Marine utilization of sea trout (*Salmo trutta*) in Tvedestrandsfjorden – An acoustic telemetry study

Av Thomas Ruud

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Summary

The sea trout is popular anadromous fish that has long traditions as game for recreational and sports fishing. However, the habitat utilization of the sea trout in fjord systems is poorly studied. It may be influenced by internal factors like size, sex and early life- history in freshwater, as well as external factors like season and weather conditions. The objectives of this study were to quantify full-year space use of the sea trout in Tvedestrandsfjorden, and how space use is affected by early life-history in freshwater and environmental agents. I used acoustic telemetry to monitor 56 tagged sea trout from April 2013 to September 2014 in Tvedestrandsfjorden. By triangulating the receiver data, habitat use metrics like utilization distribution and volume, total daily distance, turboness and mean depth utilization could be estimated. The results revealed that length at tagging, probability of using the no-take zone and smolt length influenced the behavior and final fates of the tagged individuals.

Sammendrag

Bruk av marine områder for sjøørret i Tvedestrandsfjorden – et akustisk telemetristudie. Sjøørret er en ettertraktet anadrom fisk med lange tradisjoner til rekreasjons- og sportsfiske. Likevel er habitatutnyttelsen til sjøørret i fjordsystemer dårlig studert. Habitatbruken kan trolig påvirkes av interne faktorer som størrelse, kjønn og tidlig livshistorie i ferskvann, samt eksterne faktorer som sesong og værforhold. Målet med denne studien var å kvantifisere habitatbruken til sjøørret i Tvedestrandsfjorden gjennom et år, og se hvordan arealbruk ble påvirket av tidlig livshistorie i ferskvanns- og andre miljøparametere. Studien brukte akustisk telemetri til å overvåke 56 tagget sjøørret fra april 2013 til september 2014 i Tvedestrandsfjorden. Ved å triangulere posisjonsdata, kunne habitatbruk i plan og volum, total daglig avstand, «turboness» og gjennomsnittlig dybdeutnyttelse estimeres. Resultatene viste at lengden ved merking og smoltlengden påvirket marin atferd i stor grad.

Introduction

The brown trout (*Samlo trutta* L. 1758) has a wide natural distribution and is therefore subject to a great variety of ecological, physiological and morphological variation within the species (Elliott 1989). A variety of local adaptations are thus abundant and this results in different colors and size (Frost & Brown 1967), life-history traits and habitat use (Jonsson 1985). The habitat use is vital to the brown trout, and may highly influence individual survival, reproduction and their ability to exploit available resources (Kramer et al. 1997). In the freshwater nursery areas, young parr of brown trout utilize the slow-flowing shallow banks in the riverbed, while older individuals tend to dwell in the faster and deeper stream habitats (Keeley & Grant 1995). As the individuals grow, their requirements for food will change and their preference of habitat change to larger rivers, lakes, estuaries and even the marine environment if it is available (Jonsson & Jonsson 2011).

Brown trout with an anadromous life style that includes migration to the marine environment, are known as sea trout. This seaward migration pattern is probably influenced by a complex interplay between genetics and environmental agents like temperature, river discharge, interspecific competition, metabolism and juvenile growth rate (L'Abèe-Lund et al. 1989; Jonsson et al. 2001; Cucherousset et al. 2005; Pulido 2011). The seaward migration of sea trout occurs every spring and is an adaption in order to increase nutrient intake and maximize individual growth (Pemberton 1976a; Klemetsen et al. 2003; Jonsson & Jonsson 2011; Boel et al. 2014). Increased individual growth will reduce mortality and increase reproductive success and thus fitness (Jonsson 1985; Klemetsen et al. 2003; Jonsson & Jonsson 2011). Before migrating to sea, the juvenile sea trout grow up in freshwater habitats and experience a smoltification prior to the migration. This is a physiological change where the individuals are adapted to a life in the marine environment with higher salinity and osmotic stress (Gordon 1959; Prunet et al. 1989). However, little is known about the fjord residency and behavior of the sea trout beyond the so-called post-smolt period. Since timing of smoltification is influenced by early-life growth and possibly behavior (Boel et al. 2014), both survival and habitat use in the fjord may be affected by earlier stages in freshwater and the size at which the individual smoltify.

Acoustic telemetry has become a useful tool to study home range and spatiotemporal habitat utilization (Heupel & Webber 2012). The method can present high resolution results in the monitoring of long-term utilization pattern (Lucas & Baras 2000) and may give a better understanding of individuals behavior and their mortality sources (Hightower et al. 2001). Home range studies of painted comber (*Serranus scriba*) (March et al. 2010), shark-like batoids (families *Rhynchobatidae* and *Rhinobatidae*) (White et al. 2014) and several shark species in different habitats (Voegeli et al. 2001; Heupel et al. 2004; Andrews et al. 2010) shows the variety and usage of the method. The latter years, acoustic telemetry have been used to find species usage of marine protected areas and the efficiency of the reserves (Friedlander & Monaco 2007; Marshell et al. 2011; Knip et al. 2012; March et al. 2014

In the present study, acoustic telemetry was used to investigate how sea trout utilize the marine habitat throughout the year in Tvedestrandsfjorden. In particular, the study aimed at quantifying the influence of environmental and individual factors, including early-life growth in freshwater on various aspects of the fjord habitat use.

Materials and methods

Study species

In Scandinavia, smolt and overwintering anadromous brown trout migrate from their spawning stream to seawater from February (Jonsson & Jonsson 2002), but mainly from April to June (Pemberton 1976a; Klemetsen et al. 2003; Jonsson & Jonsson 2011; Boel et al. 2014). The onset of this migration is likely influenced by both genetics and environmental agents such as water and air temperature, river discharge, interspecific competition and juvenile growth rate (Jonsson et al. 2001; Cucherousset et al. 2005; Pulido 2011). The migration is likely an adaption to increase nutrient uptake, whereas increased growth may increase reproductive success and reduce mortality (Jonsson 1985; Jonsson & Jonsson 2011). The disadvantages of migration are increased mortality while migrating in the marine environment and increased energy cost of the journey (Bohlin et al. 2001).

Sea trout are individuals that mature sexually at sea, while residents mature in the river or stream of origin without migrating (Jonsson 1985). Mature and older individuals migrate earlier than first time migrants to the sea (Jonsson & Gravem 1985; Jonsson & Jonsson 2002), where they can migrate great distances into coastal areas. Studies have shown migration up to 100 km from the outlet of their spawning river (Jensen 1968; Nordeng 1977; Jonsson 1985). This pattern suggests a continuum of migration patterns from freshwater areas to the outer coastal areas and the sea (Boel et al. 2014; del Villar-Guerra et al. 2014). However, some sea trout rarely dwell more than 10-15 km from the spawning river outlet (Frost & Brown 1967; Jensen 1968; Jonsson 1985). These individuals have a partial migration within the fjord with brackish water, and thus a fjord residency than rather a migration continuum to the sea (Boel et al. 2014; Davidsen et al. 2014c; del Villar-Guerra et al. 2014). The migratory tendency is often negatively correlated with distance and cost of migration (Kristoffersen et al. 1994; Jonsson & Jonsson 2006). The migratory distance may thus be subject of the physical conditions of the brown trout before leaving the stream, whereas individuals with the lowest energy levels migrate a shorter distance than individuals with higher levels of lipid deposition (Sheridan et al. 1983; Sheridan 1989; Boel et al. 2014). Studies also show that the migration distance is shortened when encountering suitable habitats that satisfy the metabolic needs (Cucherousset et al. 2005).

Study area

The current study used of acoustic telemetry data from Tvedestrandsfjorden (Figure 1), in Southern Norway, at the 58° 36' 23"N and 08° 56' 56"E. The study area is about 4.5 km long (from Tvedestrand to Saltneset in a straight line) and 3.9 km2, with a maximum depth of 85 m (Ciannelli et al. 2010), and a catchment area of 38 km2 (Helland et al. 2003). The complete fjord system is about 8 km from Tvedestrand to the Skagerak sea (Knutsen et al. 2010).

Tvedestrandsfjorden is narrow and sheltered in the inner coastal areas of the Skagerrak Sea. Two islands, Furøya and Hestøya situated in the center of the fjord, divide the fjord and create areas with shallow water. The shallow areas hold dense meadows of eel grass (*Zostera marina*) (Miljødirektoratet 2015), considered as a locally important nature type and suitable habitat for smolts of sea trout (Pemberton 1976b). These shallows also create a 15 m deep threshold in the fjord inlet, which creates the inner and outer basins in Tvedestrandsfjorden (Helland et al. 2003). Several small freshwater streams have their outlets into the fjord, giving freshwater discharge to the top layers nearby the outlets. The stream Østeråbekken is the largest and main spawning stream of the sea trout in the fjord (pers. comm Even Moland).

Tagging

The fish handling and tagging procedure (Figure 2) in the present study where conducted by my co-supervisors from the Institute of Marine

Figure 1: Tvedestrandsfjorden with the three fishing zones. Red zone indicate no fishing, turquoise indicate hook-and-line permit.

Research (IMR) in Flødevigen: the scientists Even Moland and Esben Moland Olsen.

During four periods (April, May, September and November) in 2013, 59 wild sea trout where caught and selected for tagging. In order to sample a study population without selecting for active or more "catchable" individuals (Allendorf & Hard 2009), active gear were used and targeted naïve fish near habitat likely used for feeding or resting (between Furøya og Hestøya). The sea trout were caught using a beach seine (60 x 3 m), with 30 m hauling ropes at each end, deployed from a rowing boat. Deployment was carried out by positioning a person on shore holding one of the ropes. The seine was deployed in a U-shape with the rower bringing the second hauling rope to shore. As the seine was hauled, the two ends where brought together at a suitable landing site. Great care was taken when beaching the seine and hauling the outermost seine wall in to form a pocket in shallow water. Any trout caught in the pocket were lifted over in 40 – 80 l basins on shore with a hand net/ scoop net. Clove oil was used as anesthetic (Munday & Wilson 1997; Bridger & Booth 2003) *in situ*, and was administered in a bath. Surgery was conducted in a U-shaped half-tube when fish showed signs of complete anesthesia (belly up, gentle ventilation). Following the implantation protocol of Mulcahy (2003), each candidate got surgically implanted an acoustic tag (Vemco V9P-2L). The tag was inserted into the abdominal cavity (Bridger & Booth 2003; Bøe 2013) through a small wound that was closed using two absorbable sutures (Olsen et al. 2012). After surgery, width and height (in mm) of the caudal peduncle using vernier calipers, and body weight (g) of each individual were measured as fork length to nearest millimeter (Olsen et al. 2012). Length varied from 230 mm to 635 mm with a mean length of 338 ± 161 mm (± SD). Scales were sampled from the peduncle for aging, and a tissue sample were removed from the anal fin for latter genetic analysis. The whole procedure lasted less than five minutes. Trout were then transferred to a container with well oxygenated sea water for recovery. After full recovery, the individuals were observed for 10-20 minutes before being released at the location of capture.

Figure 2: Fish handling and tagging by Even Moland and Esben Moland Olsen. The middle picture on the upper row shows a V9P-2L transmitter that was used for tagging (Photo credit: Even Moland and Carla Freitas).

Scales readings

I used the scales samples to determine the age of the fish, back-calculate the smolt length and register life-history events (e.g., spawning events). From the scales the age is estimated by reading the among-circuli density pattern in each scale (Jonsson 1976). During winter the circuli are formed tighter as the growth is reduced (Jonsson & Jonsson 2011), and when spring and summer comes, the distance between two circuli is much broader. Often, clear winter and summer zones can be read. In anadromous individuals, the fish experience increased growth as post smolt, up to 20-25 cm during the first year at sea (de Leeuw et al. 2007), illustrated in Figure 3. Scales comprise handy tools for estimating age when dealing with fast-growing individuals (Jonsson & Jonsson 2011), like the individuals in my study. I also estimated the smolt length of each individual (Figure 4), by back-calculating the fish length from the scales (Francis 1990), assuming a proportional growth of scales and body.

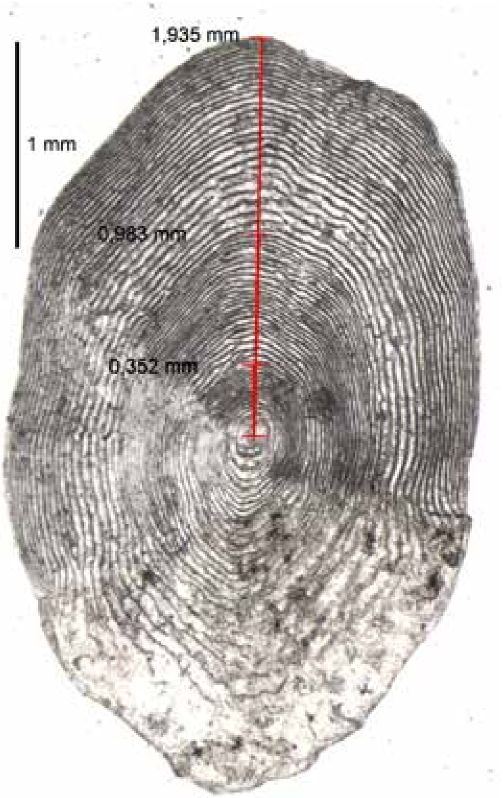

Figure 3: The scale from fish ID 1158183. The crossing red lines indicate end of winter zones. This individual spent two years in freshwater and then migrated to the sea, as indicated by a substantial increase in growth during the third yea.

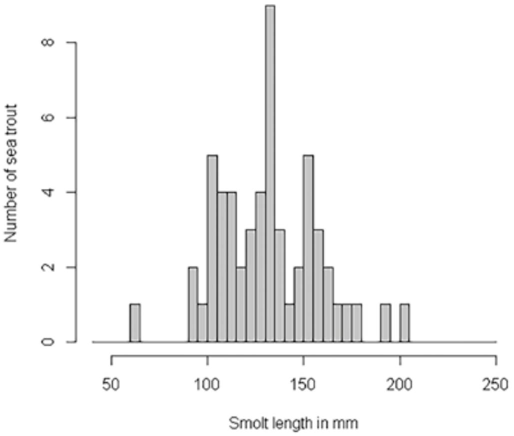

Figure 4: The back calculated smolt lengths (mm) of the 56 individuals studied in Tvedestrandsfjorden.

Tracking and monitoring

The 59 sea trout individuals were equipped with V9P-2L transmitter tags (Figure 2) (Vemco Division, Amirix System Inc., Halifax, Canada) implanted for acoustic monitoring. These cylindrical transmitters were 29 mm in length, with diameter 9 mm, weighing 4.7g in air. Hence, tag weight-to-fish ratio was < 3.8%. Each transmitter had a unique identity code that was transmitted as ultrasonic signals or "pings" every 100-250 second. The random interval of the signals reduced the chance of code collisions (Olsen & Moland 2011). In addition, the tags have a pressure sensor that provides vertical positions as well (accuracy ± 2.5 m when deployed at max. 50 m depth). The acoustic transmitter's battery life lasted for approximately 660 days. When the battery is empty, it simply stops sending signals (Olsen et al. 2012), but the tags remains within the fish until death.

A network constituting 51 passive stationary VR2Ws receivers (Figure 5) (Vemco Dicision, Amirix Systems Inc.) were constantly logging transducer signals received via omnidirectional hydrophones. These receivers where moored to the sea floor and deployed at around three meters depth (Olsen et al. 2012). The receivers were placed to give maximum coverage of the fjord (Figure 7), and secure a large enough minimum convex polygon (MCP) for the mean-position estimates (Simpfendorfer et al. 2002). Sentinel receivers where placed at Hantosundet, Saltneset and the outlet of Østeråbekken (Figure 1) to ensure recordings of roaming sea trout (Olsen & Moland 2011). The receiver at Østeråbekken and Hantosundet were used to register movement to the spawning streams, and the receiver at Saltneset to register movement in and out of the study area. The narrow little strait called Røskilen, was not covered with hydrophones. The receivers collected data from 30.04.2013 to 12.09.2014 and the data were downloaded during several periods: 17-27. June and 3-17. December 2013, and 7-14, April and 9-12. September 2014. Downloaded data where stored in a VUE database (Vemco Division, Amirix System Inc.) (Olsen et al. 2012; Simpfendorfer et al. 2012) and later exported to R (R- Core Team 2012).

Fate assignment

To determine if the fish was dead by anthropogenic or natural causes, a careful inspection of all individual depth- and position time trajectories were undertaken by Thomas Ruud, Thrond Haugen and Even Moland. If the tag suddenly disappeared from the study area, we decided that the fish where caught by a fisherman. If the tag, after long periods of normal behavior, abruptly was fixed at a position and depth for a long period, we concluded that the fish was caught and gutted on the same place at typical fishing sites. The tag was assumed thrown into the water after gutting or just followed unobserved with the gutting into the water. If the dataset showed a tag at nearly the same position during a long period, but with some differences in depth, we concluded that the fish was dead by natural or elusive causes. The depth variance where probably caused by the tidal water or currents. Lee and Bergersen (1996) did some of the same assumptions in their study. When a tagged fish was still at the same location for more than 48 hours, it was assigned dead. A candidate was assumed emigrated when the movement steered straight out to sea, and the last detection was at the furthest receiver in the system with no further detections during the study period (Olsen et al. 2012). Concluding the fate assessment, a total of three sea trout individuals were removed from the dataset due death following shortly after release. These candidates gave insufficient data to the study. The total number of sea trout retained for further analyses were 56 specimens. Following the fate assessment, the study specimens where categorized as “Dead”, “Alive”, “Caught” or “Emigrated”.

Figure 5: A VR2w receiver for passive monitoring of tagged sea trout (Photo credit: www.Vemco.com)

Position averaging

To estimate the sea trout positions, I used the mean-position-algorithm, available from Simpfendorfer et al. (2002) This was done at 15 minutes intervals per individual. The method uses the presence or absence of signals from the transmitters to the hydrophones at a given time, and estimates mean positions weighted by the number of signals received at each hydrophone. These signals are omni-directional pressure waves that travel through water and are received at omni-directional submerged hydrophones (VR2W) (Thorstad et al. 2013). The receivers partly overlap, so one unique signal can be detected by multiple hydrophones and subsequently estimate a mean position between the hydrophones for each fish over a given period. In my study, 15 min time slots were used. These signals are then summed and weighted by the number of detections at each receiver to give a mean position (Olsen et al. 2012). The accuracy of the positioning increases with the number of received signals within the time slot. This method is also called "the weighted-mean method" (Hedger et al. 2008). In a triangulation situation, if a receiver has more signals than other neighboring and overlapping receivers, this indicate that a fish has been proximal to this receiver (Simpfendorfer et al. 2002). The method will not give an exact position of the fish, but an approximate position between all hydrophones that received a signal during the chosen time slot (Olsen et al. 2012), also called position averaging (PAV).

Utilization distributions and movement metrics

The volumetric UD (XYZ-dimension) where given with horizontal UD (XY) added approximate mean depth (Z-dimension) during the same time slot (15 min). Overlapping horizontal position estimates are corrected with volumetric data, which can give individuals different depth distribution (Simpfendorfer et al. 2012). Figure 6 illustrates the mean volumetric utilization distribution of the individual with ID 1158183 during week 16. The depth data where given from depth sensors within the V9P-2L transmitters that each fish where tagged with. The estimates of the volumetric UD, were fitted and smoothed using the kde-function within in the ks-package in Rstudio (R- Core Team 2012).

The estimated PAVs were used for estimating individual utilization distributions (UDs), for the area within one removes outliers and only includes the area mostly used by the individual (Rogers & White 2007). I estimated UDs using the same smoothing parameter, h=28.7, across all individuals. This h-value constitutes the median value when running individual-wise least squared cross validation kernel fittings across all individuals. By forcing the same h- parameter on all individuals, direct comparison of home range sizes among individuals becomes relevant, without having to consider eventual effects from differential smoothing parameter on the UDs. Daily UDs were estimated using the kernelUD function embedded in the R package adehabitatHR (R- Core Team 2012).

The PAVs were also used for estimating daily linear distances at individual level, i.e., the total distance an individual swims per day. These linear distances were estimated using the R-package adehabitatLS (R- Core Team 2012). Volumetric UDs were estimated using the 3D PAVs. Technically, this was done using the kde-function available from the ks-package in R. In order to explore the activity level with the home ranges, I estimated a metric framed "turboness" which was simply the daily linear distance divided by UD 95.

In the triangulation of the horizontal home range estimates, a minimum of three VR2Ws had to be involved with every triangulation. That gave a potential of 96 unique relocations every twenty-four-hours. Days with less than 20 observations and 20 unique relocations from each ID where removed from further analysis. In the volumetric estimates, we used the average positioning of every 15 min, and days with more than 30 observations and each ID needed at least 10 unique relocations to be included. In the volumetric and depth estimates, the dataset showed 34907 positions above sea surface, and 11686 positions 50 meters below the surface. These positions where removed as well to simplify and avoid corrupted data.

The definition of activity within the 95 % favoring utilization area (delta displacement), has in this study been called "turboness". The turboness unity is meters/hectare/day, and has the importance to show how much the sea trout utilize their favoring areas. The 50 % home range where not covered with turboness analysis since the areas were considered too limited.

Statistical analyses

Space-use variables (depth, horizontal UDs and volumetric UDs) were included in univariate linear mixed effect models (LME) fitted to estimate effects from a range of external (e.g., air temperature, wind speed and precipitation) and internal (smolt length and length at capture) variables on the within Tvedestrandsfjorden habitat use. For UDs, the 50% and 95% distribution levels (i.e., the core distribution area/volume) were used as responses in the LMEs. Individual IDs were used as random intercepts to account for within-individual dependency of observations (Nakagawa & Schielzeth 2010). Model selection followed the procedures described in Zuur et al. (2009) utilizing Akaikes information criteria (Akaike 1974) for model selection. Model selection tables along with parameter estimate using tables of the selected models are shown in the appendix, and corresponding prediction plots of the selected models are displayed in the results chapter.

In order to quantify eventual effects of using the no-take zone on individual fate, a multinomial modelling approach was undertaken by the fate data as response and fraction of time spent inside no-take area as predictor. The fraction spent inside the no-take zone was based on PAV assignments to either "inside" or "outside" using the over-procedure in sp- package in R. This procedure overlays the PAVs with the no-take GIS-polygone. I also fitted generalized linear mixed effect models to explore which environmental and individual characteristics that most efficiently predicted the probability of using the no-take zone. This was done by using the glmer-function in the lme4-package. I followed same model selection procedures as described for the UD modelling.

In the analysis of examining the probability of using the no-take zone, I simplified the data to make the process easier, and used the triangulation positions inside the no-catch area compared with positions outside for fate of the individuals. Outside positions were called Buffer zone and inside positions called No-take zone (Table 1). In the selection of parameters for this test, I wanted to see what individual characteristics would determine the probability of using the no-take zone. Therefore, no climatic parameters were included in the model selection.

Results

Studied individuals

Of the 56 sea trout that remained, I got 498 days of continuous passive monitoring of their horizontal and vertical movements, resulting in estimations of their favoring utilization distri-

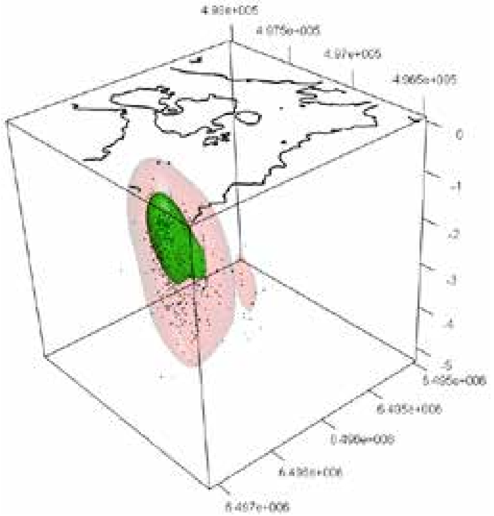

Figure 6: The mean volumetric distribution of the sea trout with ID1158183 during week 16. Green area indicate UV 50 and pink area UV 95. XY-axis are coordinates in UTM 32, datum WGS 84, and Z-axis depth in meters.

Table 1: A summary of the numbers of positions inside and outside the No-take zone according to their preliminary fate

Fates	Buffer zone	No-take zone
Alive	41280	17665
Caught	87322	80470
Dead	59449	84693
Emigrated	100795	50582
Total	288846	233410

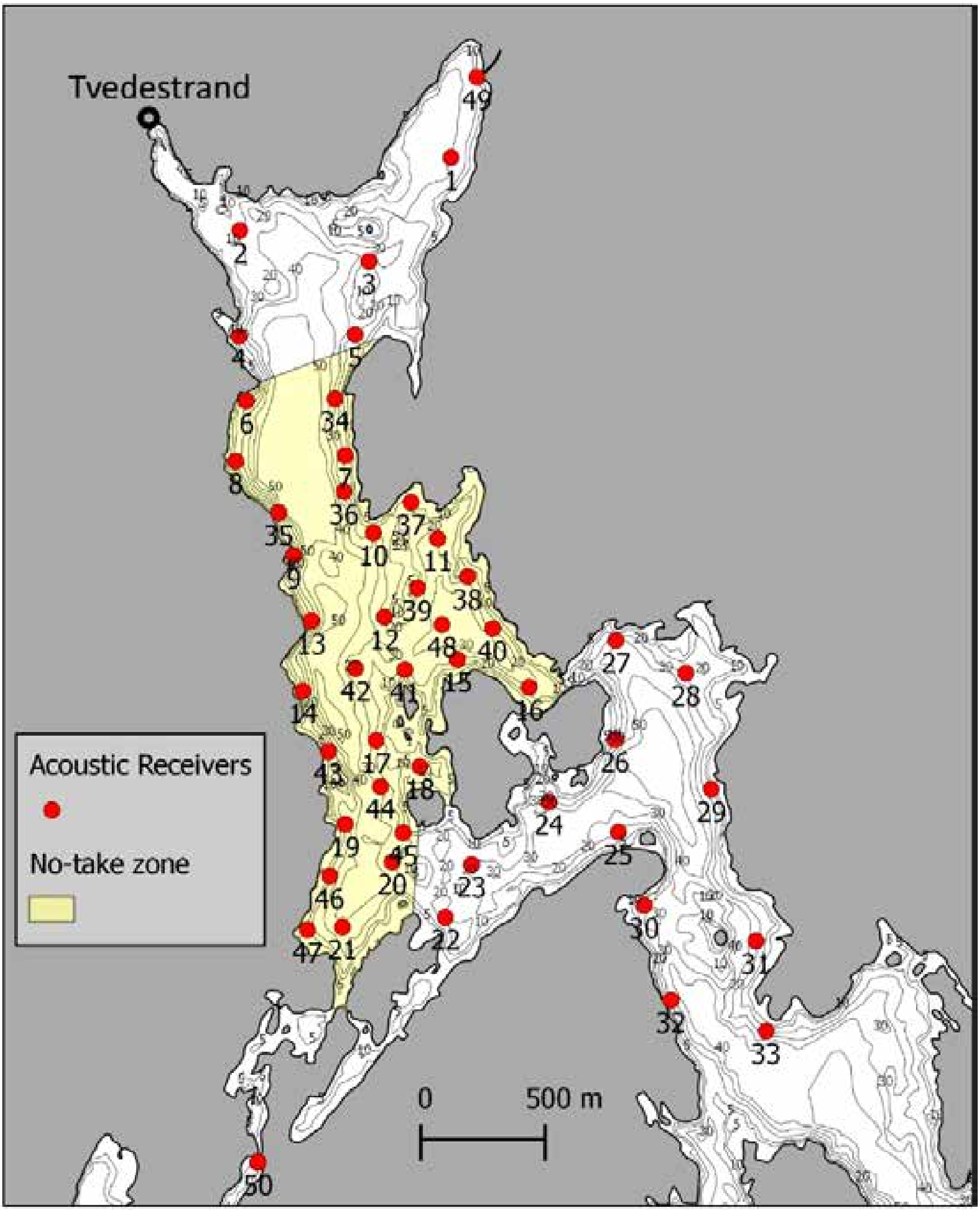

Figure 7: The location of the first 50 stationary receivers in the study area. (Figure credits: Carla Freitas, IMR)

bution. Of the 56 studied specimens, 38 sea trout remained in the fjord system during the whole study period, while 18 fishes emigrated from the system, never to return. Of the resident sea trout in the fjord, only 8 individuals were alive at the end of the study. In total, 30 fishes were either captured by fishermen or dead due to other elusive causes. A simplified overview of their fates is presented in Table 2.

Table 2: The final fates of the 56 individuals equipped with transmitters in Tvedestrandsfjorden.

Total	Alive	Caught	Dead	Emigrated
56	8	16	14	18
100%	14%	29%	25%	32%

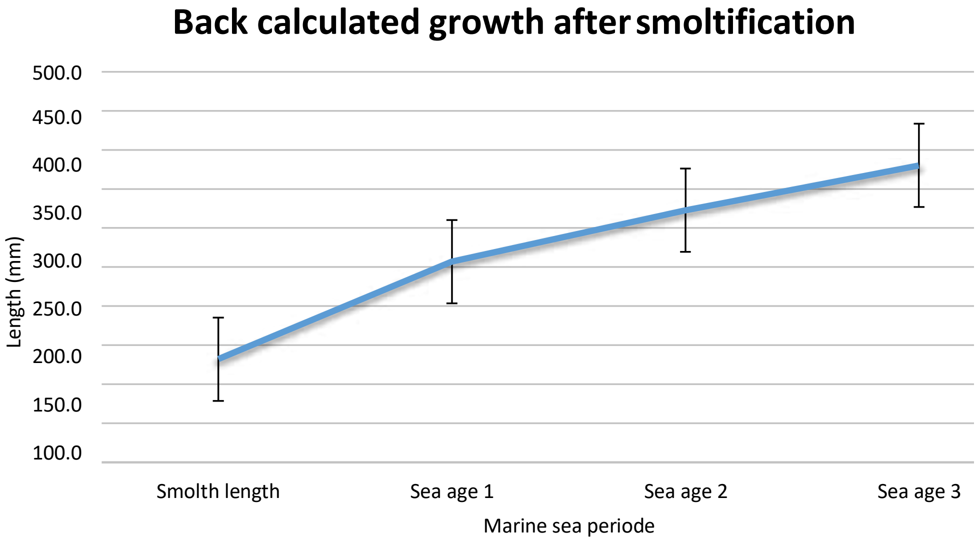

Figure 8: Back calculated growth in the sea from smolt lengths, estimated from scales.

Smolt lengths

The mean back-calculated smolt length was estimated to 131.9 ± 27.7 mm, with a minimum length of 60.3 mm and maximum length of 203.0 mm (Figure 8). The growth in length during the first season in the marine environment is was expressive, as illustrated in Figure 8. The individuals have a continuous growth the forthcoming years after their first season at sea, however with a reduced growth rate as they age. The estimated mean growths was 125 mm from smoltification to first year at sea, 65.9 mm from first to second year at sea, and 57.4 mm mean growth from second to third year at sea.

Home range 50

When analyzing the UD kernels that contained 50% of the probability distribution of the triangulated positions in the horizontal plane, the most supported linear mixed effect model showed an additive effect between month and smolt length to explain the log- transformed home range 50. The results indicated a trend towards reduced home range with increasing smolt length (Figure 9). The home range 50 had highest effect in April, May and September. These effects were also significant.

Home range 95

The results from the model selection of the 95% horizontal utilization distribution area also revealed an additive effect between month and smolt length. The prediction plot of the most supported model to predict the log-transformed home range 95 also showed a trend that indicated reducing home range with increasing smolt length. This effect where strongest in April, May and June, as they were also significant. In February, the effects where highly negative, indicating a significant reduced home range compared to January (Figure 10).

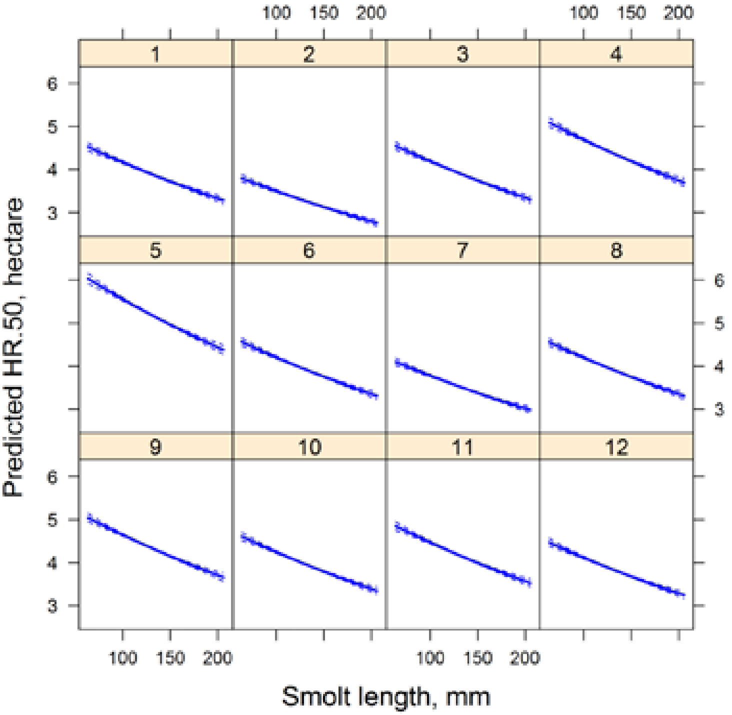

Figure 9: Prediction plot showing predicted 50 % home range (hectare) dependent on smolt length (mm) for each month of the year.

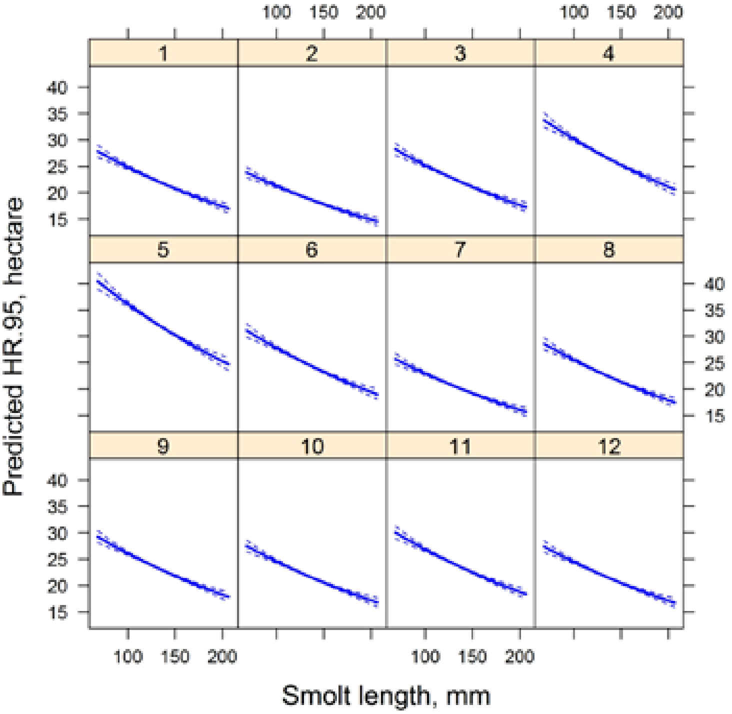

Figure 10: Prediction plot showing predicted 95 % home range (hectare) dependent on smolt length (mm) for each month of the year.

Turboness

The model selection results showed two supporting models fitted to predict log-transformed turboness. The most supported model revealed purely additive effects of month, smolt length and air temperature^2, and an additive effect of month and smolt length for the second-most supported LME-model. The turboness-effect in the most supported model was almost entirely dependent on the smolt length, as illustrated in Figure 11. The turboness increased with increasing smolt length, however decreased with increasing temperature. The temperature effect were low though. The effect of turboness were high in the summer, and increase from June to September, where the significance also was highest. The prediction plot for the second most supported model showed a trend that increasing smolt length increased the turboness (Figure 12). The turbo-effect also grew stronger from June towards September , where the significance also is strongest.

Total daily distance

Two models where fitted to predict the log-transformed results for the total distance per day (in meters). The most supported LME-model revealed additive effects of month, smolt length and air pressure^2, and the second most supported model showed factorial effects of month, smolt length and air pressure.

The prediction plot for the most supported LME-model illustrate additive effects that describe the mean total distance per day, where the air pressure weights the prediction of mean total distance per day compared with the smolt length (Figure 13). At a given air pressure of approximately 1000 hPa, the mean total distance were at its lowest, with increasing distance with increasing and decreasing air pressure interconnected with increasing smolt length. The effects of smolt length and air pressure on the mean total distance where however low. The effect of total distance per day where high from April to June, and from August to October. The total

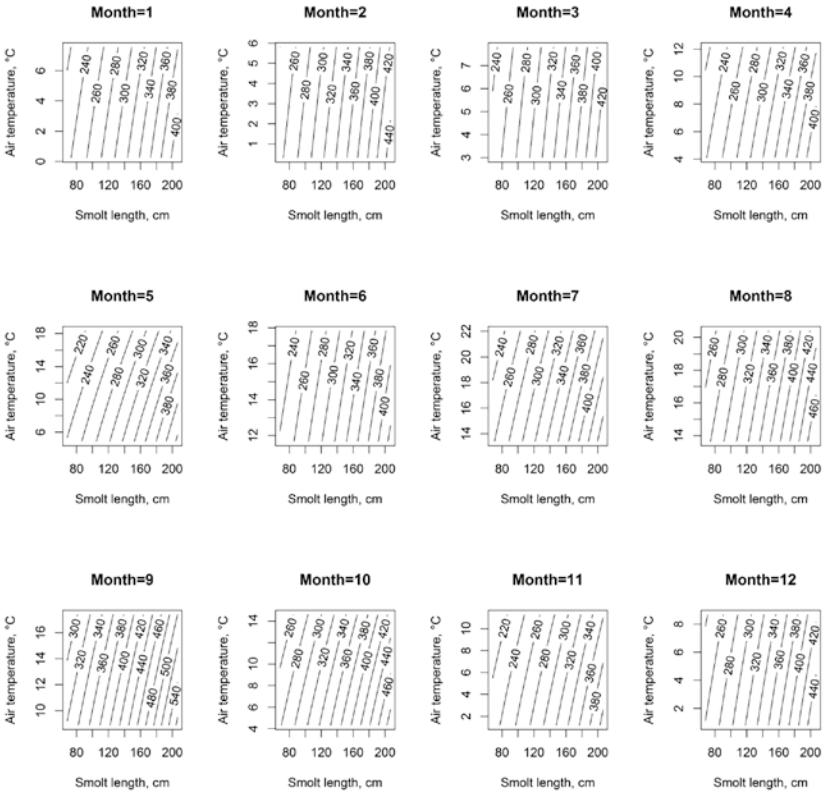

Figure 11: Prediction plot showing predicted turboness (m/hectare/day) within home range 95 dependent on smolt length (mm) and air temperature (ºC) for each month of the year.

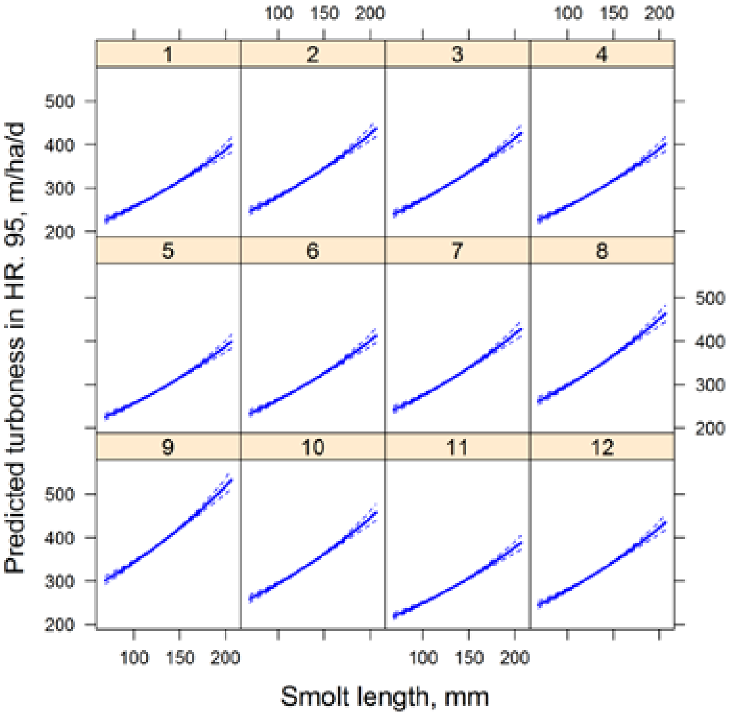

Figure 12: Prediction plot showing predicted turboness (m/hectare/day) within home range 95 dependent on smolt length (mm) for each month of the year. Head numbers indicating months.

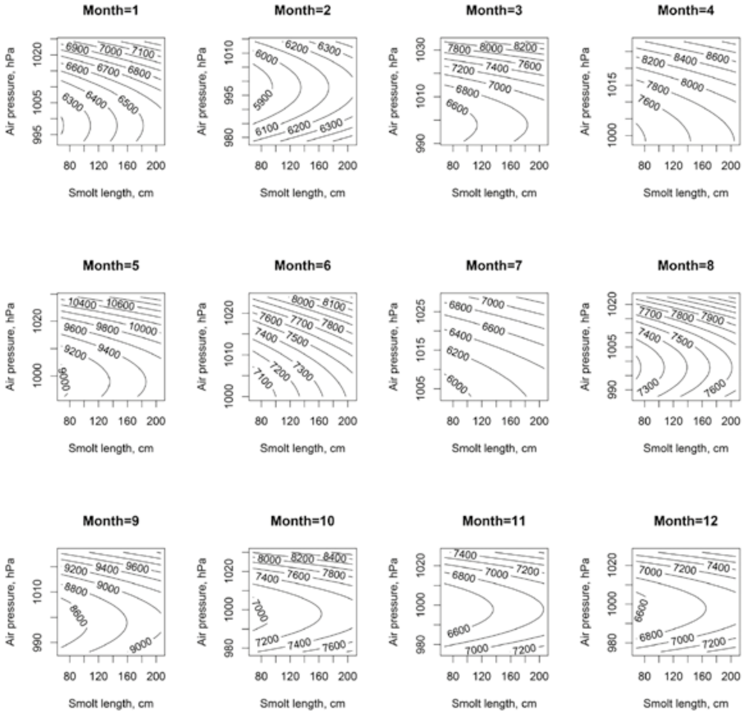

Figure 13: Prediction plot showing total distance (meters) dependent on smolt length (mm) and air pressure (hPa) for each month of the year. Head numbers indicating months.

distance was at its peak in May, and at its lowest in July.

Figure 14 shows the far more complex interactions that describes the second most supported model. The plot reveals saddle points, which mean that the mean total distance per day increases with increasing air pressure and increasing smolt length, but also increases with decreasing air pressure and decreasing smolt length. These effects where however low. The monthly effects were also in this model strongest from April to June, and August to October, where the effect was strongest and most significant in May and lowest in July.

Depth use

The model selection for the log-transformed mean depth use, showed complex and exclusively factorial effects of month, smolt length and air pressure^2. The corresponding ANOVA-test revealed highly significant interaction effects.

The depth use is, throughout the year, almost entirely dependent on smolt length. However, in the months May, August and September, the air pressure may explain the depth use also (Figure 15). In August, there is an optimum depth use at around 1010 hPa. At the same optimum, the depth use increases even further with increasing smolt length. The maximum mean depth utilization from January to April is heavily dependent on smolt length, whereas fish with longer smolt length had a deeper mean depth. The depth use trend from Figure 18 indicate a shallow use in the water layers, with depths ranging from around 0.7 to 7 meters, independent of the max depth at the location.

Utilization volume 50

The results of the utilization volume 50 (UV 50) were backward-selected because of complex interactions. The complete list of fixed effects parameter estimates for the most supported LME-model fitted to predict log-transformed UV 50, is presented in Table A9. The most supported LME-model showed complex interactions effects of month, smolt length and air

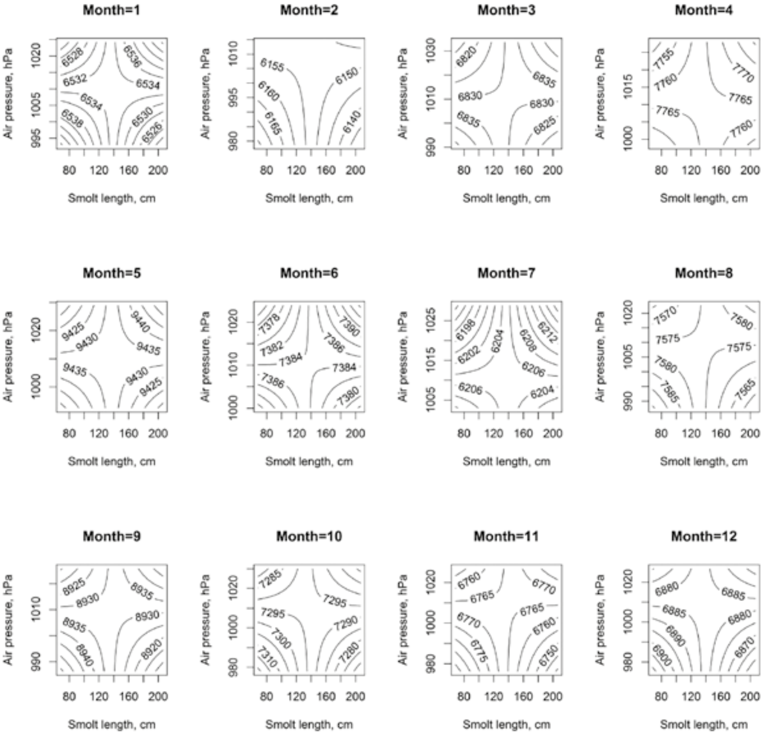

Figure 14: Prediction plot showing total distance (meters) dependent on smolt length (mm) and air pressure (hPa) for each month of the year. Head numbers indicating months.

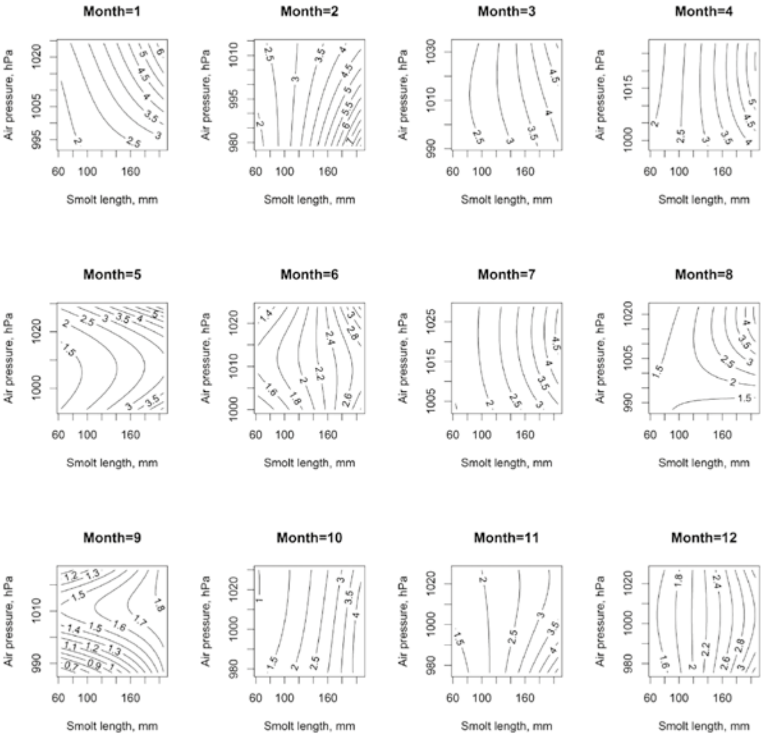

Figure 15: Prediction plot showing the mean depth utilization dependent on smolt length (mm) and air pressure (hPa).

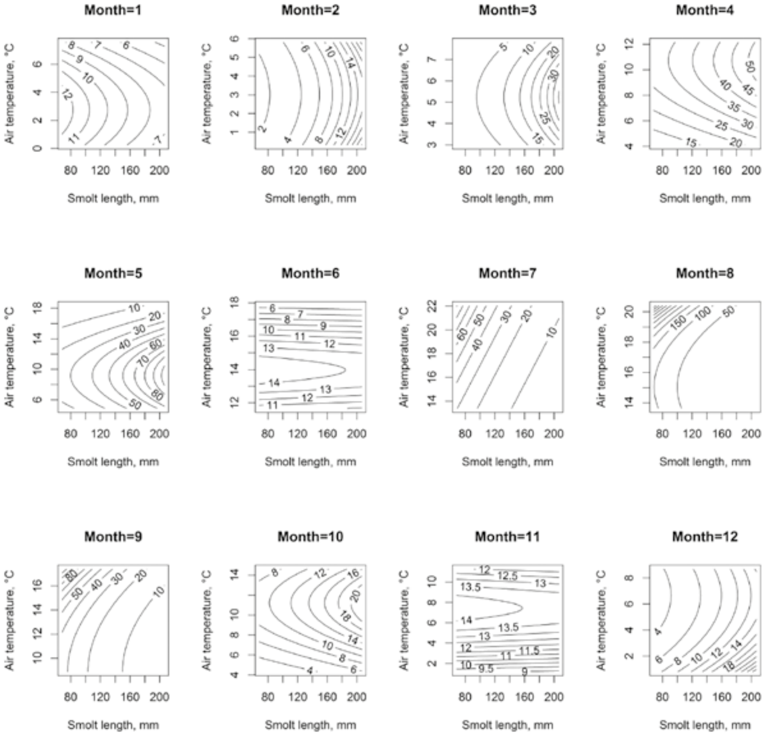

Figure 16: Prediction plot showing UV 50 (gigaliters, 10^9 L) dependent on smolt length (mm) and air temperature (^{o}C).

temperature[2]. The corresponding ANOVA-test revealed significant interaction effects.

From February to May, UV 50 increased with air temperature and smolt length, however best explained by the individual's smolt lengths (Figure 16). During the warm summer moths of June and July, the UV 50 became reduced. In June, the UV 50 was optimal at approximately 14 °C. In August, the UV 50 is again increased, but was reduced in September and the following autumn months. However, with an optimum temperature each month to explain the spatio-temporal usage. In November the usage is union with the smolt length, and only dependent on the air temperature.

Utilization volume 95

The most supported LME-model to explain utilization volume 95 (UV 95) showed fully factorial effects between month and smolt length. In the prediction plot (Figure 17), there were trends towards increased UV 95 from February to May with increased smolt length. In June, UV 95 was compressed and reduced. From July to October, the trend where opposite. The UV 95 decreased with increasing smolt length. From October to January, the UV 95 was again compressed and reduced, however with a weak increase with increasing smolt length. However, the effect of the smolt length on the UV 95 was low, with low significance. The effect of the UV 95 where highest in April and May, whereas significance also where high.

Discussion

Fates and utilization

In the present study, smolt length, air temperature and air pressure had strong effects on the space use in Tvedestrandsfjorden. In addition, did smolt length and length at capture highly influence the fates and behavior of the sea trout in the fjord. Of these variables, smolt length was the one variable that showed significance and decisive effects on all behavior traits.

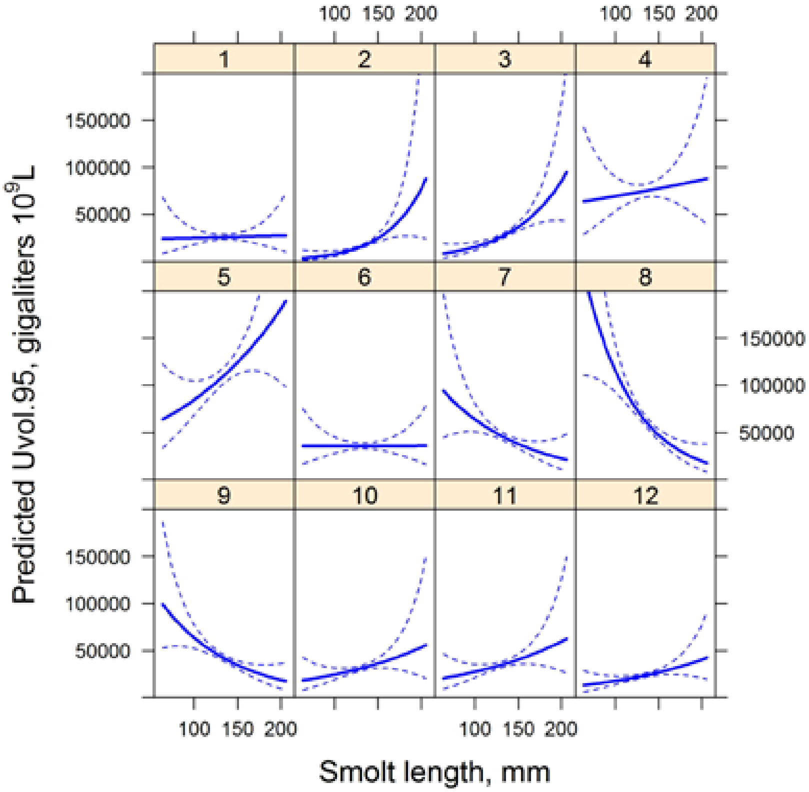

Figure 17: Prediction plot showing UV 95 (gigaliters, 10^9 L) dependent on smolt length (mm). The predictions where gathered from the most supported LME-model reported in Table 17.

Horizontal and vertical activity of the sea trout varied throughout the year. The results indicated increased activity from April towards June, and in early autumn from August towards October, while activity was reduced in July and the winter months. This may be interconnected with seasonal feeding intensity. Earlier examinations of feeding activity of sea trout indicated that the fish fed most heavily during spring (April-May)(Pemberton 1976b) and autumn (August-September) (Borgstrøm & Heggenes 1988; Knutsen et al. 2001b; Olsen et al. 2006), with a minimum during July (Knutsen et al. 2001b) and the winter months (Rikardsen et al. 2006). However, the activity peaks also coincide and may be explained with smolt migration from freshwater to the sea in the spring (Jonsson 1985; Jonsson & Gravem 1985), spawning activity in the autumn (Jonsson 1985; Elliott 1994; Klemetsen et al. 2003), and possibly optimal growth temperatures (Elliott 1975; L'Abèe-Lund et al. 1989; Forseth et al. 2009; Jensen et al. 2014).

With increasing smolt length, individuals had characteristics towards increased turboness, mean depth, mean total daily distance and increased utilization volume in autumn. However, increased smolt length gave reduced utilization distribution. Moreover, individuals with smaller smolt length had increased utilization volume in spring, however not in autumn. The utilization distribution increased during both spring and autumn with decreasing smolt length. The depth use was also at a minimum in September with decreasing smolt length. The present findings correlates with observations recorded by Dzadey (2014), who also found that smolt length highly influenced the distribution and activity of sea trout in the marine environment.

Individuals with large smolt length may have been more exposed to fishing as they had high activity and increased utilization volume in the spring. However, individuals with smaller smolt length were also exposed. These individuals had the largest utilization distribution during the entire year, and high utilization volume in the autumn.

The mean back-calculated smolt length (Figure 8) at 131.9 ± 27.7 mm, with a minimum and a maximum length of 60.3 mm and 203.0 mm, respectively, are within the smolt lengths recorded in several other sea trout studies in the Aust-Agder. Ingebrigtsen (1998) recorded the mean smolt length to be 120 ± 38 mm in Østeråbekken. In the nearby river Langangselva, the smolt length was somewhat larger and had a mean length of 143 ± 0.90 mm (L'Abèe-Lund et al. 1989). L'Abèe-Lund et al. (1989) explained varying smolt lengths to be influenced by abiotic factors, in which increasing river length, water discharge and latitude seemed to give increased smolt length, while smolt length decreased highly with decreasing temperature at sea.

Fjord residency

In later years has the concept of partial migration in the marine environment received much attention and recognition. Several studies have documented that the sea trout actually may remain in high numbers in a fjords inner coastal systems during their entire marine stay (Knutsen et al. 2001b; Knutsen et al. 2004; Olsen et al. 2006), without a continuum migration to the sea (Urke et al. 2010; Aldvén et al. 2014; Davidsen et al. 2014c; del Villar-Guerra et al. 2014). The sea trout in Tvedestrandsfjorden had a tendency towards fjord residency, whereas 32% of the tagged sea trout emigrated and 68% remained in the system. This differ somewhat, but not greatly from the observations published by del Villar-Guerra et al. (2014), who found that 53% of the tagged sea trout emigrated and 47% remained. They found no evidence that size (length or weight) nor body condition (Fulton's K) affected the fate.

However, Bendall et al. (2005) saw that migration in coastal waters were size dependent, whereas larger fish migrated faster and further than smaller fish. Davidsen et al. (2014c) also found migration to be size dependent, but at smolt level. Larger and older smolts had a longer continuum migration, though these individuals also had poorer body conditions than the fjord residents. These findings differ somehow from the present study. I found that the smolt length highly influenced the marine behavior, and that short lengths at tagging in the marine environment induced emigration from the fjord. The seaward migration alternatives may also be affected by nutritional status (Boel et al. 2014; Davidsen et al. 2014b) and lipid depletion (Boel et al. 2014) in addition to smolt length prior to the downward journey from the spawning stream to the marine environment. Individuals with high growth rate as 0+ and poor growth as 1+, but still had high metabolic needs, sought better conditions at sea and migrated (Jonsson & Jonsson 1993; Forseth et al. 1999; Cucherousset et al. 2005). The energy storage and condition of the fish may thus decide the distance of migration when entering the marine environment, whereas individuals with low energetic levels and low lipid depositions as smolts are inclined to a shortened partial migration within the fjord (Sheridan 1989; Jonsson & Jonsson 1998; Forseth et al. 1999; Boel et al. 2014; Davidsen et al. 2014b). If these individuals also have a high metabolic demand, the chance of fjord residency increase even further, if these needs are fulfilled with early encounters of suitable habitats (Cucherousset et al. 2005). This can also explain the negative tendency of migration if the distance and cost of wandering exceeds the internal energetic status of the smolts (Kristoffersen et al. 1994; Jonsson & Jonsson 2006), and force the individuals to an early partial migration and fjord residency.

Other studies (Davidsen et al. 2014a; del Villar-Guerra et al. 2014) including the current results, indicate a relative high ratio of lacking returns of the local sea trout to their natal spawning areas. After an emigration and migration continuum to the outer coastal areas and the sea, these individuals have an uncertain fate, but may have dispersed to other coastal areas. Earlier examination from coastal Aust-Agder shows colonization and dispersal of sea trout to new fjords and river systems (Knutsen et al. 2001a). This may help explain the high emigration ratio, and might as well be a genetic dispersal mechanism within the sea trout species (Bekkevold et al. 2004).

Acoustic telemetry

Acoustic telemetry is now one of the most cost and labor-effective methods to monitor marine habitat utilization (Kessel et al. 2014), however climatic and biological factors may alter the detection rate and results of the ultrasonic hydrophones. Wind and waves may highly affect the detection rate of hydrophones, together with rain and the depth of the hydrophones (Gjelland & Hedger 2013). Stratification and thermocline creation following different seasons, with tidal and flood currents may also create variability and reduced detection rates. (Mathies et al. 2014). Sound travels faster in increasing water temperature, fish at depths of 4- 5 meters have therefor the highest probability of detection. However, probability of detection may decrease if the receiver is located deep and the transmitter is above the thermocline (Gjelland & Hedger 2013). In the present study, the depth utilization showed favoring depths between 1-5 meters. The data may therefore have some errors caused by wind and waves, however the depth utilization where at levels of high detection rate. Optimal days of detections of sea trout may thus be clear warm days with little wind disturbance.

To minimize errors, detection ranges should be tested before, during and after a study. A sentinel receiver may also be placed and act as a reference to detection tests (Kessel et al. 2014). The kernel method which smooth's the utilization distribution will easily uncover areas with high activity (Worton 1987), though optimized interpolation of the spatiotemporal utilization will highly depend on the kernel size. A box kernel will give higher errors than a "normal" kernel, and additionally a high density of hydrophones will give significantly reduced errors (Hedger et al. 2008).

Biological errors caused by predation could however be difficult to counteract. Cod, sea birds and seals are present in Tvedestrandsfjorden and could predate especially young sea trout (Lyse et al. 1998; Dieperink et al. 2001). Data may have been corrupted if a tagged individual was consumed by a cod or caught by larger predatory animals. There may actually be a chance that some of the data were recordings from within a cod, however such inconceivable errors may not last longer than a few days before the tag has passed through the cod (Zeller 1999).

Reproducibility

This study is unique as there have been few studies on the spatiotemporal use of sea trout in their marine habitat, and in a short fjord system with a mosaic of depths, habitats and no estuaries. The reproducibility to other studies may therefore be limited. However, studies conducted in similar fjord systems or in Southern-Norway east of Lindesnes may officiate. Studies conducted in quite different systems, such as long shallow fjords, almost as lake systems towards the sea in Denmark (Boel et al. 2014; del Villar-Guerra et al. 2014), or long and very deep fjords at the west coast and in northern parts of Norway (Jensen & Rikardsen 2008; Urke et al. 2010; Davidsen et al. 2014c) may be less comparable. The arrangement of the receivers are also highly important. The current study has used a long-term triangulation setting of receivers to maximize coverage of Tvedestrandsfjorden, whereas other studies used "curtains" of receivers as transects crossing the fjords at certain sections (Aldvén et al. 2014; Davidsen et al. 2014c; Jensen et al. 2014). Curtain arrangement of the receivers will not give the same detailed XY positioning opportunity, and will therefore not have the same basis of comparison. The latitudinal difference between Europe and Norway also has consequences for the life-history of the sea trout as well (Jonsson & L'Abèe-Lund 1993).

Conclusion

The marine behavior of the sea trout seems to be highly influenced by smolt length, and hence the life and development in early stages in freshwater. More studies on individual traits like growth, metabolism and lipid deposition of sea trout compared to their utilization of the marine environment, will give a better understanding of the behavior and life history of the sea trout in coastal waters.

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