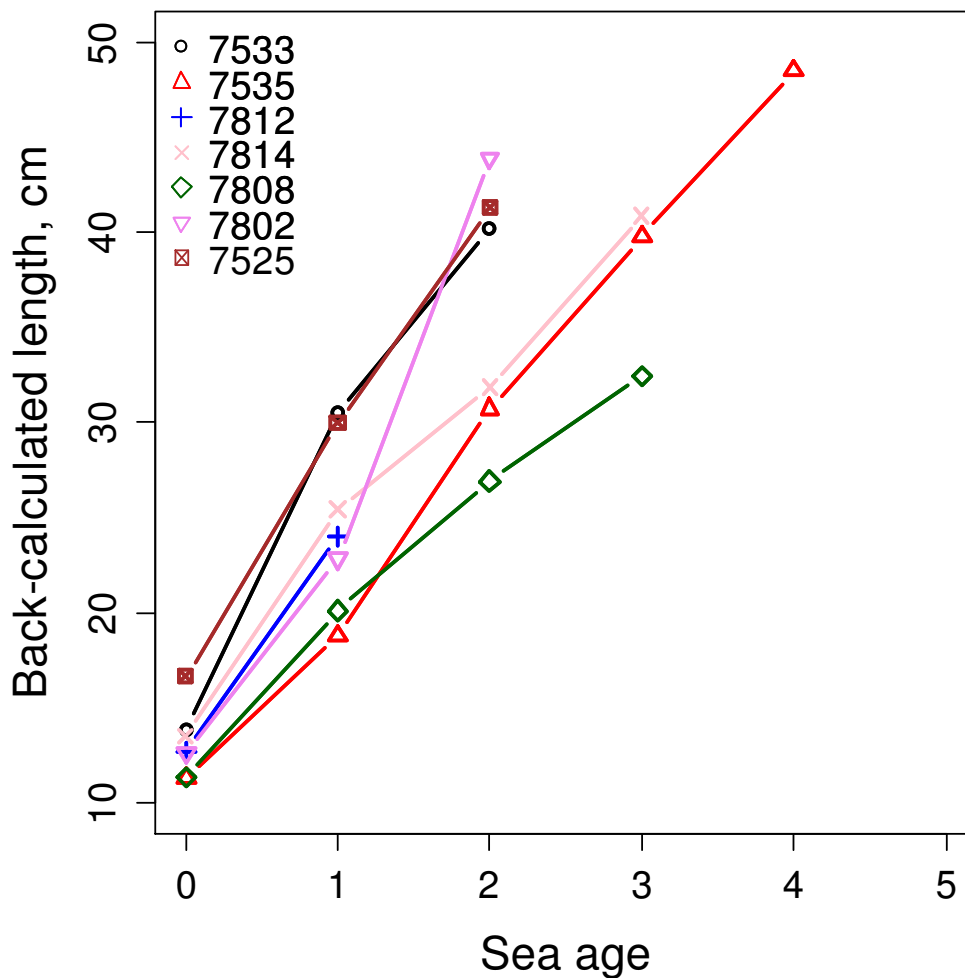


Figure 6: Individual back-calculated growth trajectories for the sea-stage growth. Age 0 corresponds to the back-calculated smolt size.

## 3.2 DETECTION-RANGE TESTING

### 3.2.1 VR100

The signal strength decreased as the distance from the VR100 to the transmitter increased. That is distance to the transmitter had a significant effect on the signal strength received by the VR100 ( $p=0.00017$ ), according to the GAM model (Table 2). The smoothing parameter ( $edf=2.3$ ) predicted that the signal strength was pretty constant over the 0-500 meters distance, but declined rapidly beyond 500 metres before disappearing at distances longer than 900-1000 meters (Figure 6). This confirms the assumption that the number of receptions or signal strength decrease within increasing distance from the receiver. Parameter estimates for the generalized additive model fitted to predict signal strength (dB) as function of distance from tag and tag type.

**Table 2: GAM model parameter estimates for prediction of the signal strength received by the VR100. Edf = estimated degrees of freedom**

Term	Parameter estimate/edf	SE/ref df	t/F	P
Intercept	43.08	3.03	14.21	<0.0001
Tag type[Vemco]	-2.30	4.17	-0.55	0.588
s(distance)	2.3	2.668	11.3	0.00017

## Detection range VR100

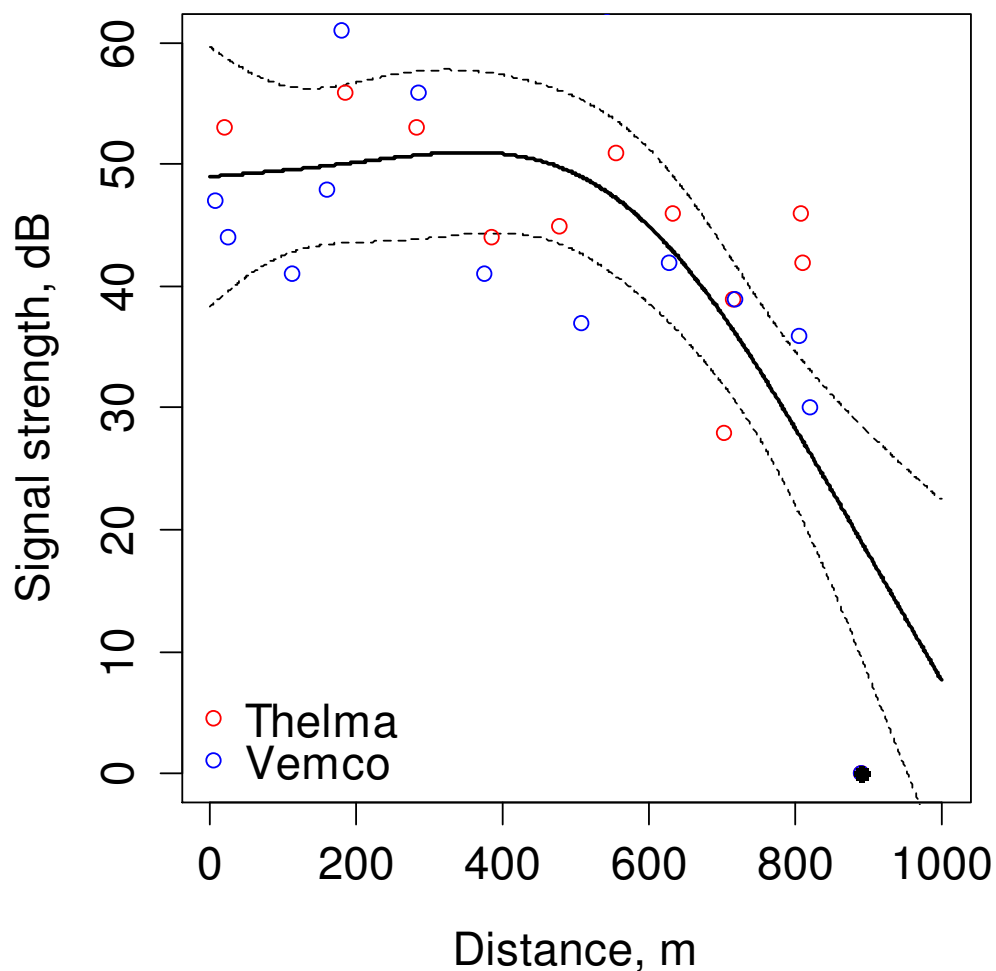


Figure 6: Signal strength as registered by the VR100 as function of distance to transmitter. Lines display model predictions from generalized additive model. Black filled symbol represent the shortest distance at which no signal was received

### 3.2.2 VR2W

A similar range test was done for the VR2s (Figure 7). It will be observed that the probability that a pinged signal will be detected decreases as the distance from the receiver increases (distance slope =  $-0.0066 \pm 0.0012$  on logit scale). Note that there will not be 100% detection probability even at very short detection distances.



Table 3: Logit parameter estimates for the logistic regression model fitted VR2W detection data as function of distance to transmitter.

Parameter	Estimate	SE	Z	P
Intercept	1.756	0.506	3.469	<0.0001
Distance	-0.007	0.001	-5.335	<0.0001

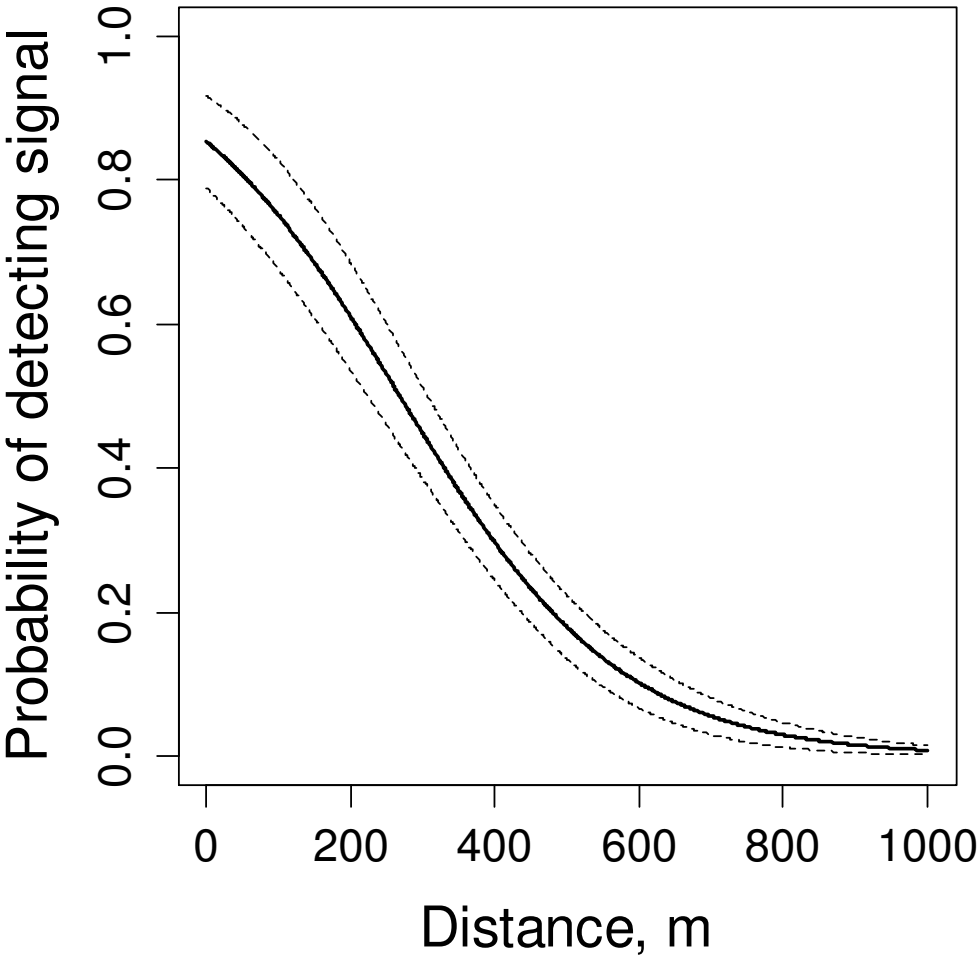


Figure 7: Predicted detection probability of VR2w as function of distance to transmitter. Predictions have been derived from a logistic regression model presented in **Error!** Reference source not found.

### 3.3 AREA USE

Weekly mean positions of the nine tagged individuals are presented in Figure 4. Since two individuals were caught by anglers during the study period (one shortly after tagging) activity areas were only possible to estimate for 6 individuals (requires at least five relocations).

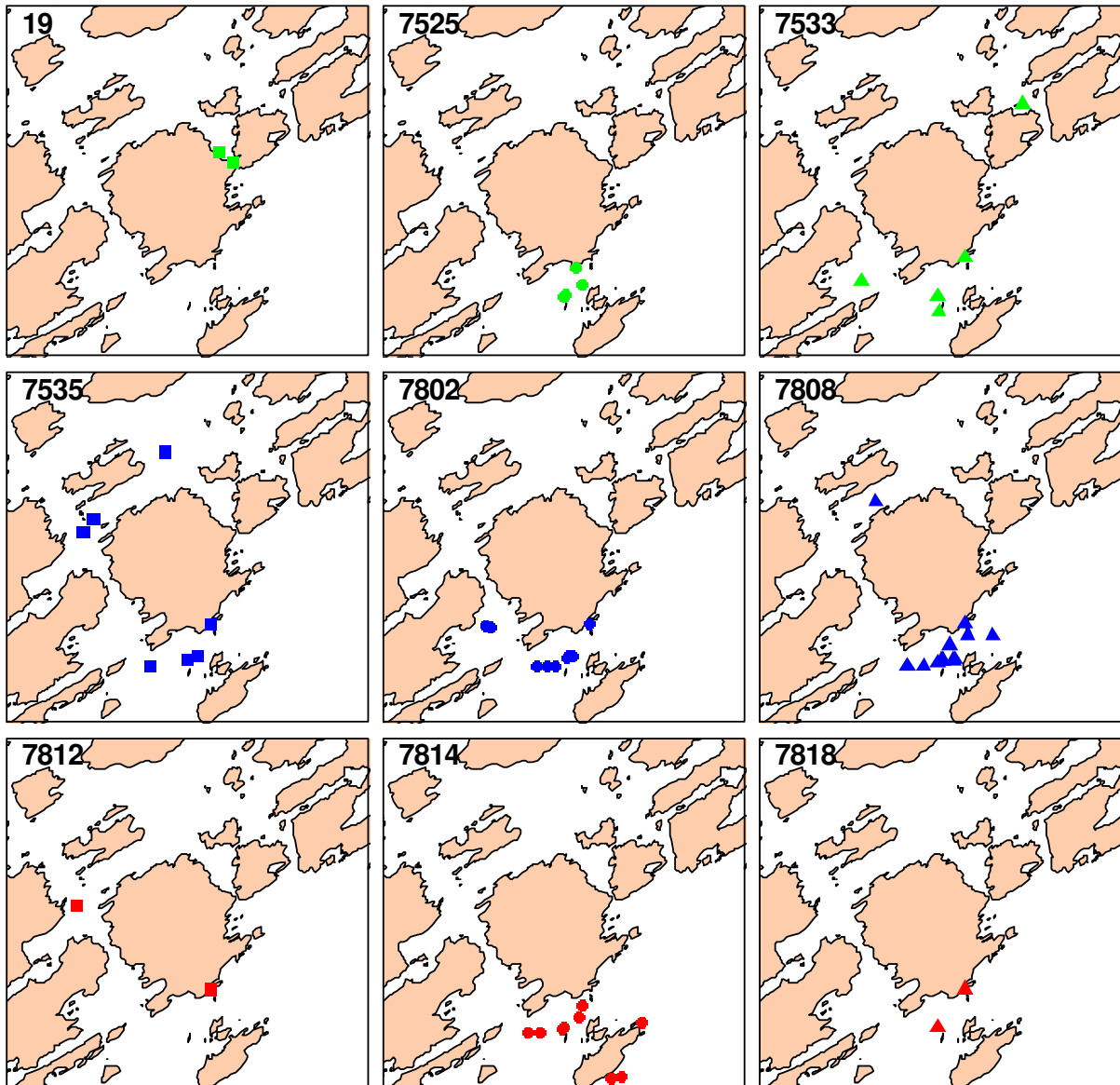


Figure 8: Weekly mean positions for 9 sea trout individuals covering the entire study period. Each individual is plotted with unique symbols and colours.

From Figure 8, individuals with less than 3 weekly mean positions were not used in the final analysis since they do not reflect the actual habitat use of the individuals.

During the entire study period no detection was made outside the core study area (but for the 2 that were caught outside the core study area by a fisherman after the entire study period). Three of the individuals (with ID= 19, 7812 and 7818) (Figure 8) had very few relocations (less than 3), hence were excluded in much of the analysis. Similarly, one individual with ID=7535, use much activity area in the core study area. Individual with ID=7814 seems to be moving a lot but much of its movement seems to be concentrated in the same activity area within the core study area as compared to individual with ID=7535 which seems to expand it activity area within the core study area.

There was large variation in activity area sizes of the sea trout during April 2012 to March 2013 (Figure 9), based on the weekly mean positions. From the minimum convex polygon (Figure 9), one will observe that, each individual sea trout uses different home range. One will also observed that one particular individual (with the black convex polygon) seems to be using home range larger than the other individuals. It seems to be exploring home ranges outside the core study area

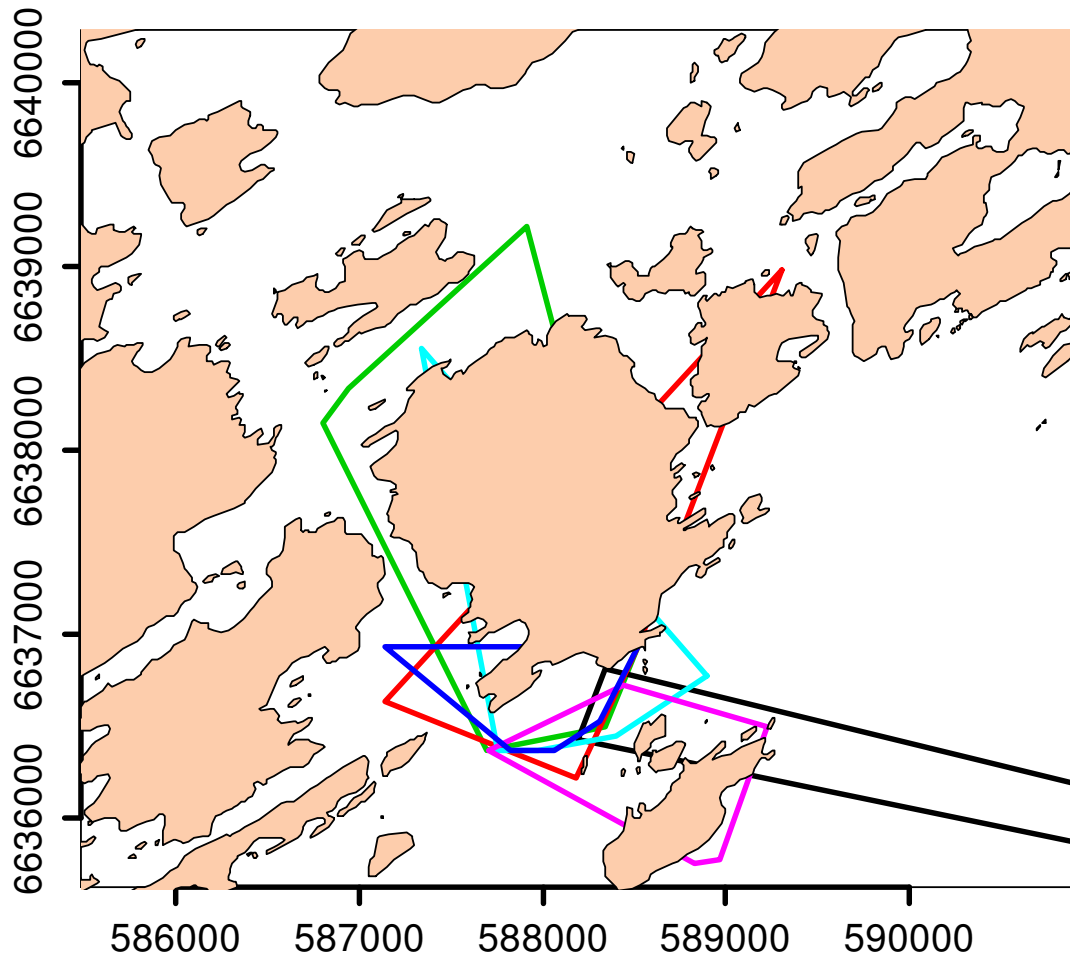
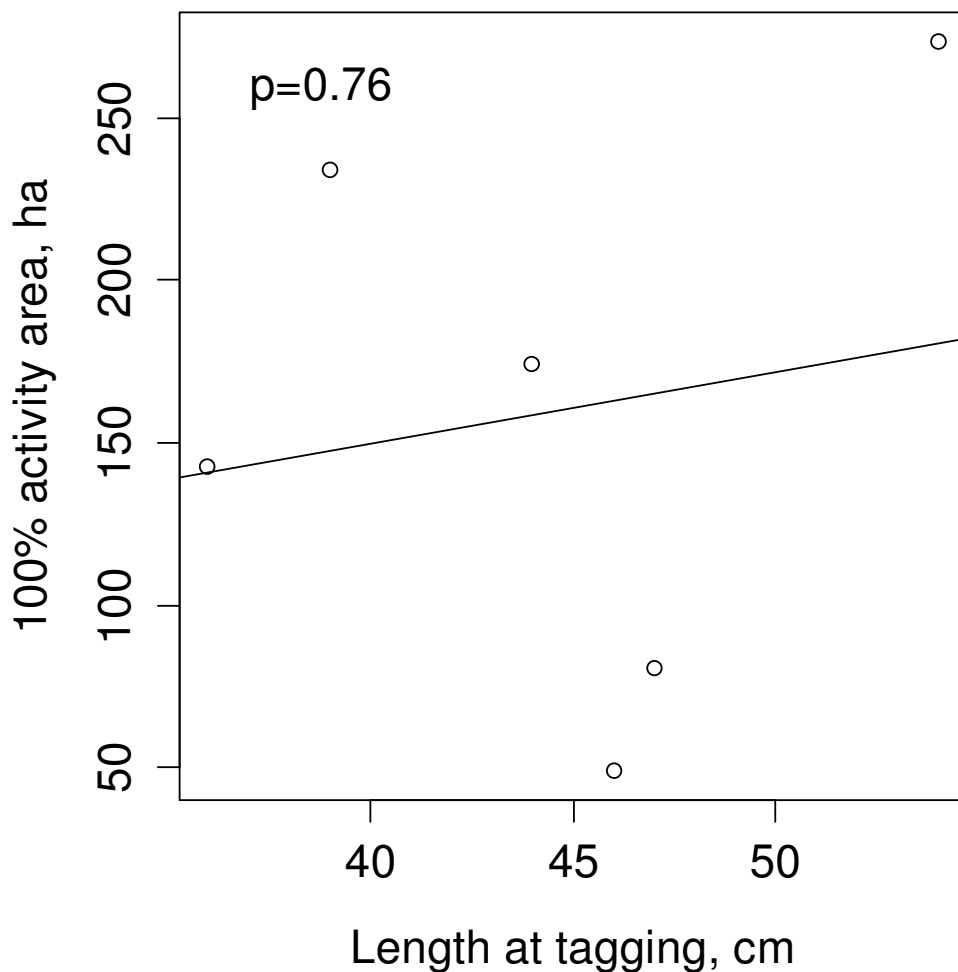


Figure 9: Individual-specific minimum convex polygon 100% activity areas for sea trout during April 2012-March 2013

Based on weekly mean positions (UTM32 coordinates) using both VR100 and VR2 data from manual tracking and triangulation. Different colours represent different individuals. Note that one individual's (black polygon, ID 7533) activity area extends outside the core study area. .

Body size (or length at tagging) did not have any effect on the activity area ( $P=0.76$ ).



**Figure 10:** The relationship between body size at tagging and 100% April 2012-March 2013 activity area in sea trout from the inner Oslo fjord. The p-value refers to the slope of the linear regression indicated in the figure.

There was no significant variation in activity area use by the sea trout between the seasons of the year (one-way anova:  $F=0.607$ ,  $p=0.4655$ ). But during the fall period, the sea trout tended to use larger activity areas (the least being 50 ha to as high as 125 ha. But during the spring period, sea trout turn to use smaller activity areas in the core study area (that is, as small as 10 ha per activity area to as high as 100 ha per activity area).

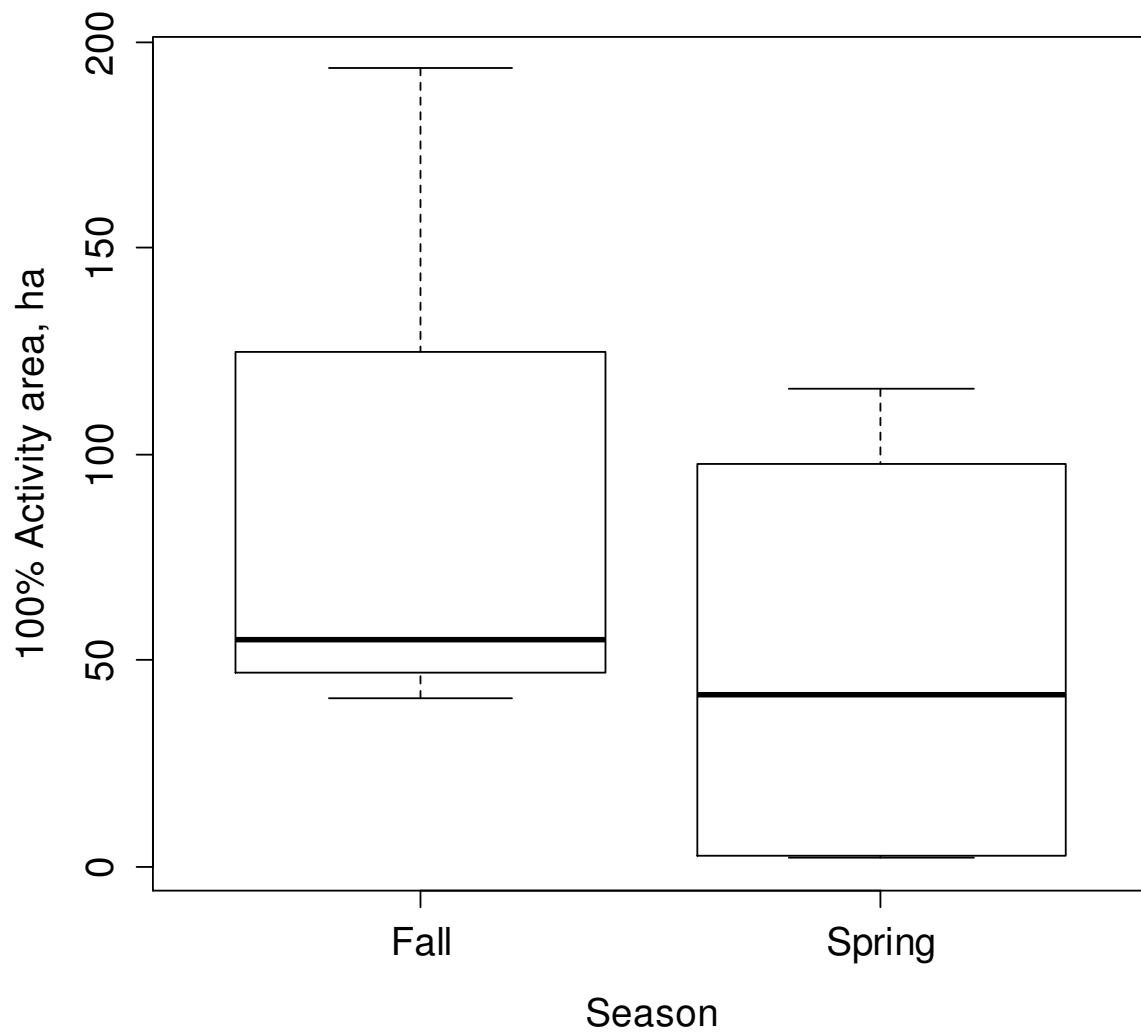


Figure 11. Seasonal variation in activity area of sea trout in the Inner Oslofjord 2012-2013.

From Fig 10, one will observe that there is not a significant variation in the length and season effect on activity area use (ANCOVA:  $p_{\text{size}*\text{season}}=0.76$ ).

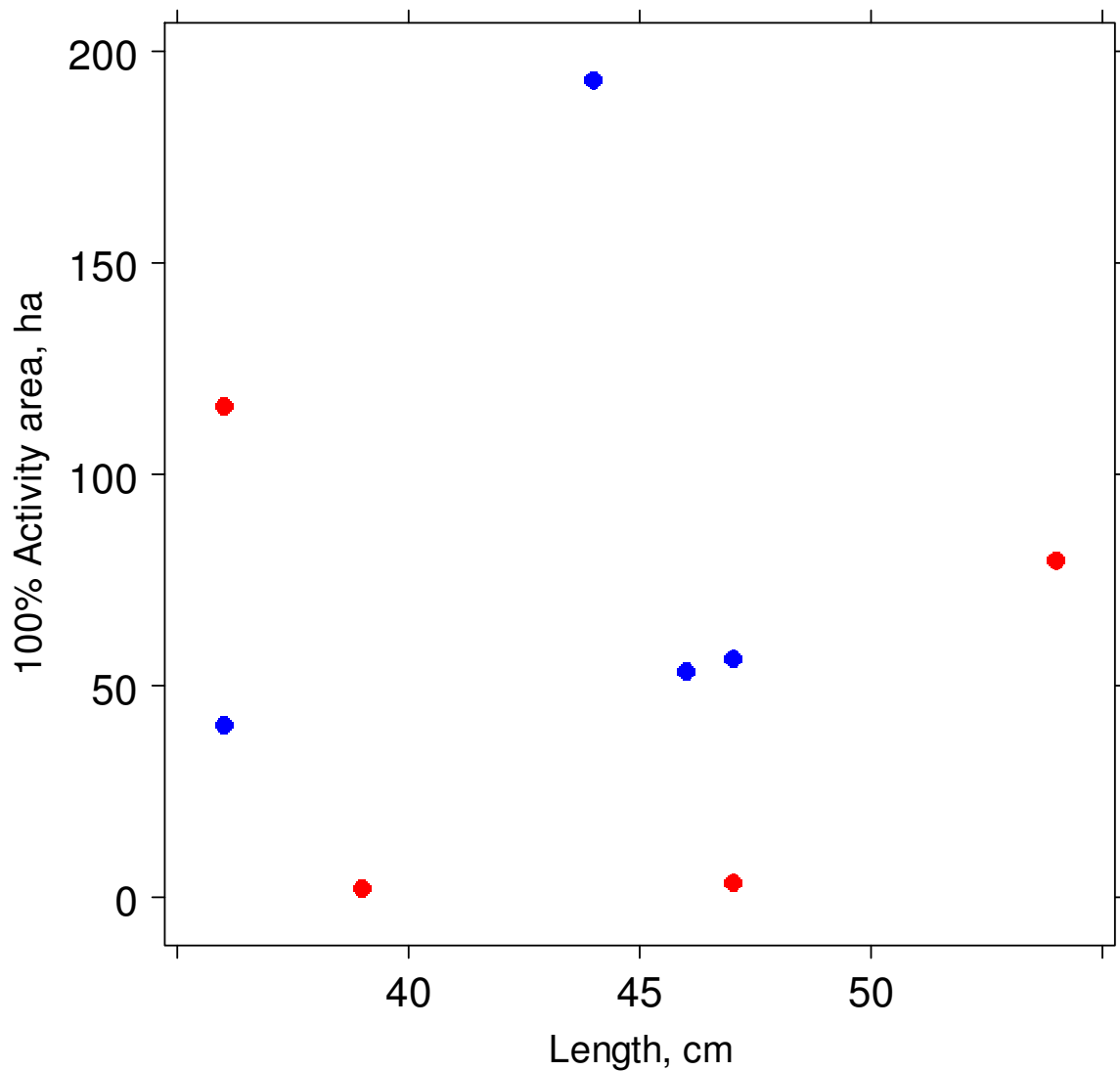


Figure 12. Sea trout body size in relation to activity area in Inner Oslofjord during 2012-2013. Blue dots represent the fall period and red dots represent the spring period.

From 13, one will observed that activity area decreased with increasing size at age. For Fig 13a, activity area have almost a significant negative effect ( $p=0.06$ ) on the size at smolt. In Fig 13b, the activity area has a significant negative effect ( $p=0.05$ ) on size at sea-age 1. While in Fig 13c, activity area has no significant effect ( $p=0.31$ ) on the size at sea-age 2.

Note that one individual (black dot at the top of the 3 figures) seems to have a large activity area compared to its size at age. Since this individual (ID7533) was recaptured far outside the

core study area it was omitted from the statistical analyses – which were conditioned on being within the core study area.



Table 4. Parameter estimates and corresponding test statistics for models fitting activity area as function of three different back-calculated sizes at age/stage estimates.

Parameter estimates					Test statistics					
Parameters	Estimate	SE	T	p	Effect	DF	SS	F	p	R <sup>2</sup>
Intercept	249.08	84.55	2.95	0.03	smolt size	1	5238.10	5.64	0.06	0.53
smolt size	-15.41	6.49	-2.37	0.06						
Intercept	227.30	71.21	3.19	0.02	size at sea age 1	1	5526.40	6.34	0.05	0.56
size at sea age 1	-7.62	3.03	-2.52	0.05						
Intercept	140.63	82.43	1.71	0.15	size at sea age 2	1	1970.40	1.25	0.32	0.20
size at sea age 2	-2.71	2.43	-1.12	0.32						

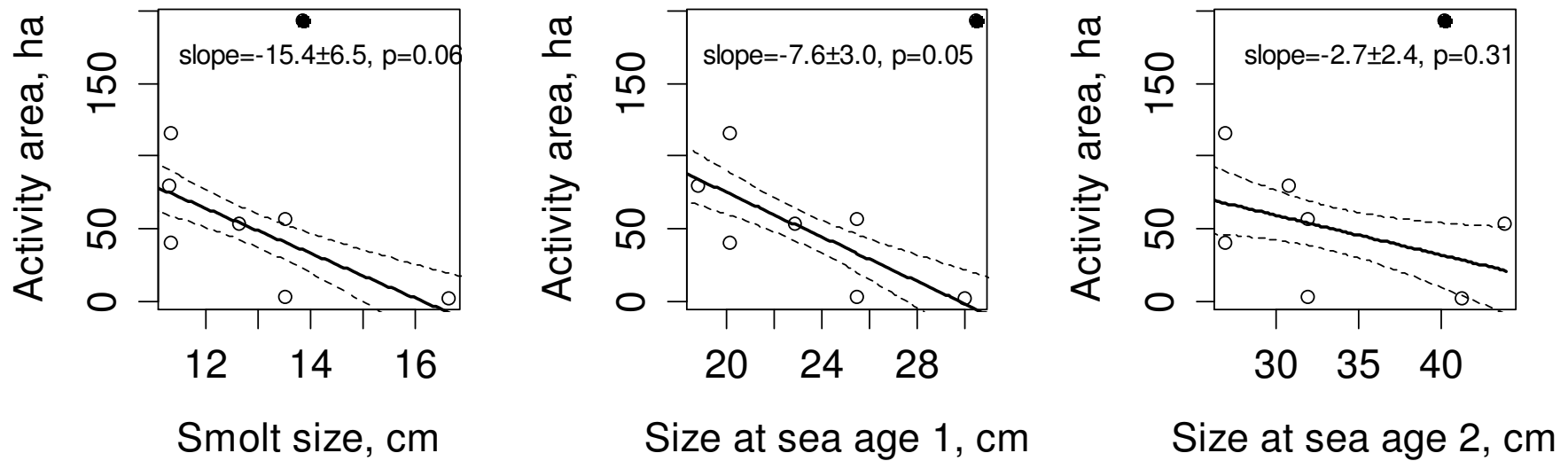


Figure 13. The relationship between activity area and individual size-at-sea-age. Bold lines represent fitted linear regression models (provided in Table ) and dashed lines the corresponding 95% confidence bounds. Slope estimates and corresponding p-values are also provided. Filled symbol at the top of the figures represent ID7533 that were not included in the analyses due to one position being outside the core study area.

### 3.4 DEPTH- AND TEMPERATURE USE

As can be seen from Figure 14, no data was received during summer and March to mid-April periods. For the periods with receiver data it can be inferred that the sea trout use depths from 0 to 30 metres, but mostly depths shallower than 20 metres. During the spring period the sea trout rarely used depths larger than 10 metres. The temperature use was generally at temperatures below 9-10 °C, but some individuals explored temperatures even above 20 °C during late summer (August).

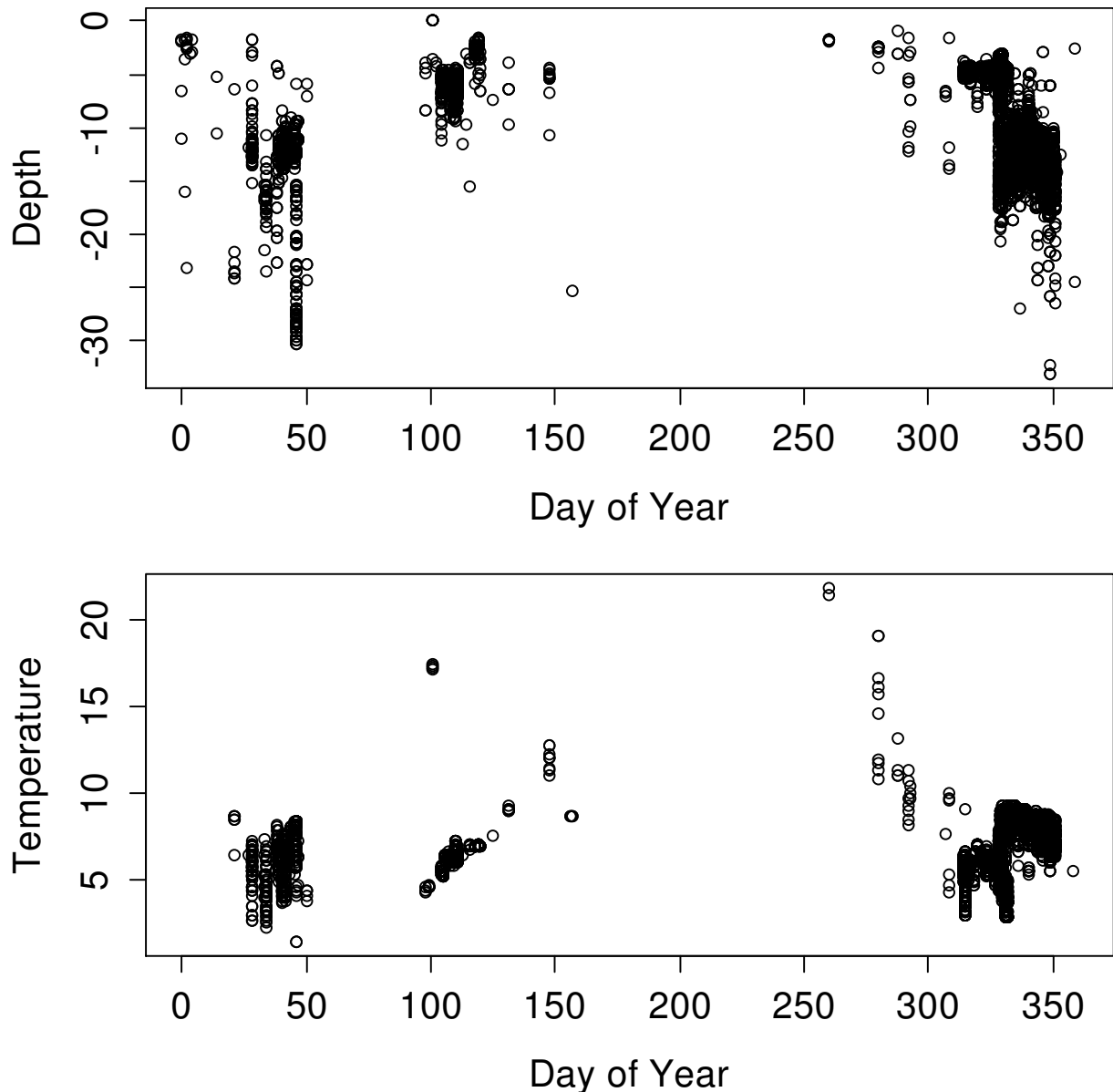


Figure 14. Temporal variation in depth and temperature use in sea trout from the inner Oslofjord during 2012-2013. Data have been retrieved from the VR2Ws in the study area.

The spatiotemporal temperature availability model revealed a shift in the temperature profiles during the December 2012 to June 2013 period where cold water was available at depth shallower than 10-15 meters during winter, an isothermal period during late April-early May 2013 and warm water available at depths shallower than 10-15 metres beyond late May (Figure 15).

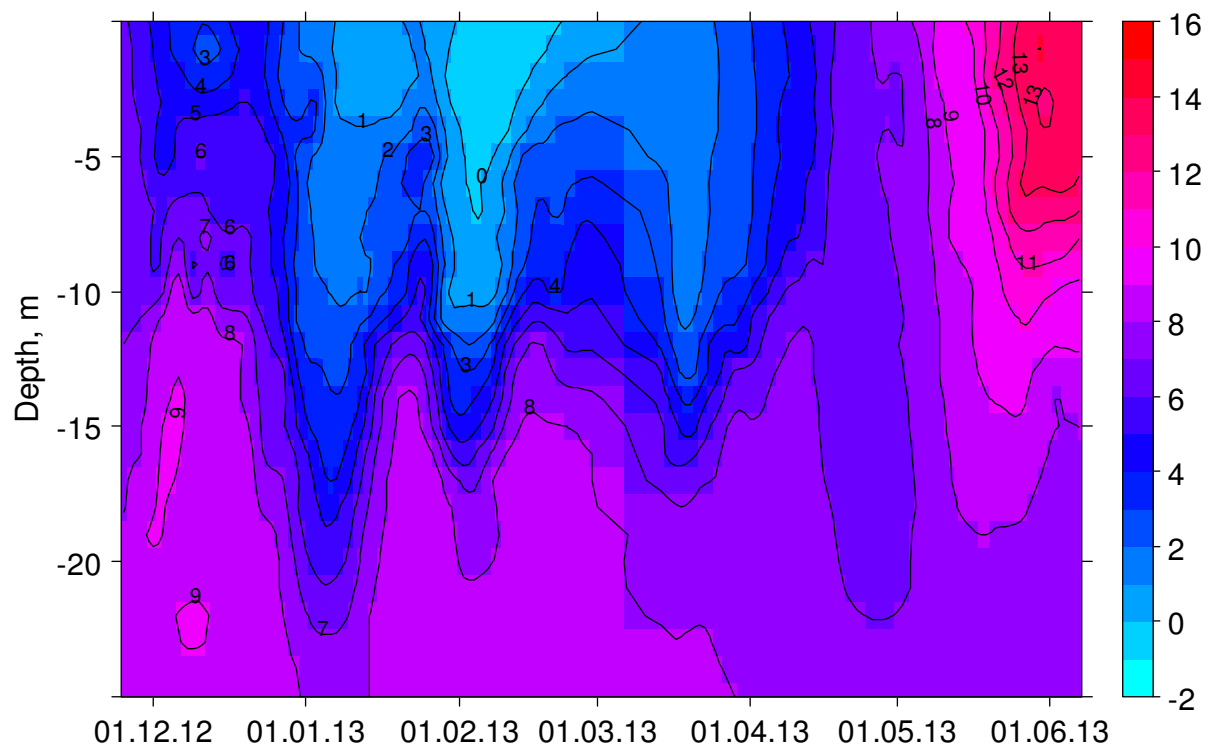


Figure 15. Date- and depth-specific temperature availability predictions as derived from spatio-temporal model fitted to CTD profiles measured in the study area during fall 2012 and spring 2013.

The habitat selection ratios (Table 5. Habitat selection ratio ( $w_i \pm s.e.$ ) table for temperature use in sea trout in the Oslo forjd during 2012-2013. Table 5) show that the sea trout generally select temperatures around 6-7 °C and avoid (apart from week 49) temperatures above 7 °C and below 4°C (apart from week 6).



Table 5. Habitat selection ratio ( $w_i \pm s.e.$ ) table for temperature use in sea trout in the Oslo forjd during 2012-2013. Bold-faced numbers indicate significant positive habitat selection (i.e., preference), red-faced numbers indicate significant negative habitat selection (i.e., avoidance). Normal fonts indicate no habitat selection (i.e., use according to availability).

Week Number	Temperature (°C)							
	2	3	4	5	6	7	8	9
5	0.237±0.166	0.406±0.198	0.498±0.18	<b>3.25±0.45</b>	<b>3.453±0.455</b>	0.129±0.063	0±0	-
6	0.46±0.222	<b>4.055±0.995</b>	<b>5.677±1.393</b>	<b>4.003±1.091</b>	<b>2.456±0.755</b>	<b>1.248±0.411</b>	-	-
7	0±0	0.146±0.059	<b>2.769±0.435</b>	<b>3.981±0.425</b>	<b>5.538±0.52</b>	<b>3.659±0.282</b>	-	-
8	0±0	0.097±0.097	0.556±0.19	0.779±0.265	<b>3.115±0.722</b>	1.062±0.29	-	-
16	-	-	-	-	<b>0.665±0.028</b>	<b>2.63±0.136</b>	-	-
17	-	-	-	-	<b>1.942±0.022</b>	<b>0.078±0.021</b>	-	-
18	-	-	-	-	-	<b>1.262±0.064</b>	0.528±0.174	0±0
48	-	-	<b>11.632±0.495</b>	<b>2.909±0.053</b>	<b>1.335±0.028</b>	0.138±0.015	0.070±0.007	0.145±0.059
49	-	-	0.397±0.028	0.037±0.011	0.059±0.015	<b>1.356±0.1</b>	<b>1.422±0.017</b>	<b>1.401±0.051</b>
50	-	0±0	0.032±0.01	0.054±0.014	<b>3.384±0.179</b>	<b>1.403±0.014</b>	0.111±0.035	-
51	-	-	0.00±0.00	0.027±0.008	<b>1.424±0.073</b>	<b>4.14±0.102</b>	0.914±0.022	-

## 4 DISCUSSION

The study aimed at demonstrating habitat preference of sea trout and aspects of habitat use that relate to both individual as well as season specific-characteristics. It also aimed at demonstrating habitat selectivity by sea trout and if season and water temperature affect how sea trout utilize sea depth.

This study demonstrated that sea trout are using areas extending far beyond the core study area in the Oslo fjord. This was further supported by the recapture of 2 individuals by fishermen outside the core study area. The study also demonstrated that sea trout seem to be selective in their temperature use. They seem to be preferring temperatures between 6 and 7°C during the winter and the spring period (Figure 14) and depths generally shallower than 20 m. Since depth and temperature in stratified water bodies have a strong correlation, it makes it difficult to separate the effect of these two factors. There is also a trend of area used relating to smolt size and growth at sea (Figure 13).

Analysis of growth component reveal that length/size at tagging does not have a positive relationship with growth and habitat selection (i.e. length does not affect how individuals use their activity area) (Figure 5). But this may not reflect the actual picture, because all the scale analysed (except one) were replacement scales. They probably lose some, but may also erode their scales. Scale loss is quite extensive during the smolt stage – and this is probably the main reason why we have so many replacement scales.

The season of the year did not have any significant effect on the activity area use by the sea trout (Figure 11 and 12). Although the habitat used by the sea trout in terms of the season of the year was different, the difference was nevertheless so small that the biological importance can be considered negligible. But there is a tendency that sea trout may use more areas in the fall than in the spring depending on the type of food available during these periods. This was support by Knutsen et al. (2001)who discovered that the diet of sea trout varies, however, according to the season, habitat and age of the fish.

#### **4.1 DO SEA TROUT USE LARGE AREAS AS COMPARED TO OTHER COASTAL FISHES?**

Foraging theory states that the habitat choice of organism involves balancing cost with versus benefit of the various parts of the environment and that organism should feed in richer habitat and shift habitat only when the profitability drops below that of the alternatives (Pyke 1984; Werner et al. 1981)

Analysis of activity area use (Figure 9) indicates that some individuals seem to explore areas outside the core study area. This was confirmed by the recapture of two individuals far outside the core study area by fishermen. This was supported by an on-going mark-recapture project for sea trout in Sandvikselva which reveal recapture all the way to Hvaler (~100 km) (Personal communication with Haugen 2013). When compared to Atlantic cod and sea bass, sea trout uses larger areas than both Atlantic cod and sea bass. In the study carried out by (Bøe 2013) in the Oslo fjord on Atlantic cod, she discovered that, throughout the study period, no detection was made more than 3 km outside the core study area, reflecting a high degree of stationarity of the Atlantic cod, as compared to the sea trout (in the same study area). Also in the study carried out by Hawkins et al. (1980), they discovered that Atlantic cod remains in home ranges of 1-1.5ha. Clark and Green (1990) also show that, although 3yr Atlantic cod range >3km per day in the summer, autumn daily home ranges were relatively small (0.05-2.5ha). Danielssen and Gjosaeter (1994) discovered an evidence of stationarity in Skagerrak cod on a year-round basis, where most (>90%) marked fish were recaptured less than 20km from their point of release. In the study by Espeland et al. (2007), all the tagged individuals (10 cods) were caught by local fishermen using eel pots in several locations within the study area. Also a study on sea bass by Ilestad et al. (2012) in Oslo fjord, they discovered that sea bass stayed in the study area during the period of June to October 2007, except for one tagged sea bass recorded on one occasion in February 2008. Isothermal occurred in October/November, at the time out migration/dispersal of sea bass away from the study area (but probably not out of the fjord system according to three winter period tracking registrations in near-to study area locations and also according to winter catches of local gillnet fishermen). Hence, sea trout seem to have a far more extended area use compared to other coastal fish species in inner Oslofjord and elsewhere along the Norwegian coast.



## **4.2 DOES SEASON HAVE ANY EFFECT ON HABITAT AREA USE IN SEA TROUT?**

Seasonal migrations are adaptations to ensure that growth, survival, and reproduction are turned to the conditions offered by the biotic and abiotic environment (Knutsen et al. 2004). The diet of sea trout vary according to the season, habitat, and age, and comprises fishes, crustaceans, insects and polychaetes, supporting the view that the trout is an opportunistic feeder (Knutsen et al. 2001)

There was no significant variation in the activity area use between the fall period and the period (Figure 11). But again from Figure 11, one will observed that the sea trout tends to use large area in the fall. The tendency for the sea trout to use more areas in the fall than in the spring may probably be related to different food composition during the spring and the fall period. In the study carried out by Rikardsen et al. (2006), they observed that prey choice of sea trout changed during the year in both fjords, and was generally dominated by fish (especially herring larvae) during spring (May/June), summer, and the autumn, and different and mostly benthic crustaceans and to some extent polychaetes during early (Nov/Dec) and late (March/April) winter. Fahy (1983) study the stomach content of 125 sea trout (length >23cm) in coastal waters in Ireland from April to July (1978). He observed that the chief food items were sand eels (62%), a polychaete, *Eunereis Longissima* (26% , more important in May), Sprats (18%) and other fish remains (13%)

The tendency of sea trout to use large areas during the fall than the spring may also be due to the fact that there is more food available in the spring than fall—therefore the need for them to move in search of food over a large area during the fall period. Knutsen et al. (2001) discovered significant variation in feed both in terms of frequency of occurrence and number of items consumed for all groups of prey. Polychaetes (which are more stationary) were mainly eaten during spring whereas fishes (which are mobile) became more important from summer to autumn. This was also supported by Knutsen et al. (2001) who identified that sea trout feed intensively in spring and early summer. A study in the north Argyll sea lochs in Scotland by Pemberton (1976b) observed that the percentage of empty stomachs was low in the spring and early summer.

The larger area use in the fall than the spring could also due to sprat been important as a food source during the fall than the spring. In a diet analysis of salmon and sea trout on the southern

coast of the Baltic Main Basin, by Haluch and Skora (1997), they discovered that Clupeidae (herring, sprat, Clupeidae) form the main dietary component of adult sea trout. They comprise nearly 80% by weight and nearly 70% by the number of dietary component identified. Knutsen et al. (2001) also discovered that clupeids were particularly important prey items for large fish (>370mm) but absent from the stomach of smaller trout feeding on the southern Norwegian coast.

If the Clupeidae (which includes sprat) is more important in the fall than the spring, it will affect the area use, as sprat are more mobile prey than invertebrates like shrimps and annelids. This will cause the trout to use large areas as they have to chase the sprat over the large areas.

Therefore although in my study, there is no significant differences in habitat use between the two seasons (fall and spring), there is a tendency that sea trout may use large surface area in the fall than in the spring

### **4.3 INDIVIDUAL-SPECIFIC HABITAT USE**

I found little evidence of size-related area use (Figure 10). Ulvund (2011) discovered that sea trout area usage has no relationship with fish length. This was a bit surprising, as it was directly opposite to what was discovered by Lyse et al. (1998). In the study by Lyse et al. (1998), they found that larger sea trout of about 2-10 kg were caught in the Aurland Fjord by anglers in the middle of the fjord, more than 100 m from the shoreline, but discovered that no fish of such size (2-10kg) was observed in the littoral zone during the study. In a telemetry study on the behaviour in the river and fjord of sea trout by Kristensen et al. (2011) scale and genetic samples were collected, and with a variety of unique historical dataset consisting of marked recapture studies conducted in the 1950s and 1960s, they discovered that growth in the freshwater phase and age/size at first marine migration, was traits that seem to differ between the two periods with increased growth and age/size at smoltification. Also Pemberton (1976a) discovered that, big-size trout (>21cm) fed mostly on fish (41.6%) compared to smaller size trout which fed mostly on crustaceans (62.1%). All of our trout are large enough to feed on fish – especially sprat – hence no reason to expect large differences in food items among individuals. That is why I did not find size effects on area use.

I found evidence of what seems to be growth-compensating habitat use (Figure 13); where individuals that were larger at sea age seem to be using smaller activity areas than those being smaller (i.e., slow growing). Alternatively to the growth-compensating mechanism, better-growing individuals may also be dominant individuals that chase the poor-growing, subordinate, individuals away. This leads to the poor-growing, subordinate, individuals moving over a large surface area in search of empty and safe feeding habitat.

Since poor-growing individuals may need to catch up with the better-growing ones, this may lead them in search of food over large area so as to catch up with growth. Since fitness in both male and female sea trout can be linked to size via access to spawning partner and number (and quality) of offspring, respectively (e.g., Jonsson and Jonsson 2012), this may be an ultimate driver for compensating for poor growth in these individuals. From my search on the ISI-web of science and other search engines such as Google scholar, I found no article/study that shows evidence of growth compensating habitat use in sea trout. This could probably mean that my study may be the first in its kind to provide evidence of growth-compensating area use.

#### **4.4 TEMPERATURE SELECTION**

Temperature use in ectoterms like fish is critical as temperature is directly linked to metabolism and thus the energetics of fish (Jobling 1994)

Salmonids like sea trout, are cold-water species with high oxygen demand, and the expected rise in temperature may extirpate populations, especially of the southern end of their distribution, where small populations face the greatest risk (Bürger & Lynch 1995). This helps to explain the findings in table 4. From Table 5, one will observed that, the sea trout in the Oslo fjord prefer temperatures around 6-7°C during winter and early spring and seem to avoid too cold and too warm temperatures.

Within populations, thermal tolerance is influenced by the size, age and physiological state of the fish. For instance, youngest life stages are most susceptible to both highest and lowest temperatures (Brett 1952), as well as fluctuations in temperature (Elliott 1994), because of the allometric relationship between volume and the surface of the fish. In the study by Ulvund (2011), he discovered a positive relationship between temperature use and fish length (slope=0.23±0.01 degrees/cm), where larger fish have overall higher temperature preference than

smaller fish. He also discovered a wide variation between sea trout and Arctic charr (*Salvelinus alpinus*) on both temperature and depth use. This finding was supported my finding in Figure (14) where one will observe a significant variation in depth and temperature use by the individual sea trout. Ulvund (2011) also discovered that about 40% of all tagged trout disappear from the sea in a two week period due to relatively high temperatures. These again support my findings in Figure (14) where there was no detection of sea trout during the summer period where temperature was high.

One reason why the sea trout may be avoiding too cold temperatures in the study will probably be due to poor ionic regulation at these low temperatures (Knutsen et al. 2004). They may be avoiding high temperatures probably because access to food is not all that good and therefore they avoid temperatures that will increase metabolism. In this situation, there may not be a huge surplus of food, but they are not starving as well.

Temperature affects metabolic processes and growth in fishes. (Wootton 1998). It influences the timing and duration of most life-history stages (Jonsson & Jonsson 2009). Maximum food consumption increases with temperature (Jonsson et al. 2001). In a study by Elliott (1975), he discovered that for sea trout, the optimal temperature for growth increases with increasing food ration and quality. Sea trout may cease feeding below their maximum rations (Elliott & Hurley 2000). Therefore the prefer temperature range from table 4 in the study shows a good compromise between metabolism costs and low feeding rate. This was also supported by the findings of Rikardsen et al. (2006) who discovered that, sea trout accomplish active feeding migration at sea during late autumn and early and late winter, although food consumption rates was discovered to have reduced during the winter period, due to low water temperature in combination with an assumed lesser availability of prey.

#### **4.5 SHORT COMINGS AND SUGGESTIONS FOR IMPROVEMENTS**

The spatial extent of my tracking and logging method (Figure 6 and 7) was not sufficient for a complete analysis of sea trout habitat use in the Oslo fjord. Methods such as mark-recapture method (as used in the on-going project for sea trout in Sandvikelva) can be used to obtain relevant information on large-scale area use over large areas; say 100km. In addition to the recapture method, use of receivers in “curtain settings” (where more receivers are placed parallel to each other in a “curtain” form so that information is receive about habitat use anytime the sea

trout pass through the receivers array) combined with high resolution, triangulating areas near key habitats such as estuaries and shallow feeding areas.

One other major limiting factor in my study was the sample size (9 individuals). As a consequence, the statistical power in my tests was low and thus effects may have been overlooked. Funds should therefore be provided so that more tags can be bought so that more individuals will be tag so as to obtain enough trout scale for a complete and relevant analysis of the growth of the sea trout at the freshwater stage.

Most scale analysed (except for 1 individual) were all replacement scale. This leads to the loss of vital information on the history and growth of the sea trout at the freshwater stage, since the initial scales were removed during spawning. These actually affect the result in relation to back-calculated growth trajectories (Figure 5). Scales should probably be sampled from different parts on the body than just one specific area (as in my study). This may cause getting access to non-replacement scales.

Also the time frame within which the study was carried out was too short to be able to obtain more relevant and complete data on the habitat use of the sea trout in the Oslo fjord. Hence more funds should be provided for the study to be carried out over a long period of time (say 2-5 years).

#### **4.6 MANAGEMENT IMPLICATIONS**

Migration has associated costs, including the actual energetic cost of displacement; risk of increased predation by both sea animals and fishermen, and the energetic and development costs of any special migratory adaptations and potential reproductive costs due to decreased lifetime reproductive effort (Rankin & Burchsted 1992)

The large area use by the sea trout makes them at risk of getting caught by fishermen (both in gillnets and by anglers) and for being attacked by predators. This was evident in the study where two individual s were caught by fishermen outside the core study area. This corresponds to a (reported) capture rate of 22%. Clearly, drawing general conclusion from 2 out of 9 individuals can lead to wrong conclusions, but the results indicates that fishing pressure on the sea trout in the inner Oslo fjord may be substantial. Slow growers may even be at more risk of getting caught by anglers/gillnets or by other parameters since they may be using or exploring large area so as to compensate for the slow growth rate. It is therefore important to determine the cause or the factors behind this growth effect, especially if the growth effect on area use can be related to

population differences and some other genetic differences. The evidence of growth-compensating habitat use suggested the need for more studies that aim at verifying and unravelling the mechanisms behind. This will also lead to a better foundation for understanding the dynamics of large activity area used by the sea trout

The large area use of sea trout in the inner Oslofjord will also have implications for the scale of management of this species. If sea trout from many populations use the entire fjord as feeding area, the scale of management of sea trout in the sea should be accordingly – at fjord level.

#### **4.7 CONCLUSION**

This study demonstrates that sea trout uses large areas in the Oslo fjord, which actually put them at risk of been caught by fishermen.

The effect of large area use on slow growers may have for risk of harvest.

The study also demonstrate that temperature have an effect on the habitat use by the sea trout. As can be observed from the result (Table 5), they sea trout seems to prefer temperature range of 6°C-7°C, and avoided warmer and colder temperatures. This can be an optimal compromise between access to food and metabolism rate.

Specifically, the study demonstrates an evidence of growth-compensating habitat use. This was an interesting discovery, as no study has ever shown this before. My suggestion will therefore be that researchers should research more into my discovery to validate the generality if this findings.

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