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Sea trout (*Salmo trutta*) area use and harvest selection: different traits lead to different fates

Ida Kessel Nordgård
Environmental Management

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Preface and acknowledgements

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Abstract

The sea trout (*Salmo trutta*) is a popular target for recreational fishing along the coast. Harvest selection is known to often fish out large individuals in a population, selecting for small size and early maturation in populations. However, selection of behavioral traits through fishing has been overlooked for a long time. In Tvedestrandfjorden, a marine protected area (MPA) has been established in order to protect fish with a none-fishing zone in the middle of the fjord and a buffer zone on each side where only hook-and-line fishing is allowed.

A total of 59 sea trout individuals were implanted with acoustic transmitters and their movement in Tvedestrandfjorden was tracked for 18 months. The data was analyzed using capture-mark-recapture analysis. The fish were assigned one of four possible fates during this period: alive, dead, dispersed or harvested.

The results showed that there were differences in habitat use between the four groups, and that it was possible to point to behavioral trends in each group both for short- and medium-scale migrations. The behavior of the fish could be connected to their fates in ways which made sense. In most cases, temperature had a positive effect on migration activity. The surviving group which did not disperse showed clear trends of staying more inside the notake area than the other groups, and were thus probably protected by the regulations within this area. This shows that the MPA does have a protective effect for sea trout, but may also cause selection for the behavioral traits found in this particular fate group, ultimately leading to adaptation of a more stationary and less bold behavior.

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Introduction

Recreational fishing like angling is a popular sport in both rivers and coastal areas in Norway (Liu et al., 2011). This has been shown to impact fish stocks and even to have the potential to deplete entire fish populations (Arlinghaus et al., 2007). However, little focus has previously been given this issue, most likely due to historical and cultural reasons regarding fishing. Studies on cod (*Gadus morhua*) have shown that mortality caused by harvesting during some periods actually may be higher than the natural mortality (Olsen and Moland, 2011). Cod populations can thus be highly affected by harvest selection by humans, and the population dynamics altered by this (Olsen et al., 2012). These results are most likely transferable to other fish species experiencing fishing pressure as well.

Fishing pressure may cause particular groups in a population to evolve in order to avoid being harvested. Large fish may develop earlier maturation at smaller sizes, or an increased investment in reproduction at a younger age (Jørgensen et al., 2007). In areas with a lot of recreational fishing, it is not a coincidence which fish get fished. Size-selective harvest of big fish over smaller ones is likely to affect the entire fish population because it favors the slow growing individuals (Fenberg and Roy, 2008). This may also be enhanced by lower size limits on fish in fishing management (Anon., 2016).

In recent years, evolutionary changes caused by fishing pressure have been given more attention. However, most of these studies only focus on size-selective harvesting, and research on evolution of fish behavior caused by fishing is often overlooked (Alós et al., 2016; Uusi-Heikkilä et al., 2008). These evolutionary changes may be developing quickly, for some fish the behavior can evolve and become visible within decades (Jørgensen et al., 2007).

Natural selection and harvest selection in many ways favor the opposite traits; while natural selection often favors the fast growing individuals, harvest selection often makes it more advantageous to be of a smaller size. Evolutionary traits can be related to behavior, and affected both by evolutionary processes within the habitat, and outside fishing pressure from humans (ibid.). Trapping, angling and gill-netting are fishing methods that most likely have direct effects on the behavior of fish because behavioral traits rather than body size, for

instance temperature use and vertical distribution (Bøe, 2013), determines whether a fish is caught or not (Uusi-Heikkilä et al., 2008). Both natural and harvest selection need to be taken into account when trying to explain evolutionary dynamics in fish populations (Ede- line et al., 2007) and determining management measures thereafter.

Owing to the size-selective nature of harvesting, growth and growth-related traits (e.g., maturation) have been demonstrated as sensitive to fishing. Growth is one of the most concretely measurable traits, and also one that is influenced by both biotic and abiotic factors like temperature, harvesting pressure or competition from other fish (Bærum et al., 2013). This is why information regarding growth is valuable when trying to determine behavioral patterns and differences between fish. For partially migrating fish species like the brown trout (*Salmo trutta*), growth at young age is one of the main traits determining whether or when the fish stays in freshwater or migrates to the sea (Jonsson and Gravem, 1985). The migrating part of the population are called sea trout, the growth of which is usually at its highest around the end of June (Berg and Berg, 1987). Individuals that grow quickly and mature late usually have a higher mortality than fish with early maturation at smaller sizes (Jørgensen et al., 2007).

Behavioral traits are to an increasing degree acknowledged as factors that can influence other traits like growth and reproduction (Biro and Stamps, 2008; Jonsson and Finstad, 1995). Examples of such traits are aggressiveness, curiosity, activity level or boldness (Biro and Stamps, 2008; Uusi-Heikkilä et al., 2008). Depending on the number of predators, active individuals can have either an advantage or a disadvantage; in the absence of predators, activity leads to increased food intake and thus growth rate, while in the presence of predators, activity increases the chance of being eaten (Sih et al., 2004). In a study of carp (*Cyprinus carpio*), Klefoth et al. (2012) found that boldness in some fish seemed embedded in the fish, as it was expressed both in situations where there were no predation risk as well as situations with predation risks. This indicates that the level of boldness in fish is a genetic trait. Klefoth et al. (2013) further found that boldness in carp was a trait that made the fish more likely to get fished, but also that the fish were able to learn to avoid capture by fishing.

Behavioral traits should be given more attention when studying fish behavior in the future. Réale et al. (2007) suggests to divide temperamental traits into five different categories: shyness-boldness, exploration- avoidance, activity, sociability and aggressiveness.

Sutter et al. (2012) found that traits like aggression, intensity of parental care, and reproductive fitness were traits common in individuals vulnerable to harvesting, and thus that selective fishing may have a negative influence on populations by removing fish with these traits.

Temperature also appears to affect fish behavior (Jonsson and Finstad, 1995). For instance, small and young sea trout have been found to depend more on high water temperatures

when descending to the sea than larger fish (Jonsson and Jonsson, 2002). Furthermore, the amount of food available to the fish usually increases when the temperature increases during the summer (Bærum et al., 2013), which also may affect fish behavior.

The sea trout is a suitable species for studying effects from fishing, as it is a popular target for both recreational- and sport fishing (Anon., 2016; Jonsson and Finstad, 1995), but not allowed to harvest using fishnets (Åpningsforskriften, 2003). Knowledge of how sea trout use their habitat is scarce, both in the sea and after their return to freshwater (Jonsson and Finstad, 1995). Habitat use may be of great influence to things like reproductive success, resource use or individual survival (Kramer et al., 1997). Compared to Atlantic salmon (*Salmo salar*), sea trout usually remain in the inner parts of fjord systems for a fairly long time after their first marine migration, after which they usually stay in the coastal areas (Jonsson, 1985; Thorstad et al., 2007). However, differences between migration patterns in sea trout have started to receive increased attention. Eldøy et al. (2015) found that even though 42 % of the fish in their study had long-distance migrations, they spent 68 % of their time <4 km from the river mouth. Furthermore, long-distance migrants had poorer body conditions than the other groups at tagging, suggesting that they thereby had a greater physical need to migrate longer in order to feed. Pelagic feeding is beneficial for long-distance migrants because in the pelagic zone they can feed almost exclusively on fish, as opposed to near-shore feeding where the diet consists of crustaceans, polychaetes, insects and fish (Rikardsen and Amundsen, 2005). Villar-Guerra et al. (2014) suggested a "*migratory decision point*" when the fish enter the fjord from the freshwater stream, at which point the fish decide whether they will migrate long-distance or stay in near-shore areas.

Marine Protected Areas (MPAs) are usually established due to one of two reasons: to manage fishing in an area in order to avoid overexploitation, or to protect biodiversity and structure of an ecosystem (Seytre and Francour, 2008). In Tvedestrandsfjorden an MPA was established June 20th 2012, lasting until June 20th 2017 (Forskrift om bevaringssoner i Tvedestrand, 2012). The MPA was established due to sinking populations of several fish species, like cod, and Tvedestrandsfjorden was considered an important area for these species, both for spawning in the inner part of the fjord, and feeding grounds for young fish around Hestøya and Furøya (Knutsen et al., 2003). It is uncertain whether the establishment of the MPA has any effect on the sea trout population, as they are a fairly migratory fish species (Berg and Berg, 1987), but they, too, have been found to stay in the fjord for feeding (Knutsen et al., 2003).

In 2015, more than 273 tonnes of wild Atlantic salmon and sea trout were fished in Norwegian fjords, a 15 % increase from 2014 (Statistisk Sentralbyrå, 2016). Thus, the establishment of an MPA in Tvedestrandsfjorden may have altered potential harvest selection in the middle

of the fjord from before the regulations were introduced. Since hook-and-line fishing is still allowed in the inner and outer parts of the fjord, harvest selection may still be going on in these areas.

In Seytre and Francour (2008), the Cape Roux MPA, was established in the Mediterranean Sea in December 2003 in order to enhance targeted fish stocks and manage the industry more closely. They found that species richness and fish abundances increased severely during the three years of monitoring, thus the establishment of the MPA was a success.

Information regarding the whereabouts and movements of fish within a fjord may be of importance when trying to determine the cause of an individual's fate, and whether its behavior has any effects on this. This information can further be used to see if any behavior appears to be advantageous. Spatial behavior may thus contain clues pointing to the future fate of the fish.

Multistate capture-mark-recapture analysis can be used to attain such information about spatial use, both small-scale and larger-scale migrations within the fjord. Mark-recapture analysis can thus be used to model behavior within the area. Placing acoustic receivers in the fjord to monitor the movement of the sea trout works because the sea trout usually stays close to the river out of which they descended. In Berg and Berg (1987), 52.8% of the fish in a capture-recapture study was recaptured within three kilometers from the river mouth. In this study, I aim at assessing whether area use is different among fate groups of sea trout within the Tvedestrandfjorden study area. Further, I quantify effects from both individual size and weather on area use and, finally, if the MPA has had an effect on sea trout fates during the study period.

Materials and methods

2.1 Study area

The study area is Tvedestrandfjorden in Aust-Agder county in the southern part of Norway, 58°36'23"N and 8°56'56"E. The entire fjord is approximately 8 km long (Kroglund et al., 2003), whereas the sampling area in this study is only the 4.5 km in the inner part of the fjord. The area is 3.9 km wide, with a maximum depth of 85m (Ciannelli et al., 2010). The catchment area is 38 km² (Kroglund et al., 2003). The fjord is a part of a large fjord system that stretches from Tvedestrand to the Skagerak sea (Knutsen et al., 2010).

Two islands, Hestøya and Furøya, are situated in the middle of the sampling area (Fig. 2.1). Around these islands, shallow areas create an approximately fifteen meter sill in the fjord system. This causes the oxygen saturation in the inner part of the fjord to become low, approximately $<1.5 \text{ ml L}^{-1}$ at 30-40 meters below the surface (Kroglund et al., 2003). The shallow areas also contain eel grass (*Zostera marina*; Anon. (2015)), where trout smolt often live (Pemberton, 1976). Eel grass meadows are an important nature type in Norway at a local level and an important marine ecosystem at a global level (Anon., 2010). In addition to this, several small freshwater streams have their outlets into Tvedestrandfjorden, which creates upper water layers of freshwater several places in the fjord (Kroglund et al., 2003). The deepest part of the fjord is the inner part, closest to Tvedestrand, where the depth is approximately 85 m (ibid.).

An MPA covers large parts of Tvedestrandfjorden (Forskrift om bevaringssoner i Tvedestrand, 2012). The MPA is divided into four zones with different fishing regulations (Fig. 2.1). The middle part of the fjord, around Furøya (1.4 km²), is a non-fishing zone with prohibition of all types of fishing gear. In the innermost part, Inner Oksfjord, (0.8 km²) and Sagesund (1.1 km²), hook-and-line fishing is allowed, but no other fishing gear. The last zone is an area called Kvastadkilen (0.5 km²) south west of Røskilen, where only hook-and-line fishing is allowed. However, the last zone is not part of the study area, hence we will refer to

Tvedestrandfjorden MPA zones

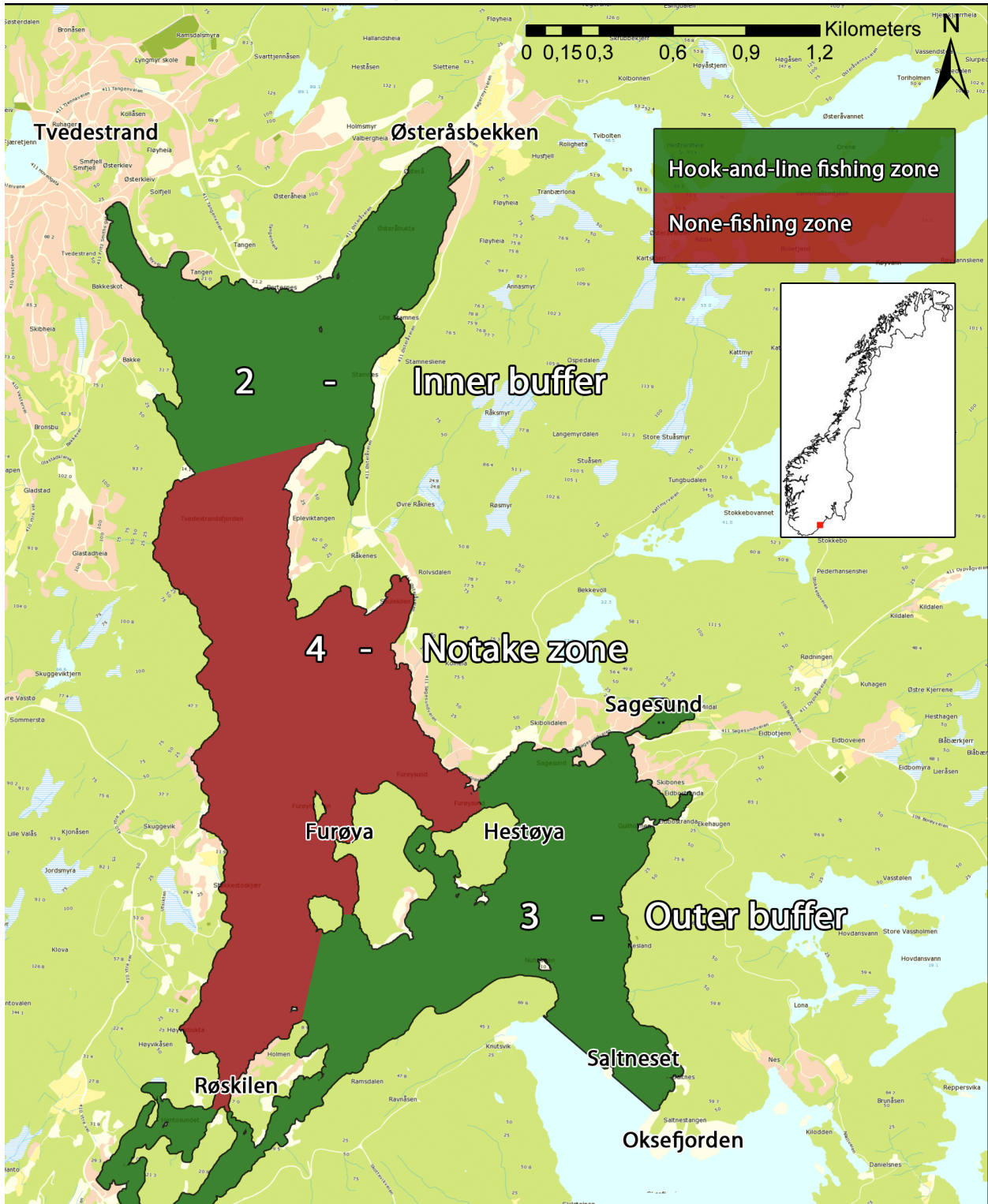


Figure 2.1: Map showing the sampling area, Tvedestrandfjorden with MPA zones. In the inner and outer buffer (green, zones 2 and 3) hook-and-line fishing is allowed, whereas in the no-take zone (red, zone 4), all fishing is prohibited.

three first three zones in this study (Table 2.1). In areas outside of the described prohibition zones, all forms of fishing gear is allowed.

Table 2.1: *The three different zones in the MPA in Tvedestrandfjorden, their individual number and fishing regulations for each zone.*

Zone	Number	Regulations
Inner buffer zone	2	Hook-and-line fishing allowed
Outer buffer zone	3	Hook-and-line fishing allowed
Notake zone	4	No fishing allowed

2.2 Weather data

Weather data containing information about air temperature and precipitation was obtained from *eklima.no*. A weather station in close proximity to the sampling area, Torungen Lighthouse, was used (Fig. 2.2; Table 2.2). Torungen lighthouse is situated approximately 24 km southwest of the sampling area. Out of the weather stations in the area, Torungen lighthouse is considered to be the one with conditions closest to the ones in the sampling area.

Data was collected for the whole sampling period, from the end of April 2013 to September 2014.

Table 2.2: *Information on Torungen Lighthouse, from which weather data was obtained. Source: *eklima.no**

Stnr	Name	Altitude	Latitude	Longitude	Municipality	County
36200	Store Torungen lighthouse	12	58°23'55.7"N	8°47'21.5"E	Arendal	Aust-Agder

2.3 Study species

The study species used in this project is the sea trout, the adult, anadromous form of the brown trout (Harris and Milner, 2006). The brown trout originates from Europe, but is now common in most parts of the world due to introduction of the species through releases in a number of countries (Elliott, 1994; Jonsson and Finstad, 1995). It lives as far north as Iceland, and as far south as North Africa (Elliott, 1989). The brown trout commonly lives in unpolluted and oxygen-rich rivers, streams, reservoirs and lakes (Elliott, 1994). The shape, size and coloration of the brown trout has been observed to differ between different rivers, and can also differ within populations in the same habitat (Elliott, 1994; Jonsson and Finstad, 1995).

Along the coast, it is common that a brown trout population is divided into two groups



Figure 2.2: *Tvedestrandfjorden sampling area in relation to the weather station Torungen lighthouse.*

which live by two different life strategies; one part is anadromous - living in both fresh- and saltwater - while the other part lives exclusively in their native freshwater stream (Elliott, 1994; Jonsson and Finstad, 1995). The anadromous brown trout is commonly called sea trout in order to separate between the migratory and the non-migratory brown trout (Harris and Milner, 2006). A combination of an individual's genes and juvenile growth are factors that determine if a fish stays in the stream or migrates to the sea (Jonsson and Finstad, 1995). The most common of these two life strategies is the anadromous (Jonsson and Jonsson, 2011), and anadromous sea trout are found from 42°N along the western coast of Europe (Elliott, 1994). The migration to sea most commonly takes place in April-June, but fish can start migrating as early as February (Jonsson and Jonsson, 2002). The benefit of such an adaptation is that feeding in the sea usually gives a higher nutrient uptake, an increased growth and thereby competitive advantages. The cost of the migration may be increased mortality during the migration itself, which also takes a lot of energy from the fish (Bohlin et al., 2001; Jonsson, 1985). They mainly feed in estuaries along the coast when at sea (Jonsson and Jonsson, 2011). The brown trout is a predator, and their diet consists mainly of fish, polychaetes and crustaceans (Jonsson and Finstad, 1995).

Before they leave the freshwater for the first time, the brown trout undergo a process called

smoltification, which is a comprehensive change for the fish. The smoltification happens between the age of one and seven years. Their back becomes dark and their abdomen light. Their behavior changes from highly territorial to social, and they often go together in schools down the river to the sea. Sea trout usually become sexually mature after 2-3 summers in the sea (ibid.), after which they usually return to the stream they were born in to spawn themselves (Elliott, 1989).

The brown trout is an important species for anglers in Norway, both in freshwater and in the sea (Jonsson and Finstad, 1995). A minimum allowed size of 35 cm has been introduced for anadromous salmonoid fish in southern Norway, whereas in the northern counties, the lower limit is 30 cm. Fishing in the sea is generally allowed by rod, hand line, salmon trolling lines, otters, wedge shaped seines and hook nets. In river systems only rod and hand line are allowed, and one must fish within the allowed fishing season determined for that river by the Norwegian Environment Agency (Åpningsforskriften, 2003).

2.4 Data collection

Fish handling

Fish handling and implanting the tags was carried out by Even Moland and Esben Moland Olsen at the Institute of Marine Research (IMR) located in Flødevigen, Norway.

Four field periods (April, May, September, November) were carried out during 2013, during which 59 sea trout were caught and implanted with a tag. The area between Furøya and Hestøya (Fig. 2.1) was chosen as the sampling location, as this is an area where most fish are likely to go to rest or feed. Thereby, the likelihood of only catching the "easy-caught" fish was minimalized (Allendorf and Hard, 2009).

Fish were caught using a beach seine (60x3 m) with 30 m hauling ropes attached to each end. A rowing boat was used to deploy the seine in a U-shape. One person was positioned on shore holding one of the end-ropes as the other person maneuvered the rowing boat. Once the seine was put out in a U-shape, the other end rope was taken back on shore and attached to land along with the first rope (Fig. 2.3a).

When catching the fish, a small "pocket" was made with one of the seine walls in shallow water. Fish caught in this pocket were moved to 40-80 L basins on shore. A hand net was used to transfer the fish from the water into the basins.

Implanting of the tags (Fig. 2.3b) was carried out after the fish had been sedated, using clove oil administered in a bath as anesthetic (Bridger and Booth, 2003; Munday and Wilson, 1997). Once the fish were under complete anesthesia, a U-shaped half-tube was used to conduct surgery in (Fig. 2.3c). Implanting of the tags was carried out as described by Mulcahy (2003), and tags were inserted into the abdominal cavity of the fish (Bøe, 2013;



Figure 2.3: *Fish handling and tagging by Even Moland and Esben Moland Olsen. a) The seine was deployed in a U-shape. b) The V9P-2L transmitter used for tagging was implanted in each fish. c) the procedure was carried out on an improvised operating table. d) When the fish had recovered from the surgery, it was released back into the water. e) The tag was implanted in the abdominal cavity of the fish. Photo: Even Moland and Carla Freitas.*

Bridger and Booth, 2003). Two absorbable sutures were used to close the surgical wound. Following the surgery, width and length (mm) of the caudal peduncle was measured using vernier calipers, the fish was weighed (g), and total length was measured (mm). Width and length were measured as fork length to nearest millimeter (Olsen et al., 2012). The entire procedure lasted less than five minutes. After the surgery, the fish was transferred to a basin with fresh sea water until it was fully recovered. After 10-20 minutes of observation, it was then released back into the water at the same location. Length varied between 230 mm and 635 mm (Fig. 2.4) with a mean length of 338 mm (\pm SD).

Tracking

A total number of 59 sea trout were implanted with a V9P-2L transmitter tag (Vemco Division, Amirix System Inc., Halifax, Canada) each in order to monitor their movements using acoustics. The transmitters were cylindrical with 29 mm length, a diameter of 9 mm, and a weight of 4.7 g when weighed in air, which means that the tag weight-to-fish ratio was $<3.8\%$. Each transmitter sent out unique signals every 100-250 seconds, which were picked up by receivers. The intervals of these signals were set to random to prevent signals from

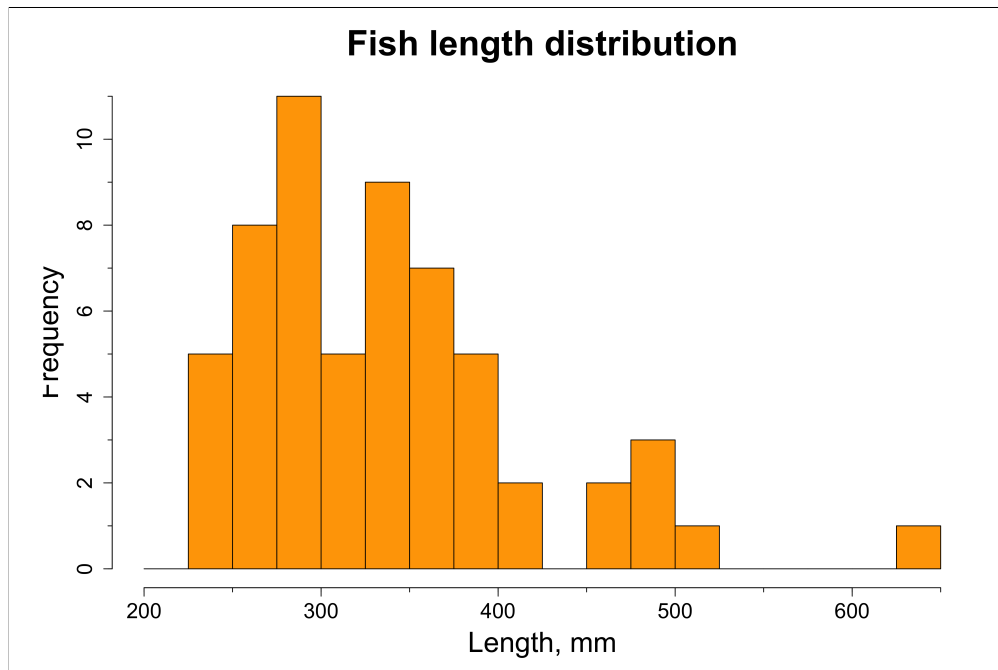


Figure 2.4: Length distribution for the 59 sea trout in this study. The data is divided into groups with thresholds of 25 mm between each group. The length distribution for all sampled fish went from 225 mm to 650 mm.

different fish from colliding (Olsen and Moland, 2011). Pressure sensors in the transmitters also enabled vertical positioning, with an accuracy of ± 2.5 at a maximum depth of 50 m. The battery time of the acoustic transmitters is approximately 660 days, after which it stops sending out signals (Olsen et al., 2012). Once implanted in the fish, the transmitters stayed there until the death of the fish.

Monitoring

A total of 51 stationary VR2W receivers (Vemco Dcision, Amirix Systems Inc.) constantly received and logged transducer signals via omnidirectional hydrophones. In order to cover as much of the fjord area as possible and still make sure a minimum convex polygon (MPC) was large enough for calculating mean position estimates (Simpfendorfer et al., 2002), the receivers were distributed all around the sampling area (Fig. 2.5). To ensure good recordings of movement in an out of the spawning stream, sentinel receivers were placed at Saltneset, where fish moved in and out of Tvedestrandfjorden, and at the outlets of Hantosundet and Østeråbekken (Olsen and Moland, 2011).



Figure 2.5: Overview of the positioning of 51 stationary VR2W receivers in Tvedestrandfjorden.

2.5 Data handling

Range testing

In 2011, 33 receivers were deployed in Tvedestrandfjorden. This was done as a test round in order to determine the range of the tags, which had the same transmitting strength as the ones used later in the study. The only difference between the testing and the study was that in the later study, the transmitter signal was fixed at five second intervals. The result of the range test was that the detection rate was high, with very few "blind zones". Only a few places along the shoreline and in narrow bays were outside of the detection range. The signals were good up to 200 m from the hydrophone, after which they started to decrease. Still, 1000 m away from the hydrophones, there was still an average detection probability

>20 %.

Position averaging

The mean-position-algorithm (Simpfendorfer et al., 2002) was used for estimation of the sea trout positions at 15 minute intervals for each individual. This method used presence or absence of signals from the transmitter and used these data to estimate the mean position of the fish, based on the number of signals received by each hydrophone. The signals, as well as the hydrophones, were omnidirectional. The signals travelled through water and were received by the hydrophones (Thorstad et al., 2013). Some of the receivers had overlapping areas, which means that one signal could be detected by multiple hydrophones. In these cases, the mean position between the hydrophones was estimated for each fish. The signals were summed, and the mean position was found by weighing the number of detections at each receiver (Olsen et al., 2012). The higher number of signals in one time slot (15 minutes), the more accurate position could be calculated. Another name used for this method is "the weighted-mean method" (Hedger et al., 2008). During triangulation, if one hydrophone received more signals than the neighboring and overlapping hydrophones, the fish was assumed to be closer to this receiver (Simpfendorfer et al., 2002). This method does not give the exact position of the fish, but it provides an approximate position during the chosen time slot. This method is called position averaging (PAV) (Olsen et al., 2012).

Fate assignment

Fish fates were determined by Ruud, Haugen and Moland based on the capture history data (Ruud, 2015). This was done after careful interpretation of the tag movements. Based on these data, each of the fish were assigned one out of four possible fates: "Dead", "Alive", "Dispersed" or "Harvested".

If the tag suddenly stopped moving much and only showed small vertical differences in position, the fish was assigned the fate "dead". The differences in depth were thought to be due to tides and currents, as previously assumed by Lee and Bergersen (1996). Fish with no apparent changes in movement which were still within the area by the end of the study period were assigned the fate "alive". Fish which disappeared from the study area, and which were detected last by one of the receivers near the entrance to the fjord, were assumed to have left the fjord, and were assigned the fate "dispersed" (Olsen et al., 2012). The fate "harvested" was assigned if the fish suddenly stopped moving after a period of normal behavior. It was then assumed that the fish had been fished, and that the tag had been removed during gutting and ended up in the water. A fish was also assumed harvested if the tag suddenly disappeared from the area abruptly without having been close to any of the fjord exits.

In addition, a number of fish had uncertain fates. These were studied even more closely in order to determine a fate.

Table 2.3: *The four different fates used in this study, and the number of tagged fish with each fate.*

Fate	Number of fish
Alive	8
Dead	12
Dispersed	19
Harvested	20
Total	59

Utilization distributions and movement metrics

The dataset was divided into 72 weeks, from 18 (the first sampling week in 2013) to 89 to ensure that there would be no crash between identical week numbers in 2013 and 2014. For further analysis, the zone for each fish each week was calculated. The last registered zone was used as the mean zone the last week they were detected. The same was done when there was no information about the fishes whereabouts the previous week.

The capture history was transferred into pivot-tables in MS Excel. The fish were given a number for each week, representing their average zone. 0 = unknown, 2 = inner buffer zone, 3 = outer buffer zone, 4 = no-take MPA zone (Table 2.1).

2.6 Capture-Mark-Recapture analyses

The detection data was analyzed using the software MARK version 6.2 (White and Burnham, 1999). The detection data was discretized into 72 encounter occasions, corresponding to weekly periods over which survival and dispersal probabilities could be estimated. A multistrata approach was used, where individual encounter histories comprised of 72-digit arrays of either "0", "2", "3" or "4" depending on whether the individual was encountered during an encounter occasion or not ("0" if not) – and if encountered, in what zone the encounter took place (see Fig. 2.1 for zone identification). An encounter history like "422434022404..." would mean that the individual was captured, tagged and released in zone 4 at first occasion, predominantly detected in zone 2 during the second and third occasion, but predominantly detected in zone 4 during occasion four, and so on. Notice the lack of detections during occasions 7 and 11. However, subsequent detections confirm that the individual is still alive, but just was not detected during these occasions. This demonstrates the nature of mark-recapture-analysis where incomplete detection histories are analyzed by simultaneously analyzing both processes related to survival and detection (Lebreton et al.,

1992). In the current study, a third process is included in the analyses: dispersal.

The parameterization of multi-state mark-recapture models is visualized in a fate diagram (Fig. 2.6). From this, we can follow individuals tagged at occasion k that are captured (and tagged and released) in zone 2. In the diagram, we follow the Markovian steps describing survival and dispersal process involved over two capture occasions. Following the Conditional Arnason-Schwarz parameterization (Arnason, 1973). S_k^2 is the survival probability over the k to the $k + 1$ period for individuals that stayed in zone 2 at occasion k , ψ_k^{23} is the probability of dispersing from zone 2 to 3 during the k to the $k + 1$ period (ψ_k^{22} is the probability of staying), and p_k^2 is the probability of being captured in zone 2 at occasion k . Encounter histories for some example fates (corresponding to fates on the same line in the figure) are provided in curly brackets to the right; 0, not caught; 2 caught in zone 2; 3 caught in zone 3; -2 means assigned as caught (and killed) in zone 2 (i.e., right censored). In Fig. 2.7, there is a comprehensive overview of parameters from the 12 first occasions for the study system, apart from the ψ -parameter for which just a couple of examples are provided to ease readability. The red rings in the figure denotes the encounter trajectory corresponding to the example provided in the previous paragraph (i.e., "422434022404").

Parameters were fitted using the maximum log likelihood method. All parameters can in theory be estimated as being constant over all occasions/periods, or to be time dependent. In addition, and more ecologically relevant, the parameters can be estimated as functions of covariates of interest. These covariates can both be occasion-specific (e.g., temperature and precipitation), and individual-specific (e.g., size). Owing to the pre-assignment of individual fates into "dead", "harvested", "alive" and "dispersed", parameters could be fitted conditionally on these fates, by including a dummy group factor into the input data. Knowing each individual's fate (i.e., over the scope of the study) opened for fixing the survival parameter to 1 for all individuals but the dispersers, as they were known to survive until the time of death ("dead" and "harvested") or throughout the study period ("alive" group). The interpretation of the survival parameter for the dispersers is probability of dispersing out of the study area. Clearly, some of these individuals will survive after dispersing, but for this analysis, dispersing is interpreted as mortality. Finally, owing to the high density of receivers, both zone 3 and 4 weekly detection probability (p) were fixed at 1. Models allowing these parameters to be freely estimated were also fitted, but they were always estimated to be 1 or very close to one. The detection probability for zone 2 was estimated freely as the density of receivers was lower in this zone. p -estimates from zone 2 were interpreted as a proxy for small-scale movement as individuals that were moving a lot would have a higher probability of detection than more stationary individuals.

Candidate model structures with combinations of individual and environmental covariates along with fate group and various temporal (e.g., season or month) effects were fitted and subjected to model selection by means of Akaike’s Information Criterion, AIC (Akaike, 1974; Anderson, 2008).

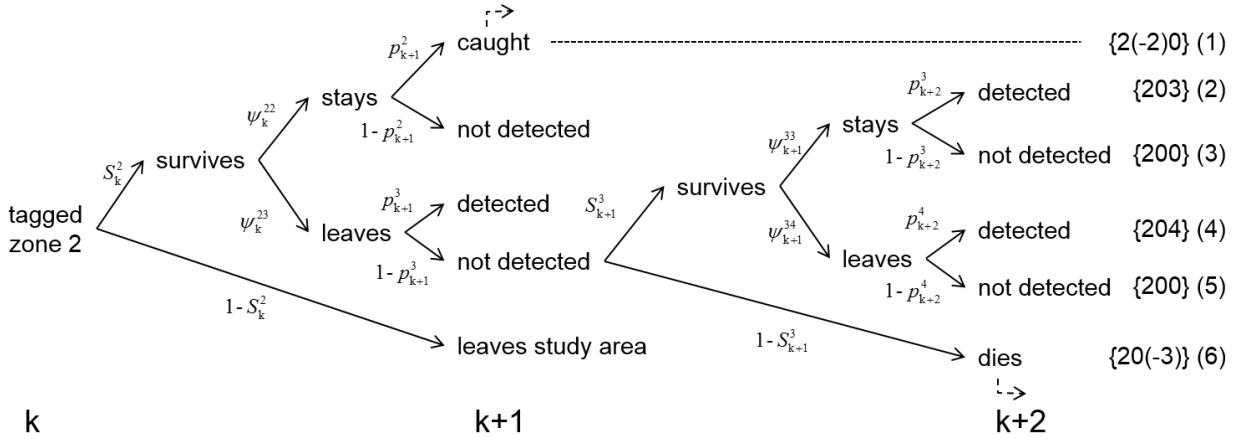


Figure 2.6: Fate diagram with corresponding Conditional Arnason-Schwarz (CAS) parameterization for a three-occasion study system (see text for a detailed description). Angled and dashed right-pointing arrows indicate right-censoring (i.e., data is used up to this occasion, but censored out of study beyond this point).

Plots were made in R (RStudio Team, 2015) and MS Excel.

Difference in length distribution among fate groups was tested in R using one-way anova and Tukey HSD-test was used for exploring pairwise differences in length distributions. These analyses were performed using the aov and TukeyHSD procedures in the stats library in R.

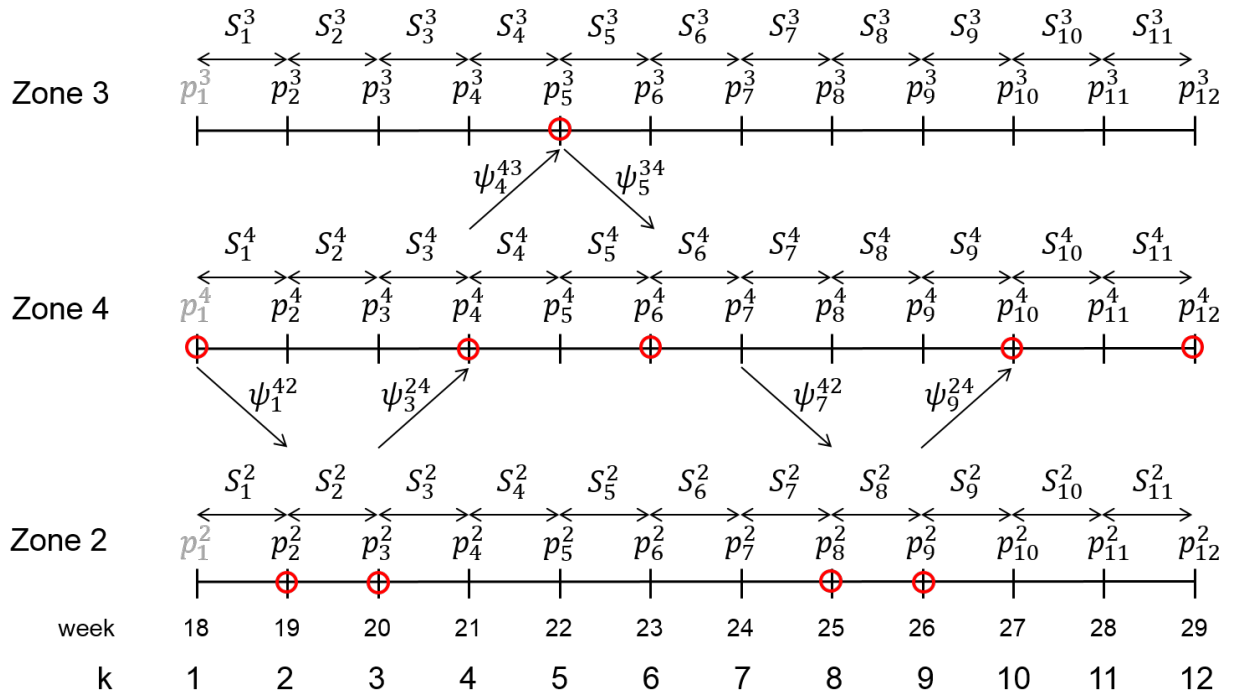


Figure 2.7: Overview of potential CAS parameters fitted for this study system (just for 12 out of 72 occasions). k = occasion number; S_k^i represents survival over the k to $k+1$ period in zone i (Fig. 2.1); p_k^i represents (re)capture probability at occasion k in habitat i (p_1 are indicated in grey as these are not estimable); ψ_k^{ij} represents the dispersal probability from zone i to j over the k to $k+1$ period. The red circles denotes an example encounter trajectory ($\{422434022404\}$) described further in the main text.

Results

3.1 Length distribution

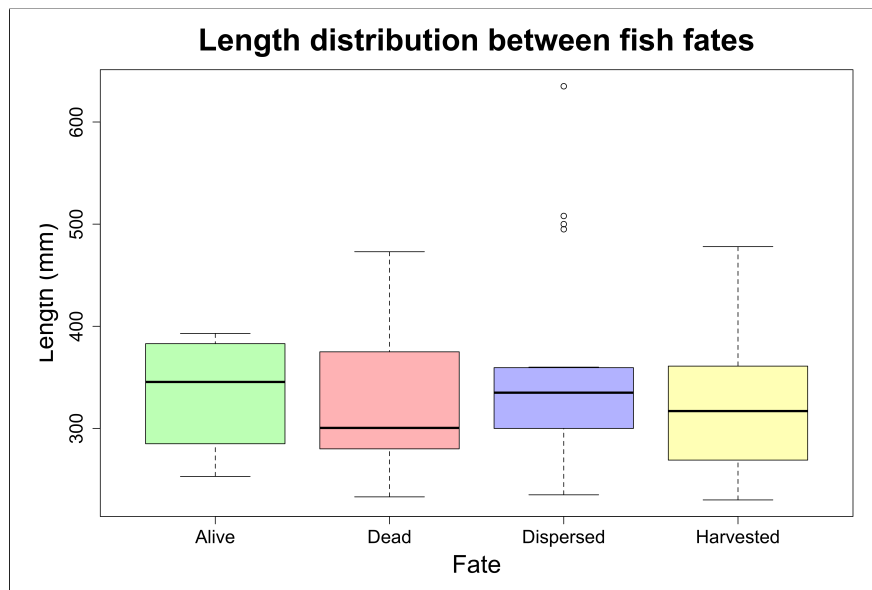


Figure 3.1: Box plot of Tvedestrandfjorden sea trout tagging length (mm) data for alive, dead, dispersed and harvested fish (Table 3.1). The boxes cover 50% of the group observations, the whiskers 90% and the bold vertical lines represent the group medians.

The length distribution between the different fates showed no connection between tagging length and the fate groups used in this study (Fig. 3.1).

A one-way ANOVA showed no significant difference between fate groups (Listing A.1), as $F = 0.70$, $df = 3$, and $p = 0.56$. A Tukey test on length showed that none of the pairwise comparisons differed from each other (Listing A.2), as $p > 0.05$.

Table 3.1: Detailed information for each fish in the study, their ID, tagging date, length at tagging, last registration before fate, number of tracking days before fate, and fate.

ID	Tagging date	Length (mm)	Last registration before fate	Tracking days	Fate
8956	30 April 2013	360	27 November 2013	211	Dispersed
8957	30 April 2013	364	07 September 2014	495	Harvested
8958	30 April 2013	478	15 September 2013	138	Harvested
8959	02 May 2013	358	17 May 2014	380	Harvested
8960	02 May 2013	286	12 May 2013	10	Dispersed
8961	02 May 2013	285			Alive
8962	03 May 2013	359	06 June 2013	34	Dispersed
8963	06 May 2013	288	03 September 2013	120	Harvested
8964	06 May 2013	243	26 September 2013	143	Harvested
8965	07 May 2013	273	15 April 2014	343	Harvested
8966	07 May 2013	268	16 May 2014	374	Harvested
8967	07 May 2013	366	18 May 2014	376	Dead
8968	07 May 2013	402	25 March 2014	322	Harvested
8969	07 May 2013	328			Alive
8970	07 May 2013	303	23 May 2013	16	Dead
8971	07 May 2013	298	09 June 2013	33	Dead
8972	09 May 2013	285			Alive
8973	09 May 2013	380			Alive
8974	09 May 2013	358	24 November 2014	564	Harvested
8975	09 May 2013	270	11 November 2013	186	Harvested
8976	09 May 2013	331	28 June 2013	50	Dead
8977	09 May 2013	295	09 March 2014	304	Dead
8978	09 May 2013	341	29 December 2013	234	Harvested
8979	09 May 2013	285	04 August 2013	87	Harvested
8980	09 May 2013	230	24 June 2014	411	Harvested
9006	15 May 2013	298	16 June 2013	32	Dispersed
9007	15 May 2013	334	11 September 2013	119	Harvested
9008	16 May 2013	305	03 October 2013	140	Dispersed
9009	16 May 2013	500	31 May 2014	380	Dispersed
9010	11 September 2013	319	10 June 2014	272	Dispersed
9011	11 September 2013	235	03 October 2013	22	Dispersed
9012	11 September 2013	384	01 June 2014	263	Dead
9013	11 September 2013	386			Alive
9014	11 September 2013	635	04 October 2013	23	Dispersed
9015	11 September 2013	495	07 October 2013	26	Dispersed
9016	11 September 2013	461	05 December 2013	85	Harvested
9018	11 September 2013	393			Alive
9019	13 September 2013	295	28 October 2013	45	Dead
9020	13 September 2013	423	07 October 2013	24	Dead
9021	13 September 2013	346	07 October 2013	24	Dispersed
9022	13 September 2013	257	10 June 2014	270	Dispersed
9023	18 September 2013	300	04 June 2014	259	Harvested
9024	18 September 2013	508	25 September 2013	7	Dispersed
9025	18 September 2013	345	06 December 2014	444	Harvested
9026	18 September 2013	259	22 December 2013	95	Dead
9027	18 September 2013	238	03 March 2014	166	Harvested
9028	18 September 2013	253			Alive
9029	18 September 2013	265	07 June 2014	262	Dead
9030	24 September 2013	302	25 November 2013	62	Dispersed
9056	24 September 2013	347	26 October 2013	32	Dispersed
9057	24 September 2013	257	10 February 2014	139	Harvested
9058	24 September 2013	233	10 July 2014	289	Dead
9059	27 November 2013	310	16 May 2014	170	Dispersed
9060	27 November 2013	363	31 August 2014	277	Alive (tag malfunction)
9061	27 November 2013	473	11 March 2014	104	Dead
9062	27 November 2013	380	20 July 2014	235	Harvested
9063	28 November 2013	335	25 April 2014	148	Dispersed
9064	28 November 2013	335	01 June 2014	185	Dispersed
9065	28 November 2013	282	27 April 2014	150	Dispersed

3.2 Tracking day differences

A one-way ANOVA (Listing A.3) showed that the difference between tracking days was significant ($p = 0.003108$) for the dead, dispersed and harvested groups (Fig. 3.2). The

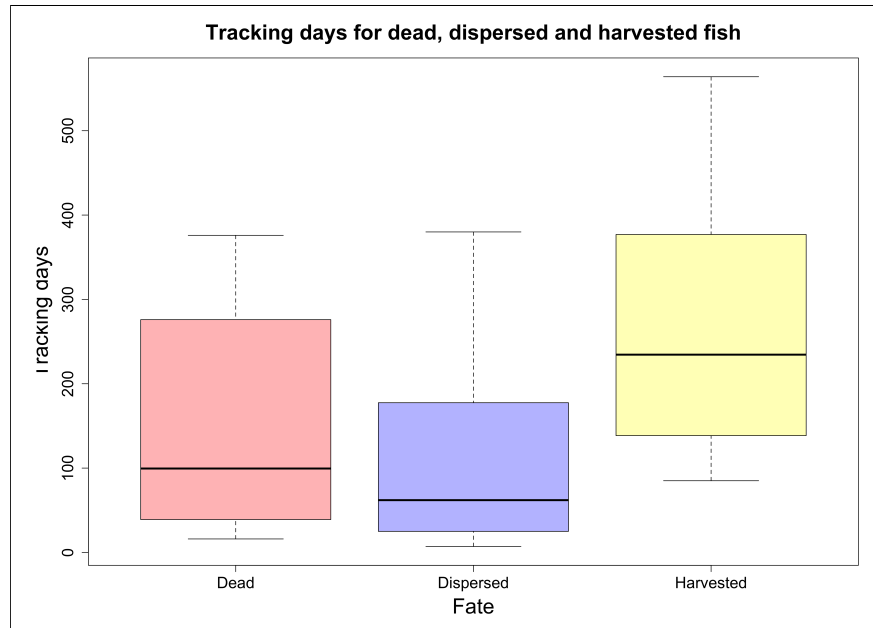


Figure 3.2: Box plot of Tvedestrandfjorden sea trout tracking days data for the dead, dispersed and harvested groups (Table 3.1). The boxes cover 50% of the group observations, the whiskers 90% and the bold vertical lines represent the group medians.

dead group had a mean value of 155 tracking days, the dispersed group for 116 days, while the harvested groups were tracked for 262 days in average (Table 3.1). The medians for the different groups were 100 days for the dead, 62 days for the dispersed and 235 days for the harvested group.

3.3 CAS analysis

Model selection

According to the AIC and Δ AIC numbers generated for the tested models,(Table 3.2), the most supported model had the lowest AIC, and produced estimates for all 95 parameters ordered.

In this model, survival (for disperse group only) was modeled as constant across months during winter and spring and with different length effects during summer (JJA) and fall (SON) months. The survivals for the three remaining fate groups were fixed to 1. Probability of detection in the inner buffer zone was modeled with interaction effects of fate and length, and additive temperature effects. For the outer- and notake zones, p was fixed to 1. ψ was modeled with interaction effects between zone, fate, temperature and precipitation, plus an additive effect of fate connected to length.

The second most supported model (Tables A.2 and 3.2) was the same as the first one, only

with precipitation as a factor for p as well as temperature, while the third had no included weather effects on p .

The models had $\Delta AICs$ of 2.076 and 3.449 (Tables A.2 and 3.2).

p , the probability of detection

The estimates (Table A.1) showed that the probability of being detected increased with increasing temperature for all fates. The effect was highest for the harvested group, and lowest for the dead group (Fig. 3.3).

The detection probability was shown to be positively affected by length for the alive and dispersed groups (Figs 3.4 and 3.5) The effect of length on the p -values (Table A.1) was

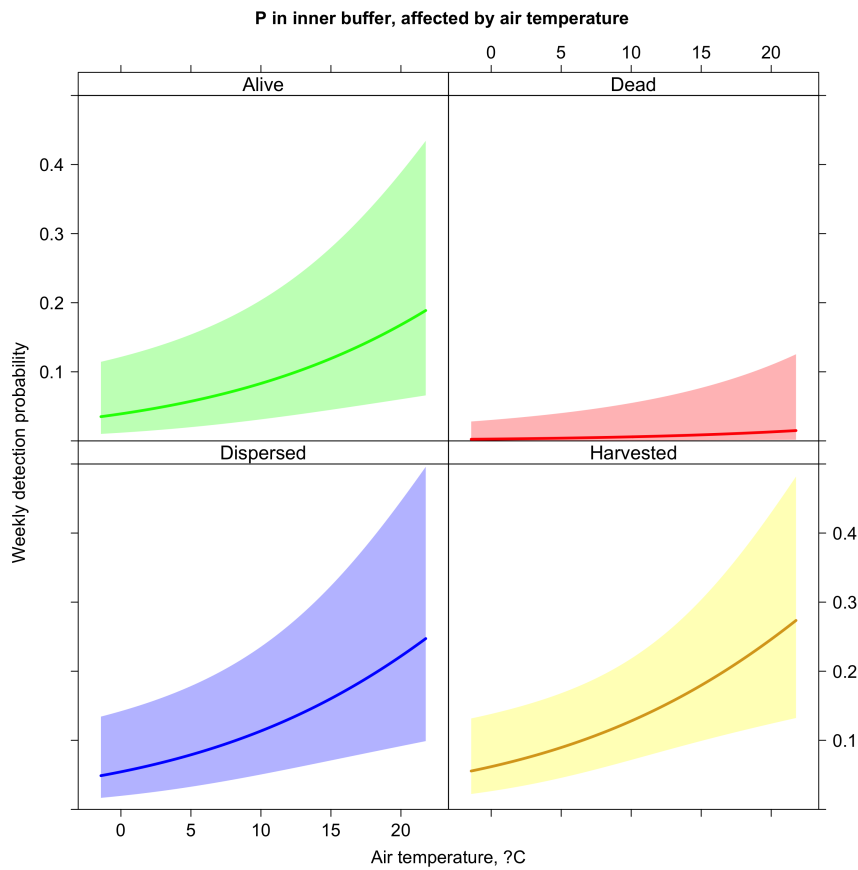


Figure 3.3: *Estimated temperature-specific p values for sea trout in the inner buffer zone for alive, dead, dispersed and harvested fish. The middle line represents the parameter estimates, while the upper and lower confidence intervals are based on the covariates (Table A.1)*

negative for the dead and dispersed fish, while the harvested and alive group showed a positive length effect (Fig. 3.4). Data is adjusted for mean temperature ($^{\circ}C$).

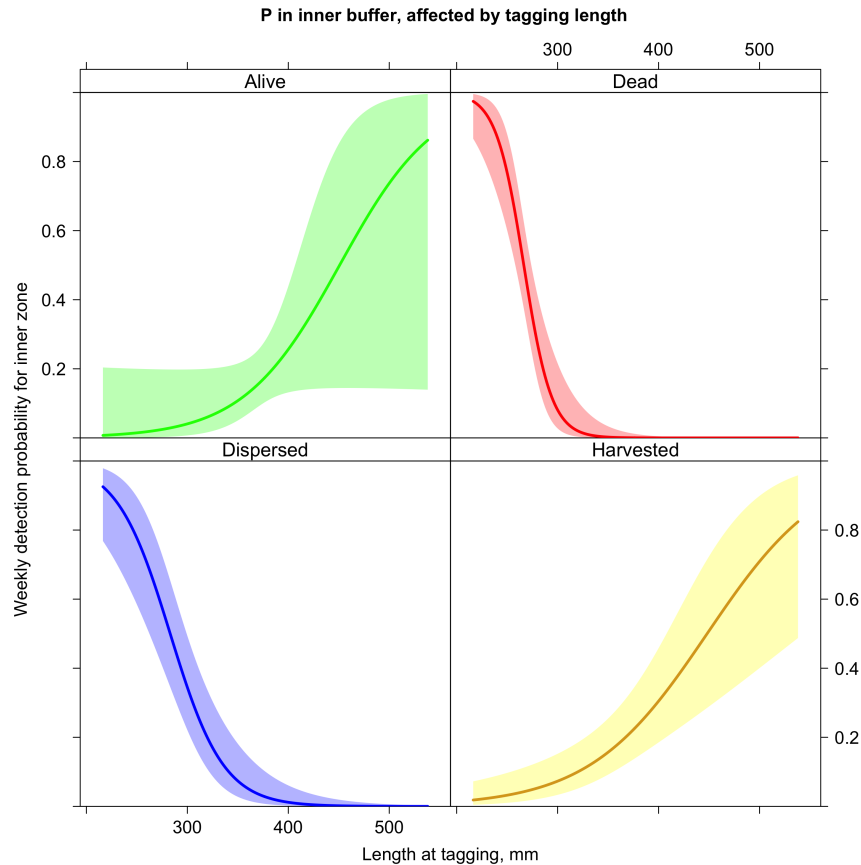


Figure 3.4: *Estimated length-specific p values for sea trout in the inner buffer zone for alive, dead, dispersed and harvested fish. The middle line represents the parameter estimates, while the upper and lower confidence intervals are based on the covariates (Table A.1)*

ψ , the likelihood of travelling between zones

The ψ values, the likelihood of travelling from one zone to another (Table A.1) showed clear fate specific responses to spatial behavior. The different fate groups' movement between zones showed differently responses to temperature and precipitation (Fig. 3.6). The data showed that the alive-group had generally very low probabilities of movement between zones, ($\psi=0.1$ and lower). The exceptions were movement from zone 3 to 4 at low temperatures ($\psi=0.5$) and from 4 to 3 at low temperatures and during little or no precipitation ($\psi=0.2$). The dead-group did not have high probabilities for movement, the highest was movement from zone 2 to 3 at high temperatures ($\psi=0.3$) and from 2 to 4 at low temperatures ($\psi=0.25$). The rest of the movement had ψ values of 0.1 or lower. The dispersed-group had a very low probability ($\psi < 0.01$) for movement from zone 3 to 4. At high temperatures and low precipitation, the probabilities of going from zone 4 to 2 (at high temperatures and low precipitation) and 4 to 3 (at high temperatures) were high ($\psi=0.5$).

The probabilities of movement for the harvested-group were generally very low ($\psi=0.15$ and

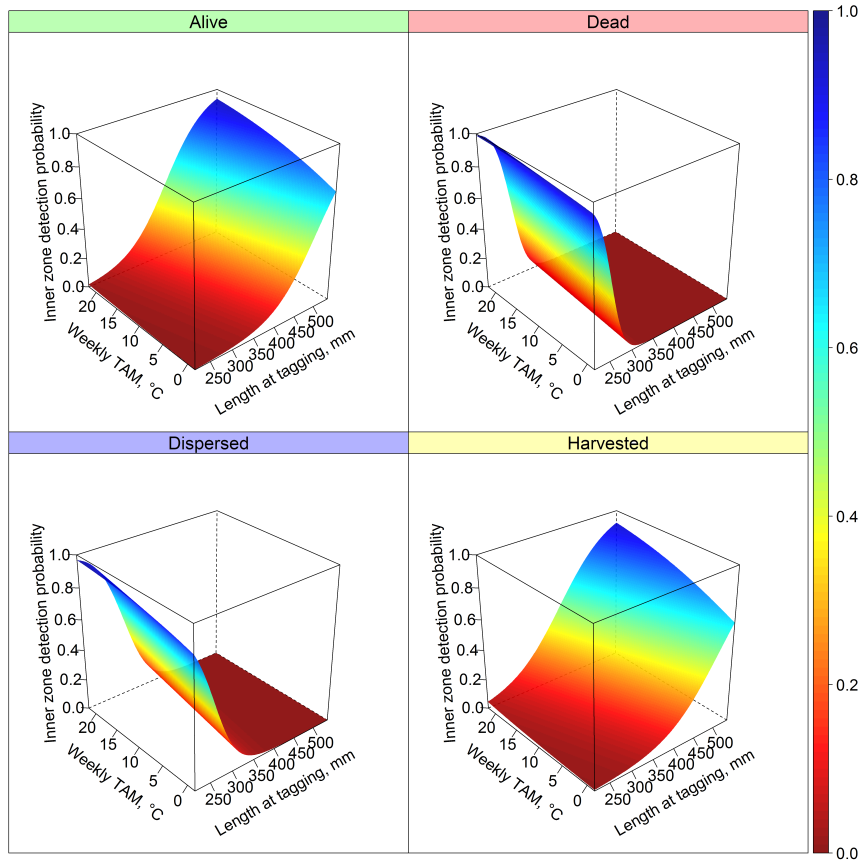


Figure 3.5: 3D plot of estimated length- and temperature-specific detection probabilities (p -values) for sea trout in the inner buffer zone. The direction of the plot indicates whether length has a positive or negative effect on p , whereas the color scale on the plot (blue = high, red = low) reflects the temperature effect on the detection probability. Estimates from Table A.1

lower). The highest probability was for movement between zone 2 to 4 at high temperatures ($\psi=0.25$).

The length effect on ψ for movement between zone 2 to 4 was positive for fate groups alive, dead and harvested, while slightly negative for the dispersed group (Table A.1). The greatest positive length effect was found in the harvested-group, while the effect on the dead and alive-groups were approximately the same (Fig. 3.7).

S, survival

The most supported model estimated survival during winter and spring to constant (i.e., 0.98 (95% CI: 0.93, 0.99)) and independent of both environmental covariates as well as individual covariates. Interpretation of survival in this study is the probability of the dispersers to stay in the system and be alive. The summer and fall data showed different length effects (Table A.1). The survival was high during both seasons, but in the summer S was lowest for small

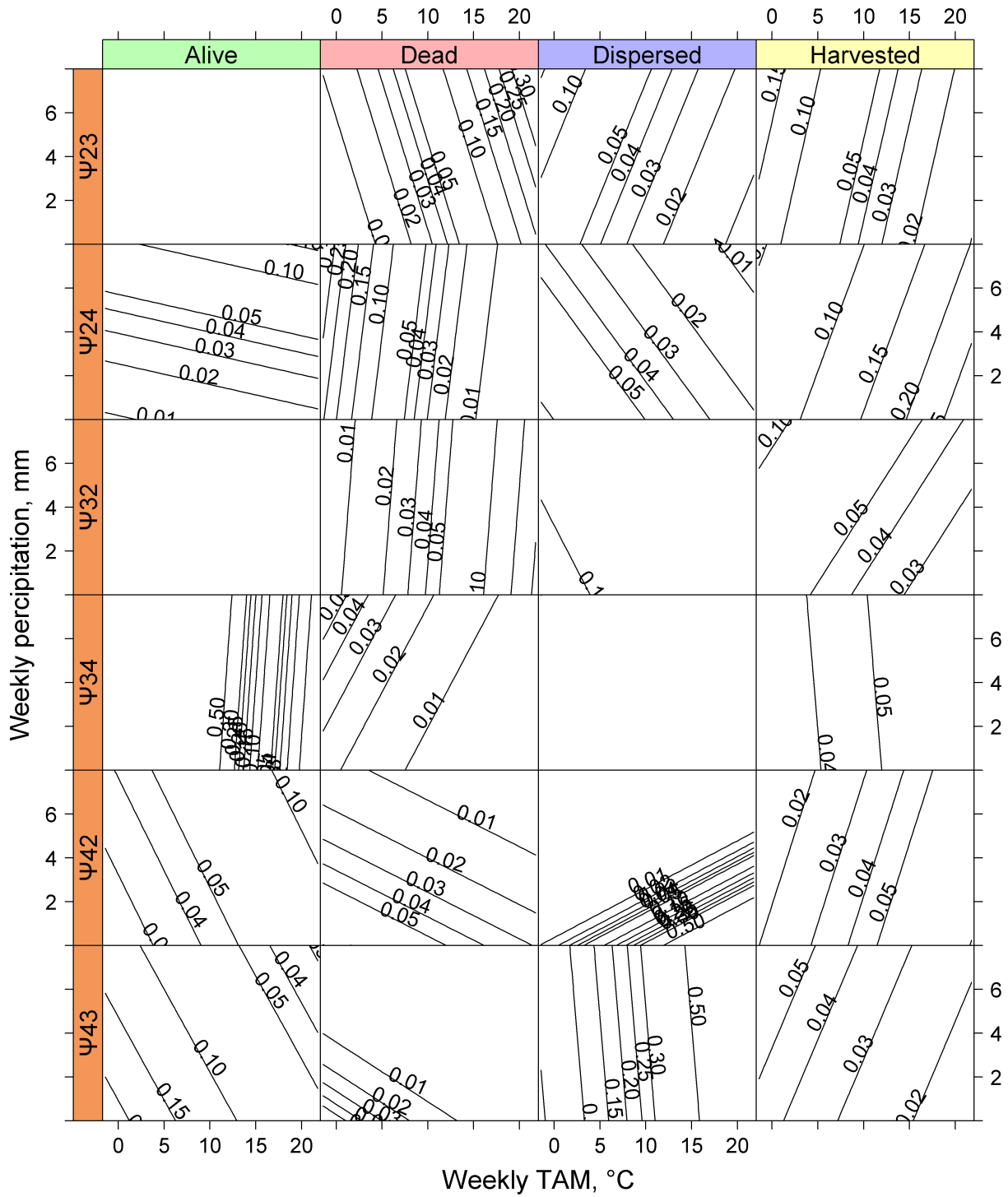


Figure 3.6: The estimated tendency to migrate between zones (2 to 3 (ψ_{23}), 2 to 4 (ψ_{24}), 3 to 2 (ψ_{32}), 3 to 4 (ψ_{34}), 4 to 2 (ψ_{42}), 4 to 3 (ψ_{43})) for each fate group, affected by temperature (x axis) and precipitation (y axis). Empty plots have <0.01 probability. The isolines in each box represents probability of movement between zones. Horizontal lines indicate strong precipitation effects, while vertical lines indicate strong temperature effects. Parameter estimates from Table A.1

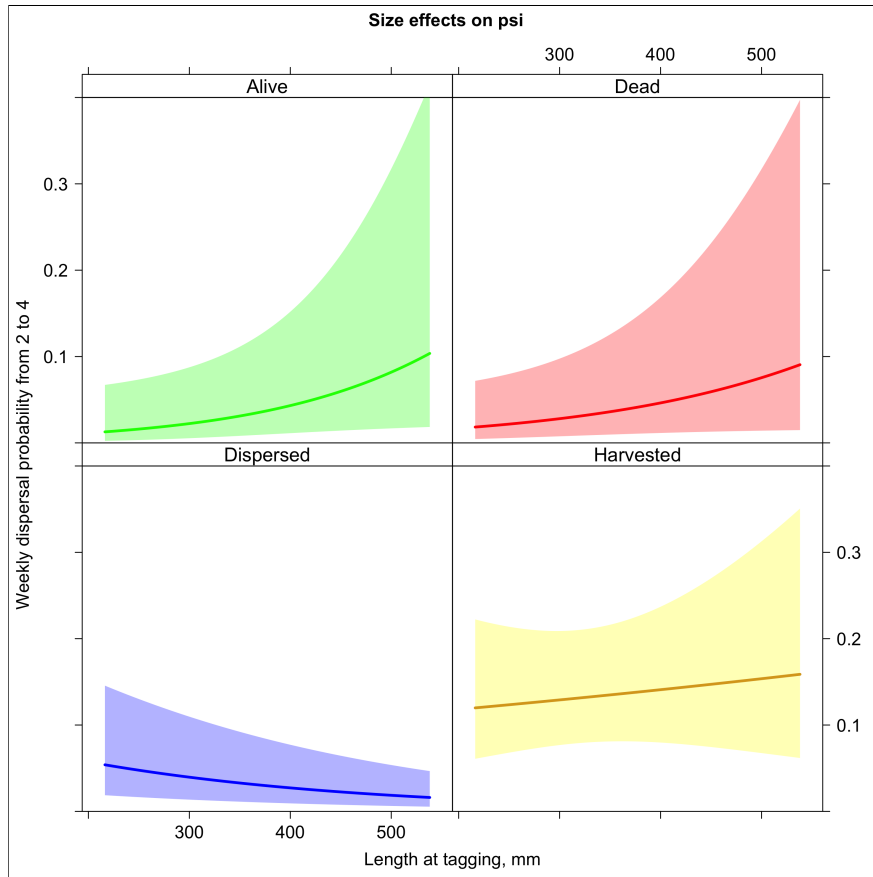


Figure 3.7: *Estimated ψ , the weekly size-specific probability of movement from zone 2 to 4, for alive, dead, dispersed and harvested fish. Length effect is additive, and will be the same for all movement between zones. The middle line represents the parameter estimates, while the upper and lower confidence intervals are based on the covariates (Table A.1)*

individuals. The summer survival increased with increasing size, while there was a weak negative effect by length during fall, meaning that bigger individuals had a slightly higher probability of dispersing (Fig. 3.8).

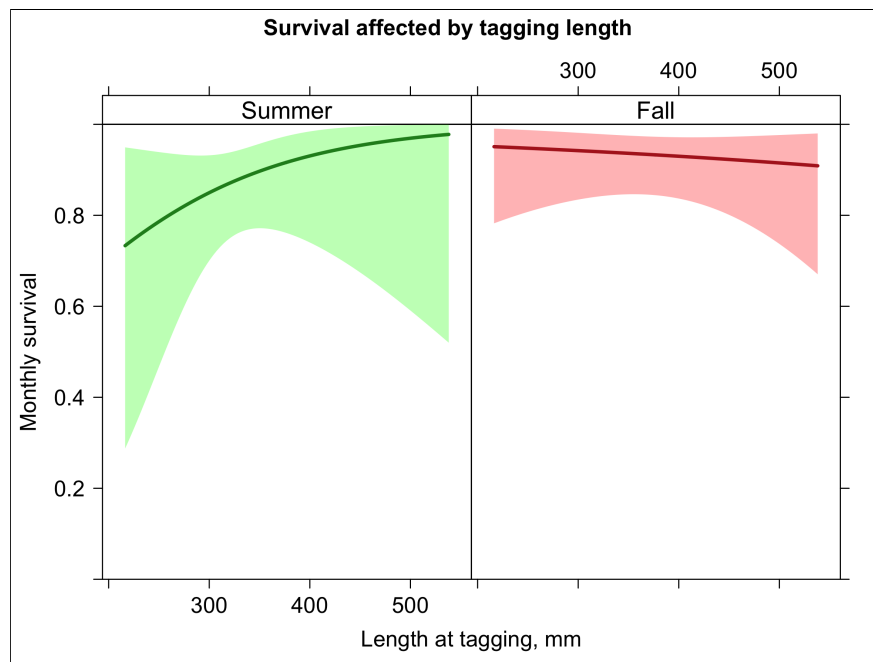


Figure 3.8: *Estimated monthly size-specific survival probability of sea trout during summer (JJA) and fall (SON) for the dispersed group. The middle line represents the parameter estimates, while the upper and lower confidence intervals are based on the covariates. Parameter estimates from Table A.1*

Table 3.2: Selection of the ten most supported models from the ones tested with AIC and Δ AIC values. The complete overview of models can be found in Appendix A.2. ψ =psi, F=fate, fa=fall, In=inner, L=length, M=month, No=notake, Ou=outer, p=detection, Prec=precipitation, S=survival, Seas=season, sp=spring, su=summer, Temp=temperature, w=winter, Z=zone.

Model	AIC	Δ AIC	AICc weights	Model likelihood	Deviance	Est. par.	Ordered par.	Fixed par.	Est. par. (%)
S(M(Wsp)+L*Seas(su=fa),=1)p(ln(F*L+Temp),No&Ou=1) ψ (Z*F*Temp*Prec+F*L)	1967.279	0	0.66203	1	1775.888	90	99	9	100
S(M(Wsp)+L*Seas(su=fa),=1)p(ln(F*L+Temp+Prec),No&Ou=1) ψ (Z*F*Temp*Prec+F*L)	1969.355	2.076	0.23448	0.354	1775.703	91	100	9	100
S(M(Wsp)+L*Seas(su=fa),=1)p(ln(F*L),No&Ou=1) ψ (Z*F*Temp*Prec+F*L)	1972.564	3.449	0.04714	0.071	1783.431	89	98	9	100
S(M(Wsp)+L*Seas(su=fa),=1)p(ln(F*L),sln+Temp+Prec),No&Ou=1) ψ (Z*F*Temp*Prec+F*L)	1973.419	6.140	0.03073	0.046	1786.541	88	97	9	100
S(M(Wsp)+L*Seas(su=fa),=1)p(ln(F*L),No&Ou=1) ψ (Z*F*Temp*Prec+F*L)	1973.78	11.463	0.02562	0.039	1784.650	89	95	6	100
S(L+M,=1)p(F*Z) ψ (F*Z)	2004.092	36.81	0	0	1926.103	38	56	1	70
S(L*M,=1)p(F*Z) ψ (F*Z)	2008.451	41.172	0	0	1924.135	41	73	1	58
S(M,=1)p(F*Z) ψ (F*Z)	2024.149	56.870	0	0	1916.414	52	55	1	96
S(F*Z,=1)p(F*Z) ψ (F*Z)	2030.110	62.831	0	0	1950.015	39	48	9	100
S(Seas,=1)p(F*Z) ψ (F*Z)	2030.354	63.074	0	0	1958.666	35	41	1	88
S(disp(L),res(1))p(F*Z) ψ (F*Z)	2031.326	64.047	0	0	1963.826	33	39	1	87
S(M+L,=1)p(F*Z) ψ (Z*F*Temp*Prec)=1	2032.300	65.021	0	0	1854.411	84	104	1	82
S(F*Z,=1)p(Z) ψ (F*Z)	2036.504	69.225	0	0	1975.262	30	31	1	100
S(Seas*L,=1)p(F*Z) ψ (F*Z)	2039.995	72.715	0	0	1966.209	36	45	1	82
S(F*Z,=1alive)p(F*Z) ψ (F*Z)	2042.806	75.527	0	0	1950.015	45	48	3	100
bottomrule									

4

Discussion

Since all the four fate groups had approximately the same length distribution (Fig. 3.1), behavioral trends for each group can be compared to each other groups.

Presently, very few studies using triangulation details to study sea trout fates and behavior exist. Due to this, there is a limited amount of literature to back up the following section.

From their acoustic telemetry study, Eldøy et al. (2015) divided anadromous sea trout into three migration categories: short (<4 km from the river mouth), medium (4 – 13 km), or long (>13 km). If we adopt this categorization and adapt it to this study, we can say that short-scale migration is within the inner buffer zone (≈ 1.2 km long), medium-scale migration is within the rest of the MPA area of Tvedestrandfjorden, the notake zone and outer buffer (≈ 4.5 km), while large-scale migration is outside of this area, where we can no longer track the fish (Fig. 2.1). The only group that can be counted as large-scale migrators is the dispersed group, as they leave the sampling area and do not come back during the rest of the tracking time.

To analyse the behavior of fish using these migration categories, the p value - detection probability within the inner buffer - the can be a measurement for small-scale migration of the fish (in the other two zones, the number of receivers was so large (Fig. 2.5) that the detection probabilities were 1) and thereby contain valuable biological information regarding fish behavior. The ψ value, likelihood of movement between zones, reflects the medium-scale migrations within the entire fjord system. The differences between the tendencies of small- and medium-scale movement in the different fate groups may help explain behavioral trends within- and differences between groups. Even though we do not have any information about the fish after they leave Tvedestrandfjorden, we are able to point to potential behavioral trends found in the long-distance migrants before fish disperse.

The behavior of the fish was affected by size, temperature and precipitation, though variations were found within each of the fate groups (Fig. 3.6).

There were clear differences in habitat use between the four fate groups, which suggests

that different spatial behavior types are found in sea trout. The presence of such behavior types has been suggested by Alós et al. (2016) in a study of pearly razorfish (*Xyrichthys novacula*). A prominent trait or a habitat preference in one group may be less expressed in others. Some of the differences found in this study also implicate that the establishment of the MPA in Tvedestrandfjorden does have a protective effect on some fish.

The large individuals in the alive and harvested groups were more likely to be detected in the inner buffer (Fig. 3.4), an indication that the large fish of these groups were both present and active in this zone. These size differences in the inner buffer zone are interesting, as larger fish in previous studies have been found to migrate faster and further away than small fish (Bendall et al., 2005; Klemetsen et al., 2003). The fact that the bigger fish in the alive and harvested groups are active in the inner buffer despite this therefore suggests that this non-migratory activity caused by another behavioral trait.

A possible explanation for low p values in some groups is that some fish may have gone up in the river Østeråsbekken, and were thereby not within the detection area for longer periods of time.

Regarding the medium-scale movement, the fish in all groups except for the dispersed group were moving more between the zones the bigger they were (Fig. 3.7). This is likely also a sign that activity and boldness are advantageous traits, as active fish are the ones to grow large, most likely due to access to more food. From earlier analysis of this dataset, Ruud (2015) discovered that the size at smoltification was more important in terms of which individuals became most active than adult size. This suggests that these behavioral traits are expressed in the fish at a young age. Smolt-length is not a factor in the analysis of this study due to an incomplete smolt-length dataset.

Each of the four fate groups showed slightly different trends as to where in the area they stayed and which areas they migrated between. Such behavioral trends may lead to altered population dynamics, especially if affected by harvest selection (Alós et al., 2016). This also underlines the importance of ecosystem-based marine management.

The alive group seemed to have clear patterns on their medium scale area use. The movement between the outer buffer and the notake zone was by far the most common one, with emphasis on movement into the notake zone. Furthermore, there was some movement between the inner buffer and notake zone, and close to none between the inner and outer buffer 3.6. These data suggest that the alive group tend to stay in or near the notake zone. An area of eelgrass meadow lies inside the notake zone, by Holmen close to Røskilen (Fig. 2.1), very close to the outer buffer. Movement around this area may further explain migration by large individuals between the outer buffer and notake zone, as large individuals have been found to use this area more frequently than smaller ones (Andrés, 2016). This also fits with the fact that medium-scale migration was positively affected by increasing length in the alive

group (Fig. 3.7). The presence of this eelgrass meadow may be contributing to keeping the sea trout inside the notake zone and thereby within the protective area. Their small-scale movement within the inner buffer zone was positively affected by increasing length, suggesting that mainly the bigger individuals were using this zone (Fig. 3.4). It is possible that the smaller individuals was using the area around Hestøya and Fuøya as feeding grounds (Knutsen et al., 2003) and staying mainly in and around the islands while the bigger ones are more active in the whole system.

The most pronounced medium-scale migration in the dead group was the migration from the inner buffer zone into the other two zones; generally, this group seemed to be moving actively out of the inner buffer zone. Other than this trend, the fish were moving between all zones, but the probabilities for medium-scale movements were generally quite low (Fig. 3.6). Increased length had a negative effect on the small-scale migrations in the inner buffer (Fig. 3.4), but a slightly positive effect on medium-scale migrations (Fig. 3.7). This indicates that large individuals in this group were either not present in the inner buffer zone, or very inactive, maybe caused by old age, while smaller individuals were moving more around in the zone. Larger individuals on the other hand, were moving, however slowly, around in the entire study area. The low probabilities of medium-scale movement, combined with the negative length effect in the inner buffer suggests that large individuals in the group were moving around slowly and randomly. The smaller individuals in the group showed a different small-scale behavior. There may be different reasons why these individuals ended up dying; some may have died due to old age, others may have been taken by predators or otherwise ended up dead. A possibility is also that the fish in this group were physically affected by the tagging procedure. The number of tracking days for the dead group was significantly lower than for the harvested group (Fig. 3.2), suggesting that tagging injury may have caused the fish to become more vulnerable. This may have lead to their death and thereby an overestimation of the natural mortality of the fish population (Jonsson and Jonsson, 2009; Thorstad et al., 2016). This being said, salmonoid fish usually respond well to this type of tagging. Even smolt down to 12 cm have been found to handle tags weighing 10 % of their body weight (Newton et al., 2016). A major effect caused by the tag is therefore not to be expected. From studies on pike, it has been shown that the recovery of the fish is quick. The method of catch-and-release is believed to not affect the results as long as the fish is not exposed to air for a very long time, <300 seconds (Arlinghaus et al., 2009). Even so, accidents may happen, and individuals may have been affected by this. The presence of a tag has also been suggested to increase predation risk, which may have affected this group (Jonsson and Jonsson, 2009).

Both at small- and medium-scales, increased length in the dispersed group had a negative

effect on activity (Figs 3.4 and 3.7), which coincides with studies claiming that large fish often are quick to migrate offshore (Bendall et al., 2005; Klemetsen et al., 2003) and that they were therefore not present in the zones. Looking at the mean number of days the dispersed group stays in the system after tagging (Table 3.1 and Fig. 3.2), it is clear that many of the dispersing fish left the study area quite rapidly. Although weak, the dispersed group was the only group with a negative effect of increased length on medium-scale migration (Fig. 3.7). It is therefore likely that the individuals which did not disperse immediately were the smaller individuals in this group. These individuals seem to be the most active group at a medium-scale, particularly migration out of the notake zone (Fig. 3.6), indicating that curiosity or boldness may be a trait in this group which later leads to their dispersal.

The probability of dispersed fish staying within the study area during summer was positively affected by length, as opposed to a slightly negative effect of length during fall (Fig. 3.8). This means that small fish in this group have a higher probability of leaving the system during summer, while bigger individuals are slightly more likely to disperse during fall. This tendency coincides with the fact that sea trout usually return to their stream to spawn from August and throughout the fall season (Jonsson, 1985; Nordeng, 1977), and is thereby not surprising. Furthermore, the estuaries of brackish water in Tvedestrandfjorden have been found to be used by young, and thus smaller, sea trout to stay during winter. The areas around Østeråsbekken in the inner buffer, and around Hestøya and Furøya in the notake zones are nursery areas for juvenile sea trout (Knutsen et al., 2003). Common differences between young and older sea trout can also be found in their feeding behavior: post-smolt tend to prefer feeding in shallow areas and at inshore places, while larger fish tend to move further out to feed on pelagic fishes (Knutsen et al., 2001). As no age-data has been used in this study, it is difficult to conclude with this, but the trends within the different groups suggest a link between age and behavior.

The harvested group was the group with the lowest probabilities for movement between zones, but as opposed to the other groups, the movement was fairly even between all zones (Fig. 3.6), suggesting that individuals in this group were using all zones approximately equally. The most likely migration was that from the inner buffer to the notake zone. Migrations between all zones is logical, considering the fate of this group. Interestingly, this was the group with the highest activity within the inner buffer, positively affected by increased temperature and size. This behavior may be also one of the reasons why the fish in this group were harvested - their high level of activity on a small scale. There was a weak tendency of the large fish to wander more between zones than the small ones (Fig. 3.7), maybe due to a higher boldness level in older fish, which has been found to be positively related to food intake and thus growth (Biro and Stamps, 2008).

The general patterns seen in the results show that increased temperature leads to increased

migration activity, both at small- and medium scales (Figs 3.6 and 3.3).

A known effect of increased temperature is increased metabolism, including enzyme activity, protein structure and cell functions (Arlinghaus et al., 2007; Harris and Milner, 2006; Jonsson et al., 2001), which is a likely explanation of this increased activity during higher temperatures, particularly the small-scale activity in the inner buffer zone (Fig. 3.3).

The medium-scale migrations most positively affected by increased temperature was the dispersed group's migration from the notake zone to the outer- and inner buffers, dead group's migration from the inner- to the outer buffer, and harvested group's migration from the inner buffer to the notake zone.

High temperatures have been found to be positively correlated to increased growth (Berg and Jonsson, 1990) as a result of more favorable habitat conditions, more food during summer, and increased metabolism.

In several cases when it comes to medium-scaled movements, migration probabilities between some zones increase with decreasing temperatures (Fig. 3.6). The most pronounced of these are the dead group's migration from the inner buffer to the notake zone and the alive group's migrations between the outer buffer and the notake zone. It is also worth mentioning that the harvested group was more likely to travel from the inner to the outer buffer at sinking temperatures.

Elevated temperatures in marine environments may cause a decrease in dissolved oxygen in the water (Arlinghaus et al., 2007). Large parts of the notake zone and inner buffer have low levels of oxygen (Knutsen et al., 2003), and it is possible that enhanced oxygen levels are part of the explanation for these trends. It is also possible that some of the temperature induced migration trends are affected by season, which we haven't assessed in this study, but which may be relevant for explaining particular behavior.

Even though precipitation had less of an effect than temperature, some migrations were affected by this too. A possible explanation for increased migration probabilities due to precipitation is the fact that the volume of freshwater from the rivers will increase during heavy rainfall. Thus, the brackish conditions in the estuaries will become more freshwater dominated. The dead dispersed groups were more likely to move from the notake zone to inner buffer during dry weather, possibly due to a more favorable brackish water condition in the area. Furthermore, movement by the alive-group from the inner buffer to the notake zone was more likely during rainfall (Fig. 3.6). Rainfall is often connected with increased wind, which may lead to the stirring of water masses and again an increased availability of food. In Ruud (2015), changes in air pressure lead to increased swimming activity in sea trout.

The one big difference between the alive group and the harvested group is the noticeable tendency of the alive group to migrate from the outer buffer to the notake zone ($\psi_k^{34}=0.5$;

Fig. 3.6). The two groups' tendencies of movement both at small and medium scale are fairly similar, and the fact that large fish are active in the inner buffer zone indicates that none of these groups are large-scale dispersers (Fig. 3.4). This suggests that the alive-group have in fact gotten some protection from the MPA regulations in the notake zone, while the harvested group, which seems to migrate more or less regularly between all the zones and thereby spends more time in the buffer zones where hook-and-line fishing is allowed, were fished. Thus, the MPA regulations in Tvedestrandfjorden can be viewed as a success in regards to protecting fish from harvesting. However, this may also lead to an adaption in the sea trout to more stationary, inactive and less bold behavior.

In Ruud (2015), individuals of medium size and smolt-length were shown to get the best protection against harvesting from staying in the notake zone. Large individuals with large smolt-lengths and small individuals with small smolt lengths were harvested regardless of their use of the notake zone. Adding on to these discoveries, the results of the current study indicates that in addition to this size-selection, fish behavior affects an individuals' likelihood of being harvested.

The use of minimum size in management is a tool with the purpose of making sure fish is not harvested before they have reached sexual maturity and reproduced at least once. However, the use of minimum size has been shown to alter natural variation in the fish stocks and reduce genetic diversity because it is a participating factor in selection for small fish with early maturation. In this study, the size effects on medium-scale movement (Fig. 3.7) for all groups except the dispersed group showed that the large individuals were more likely to migrate between zones, and thus be more exposed to harvesting than small individuals. Large fish in Tvedestrandfjorden have also been found to receive little protection from the notake zone (ibid.). Large females are considered particularly important for a population because they are known to produce many eggs with good quality, and these will benefit from the introduction of maximum size in management (Anon., 2016). A combined use of both minimum and maximum sizes in the management has been suggested, to even out the harvesting pressure on the different size groups in the population (ibid.), and is a suggestion for the future development of fish management in Tvedestrandfjorden.

Conclusion

As this study has shown, the MPA established in Tvedestrandfjorden most likely provides protection against harvesting for sea trout, particularly the ones that use the notake zone frequently. Differences were seen between the different fate groups regarding area use, which suggests that behavioral traits as well as physical ones are being affected by harvest selection. This may cause population dynamics to be altered both size-wise and behavioral-wise.

For three of the four groups, large individuals were generally more active than smaller ones on a medium scale, and thus more likely to be harvested. As large individuals (particularly large females) are just as important for a population as young individuals, the introduction of maximal harvesting size will most likely stop ongoing selection for smaller sizes and earlier maturation caused by only a minimum harvesting size restriction. As the MPA in Tvedestrandfjorden is due to be lifted in June 2017, I suggest to prolong this management area, as the project must be viewed as a success. Marine life in the area would still benefit from continued protection.

More research focusing on behavioral traits rather than only physical ones is needed in order to understand the complete ecological dynamics found in the marine ecosystems and thereby continue to improve the management of these areas.

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A

Supplementary data

```
1 > anova(lm(length~Fate, length.data))
2 Analysis of Variance Table
3
4 Response: length
5           Df Sum Sq Mean Sq F value Pr(>F)
6 Fate       3  13701   4567.1   0.6948 0.5592
7 Residuals 55 361543   6573.5
```

Listing A.1: *R-code of one-way ANOVA, length · fate*

```
1 > TukeyHSD(aov(length~Fate, length.data), ordered = FALSE, conf.level = 0.95)
2 Tukey multiple comparisons of means
3 95% family-wise confidence level
4
5 Fit: aov(formula = length ~ Fate, data = length.data)
6
7 $Fate
8           diff           lwr           upr           p adj
9 Dead-Alive    -7.041667 -105.08494   91.00161 0.9975275
10 Dispersed-Alive 24.506579  -66.02467  115.03783 0.8898531
11 Harvested-Alive -10.475000 -100.33314   79.38314 0.9896709
12 Dispersed-Dead  31.548246  -47.65662  110.75311 0.7178277
13 Harvested-Dead  -3.433333  -81.86795   75.00128 0.9994352
14 Harvested-Dispersed -34.981579 -103.79591   33.83276 0.5376640
```

Listing A.2: *R-code of Tukey HDS, length · fate*

```
1 > anova(lm(Tracking.days~Fate, td.data.DH))
2 Analysis of Variance Table
3
4 Response: Tracking.days
5           Df Sum Sq Mean Sq F value Pr(>F)
6 Fate       2 220884  110442   6.5276 0.003108
7 Residuals 48 812118   16919
```

Listing A.3: *R-code of one-way ANOVA, tracking days · fate*

Table A.2: AIC table for the tested models with AIC and Δ AIC values. $\psi=psi$, $F=fate$, $fa=fall$, $In=inner$, $L=length$, $M=month$, $No=notake$, $Ou=outer$, $P=detection$, $Prec=precipitation$, $S=survival$, $Seas=season$, $sp=spring$, $su=summer$, $Temp=temperature$, $w=winter$, $Z=zone$

Model	AIC	Δ AIC	AICc weights	Model likelihood	Deviance	Est. par.	Ordered par.	Fixed par.	Est. par. (%)
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L + Temp), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L)$	1967.279	0	0.66203	1	1775.888	90	99	9	100
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L + Temp + Prec), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L)$	1969.355	2.076	0.23448	0.354	1775.703	91	100	9	100
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L)$	1972.564	3.449	0.04714	0.071	1783.431	89	98	9	100
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L.siIn + Temp + Prec), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L)$	1973.419	6.140	0.03073	0.046	1786.541	88	97	9	100
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L)$	1973.78	11.463	0.02562	0.039	1784.650	89	95	6	100
$S(L + M, = 1)p(F * Z)\psi(F * Z)$	2004.092	36.81	0	0	1926.103	38	56	1	70
$S(L * M, = 1)p(F * Z)\psi(F * Z)$	2008.451	41.172	0	0	1924.135	41	73	1	58
$S(M, = 1)p(F * Z)\psi(F * Z)$	2024.149	56.870	0	0	1916.414	52	55	1	96
$S(F * Z, = 1)p(F * Z)\psi(F * Z)$	2030.110	62.831	0	0	1950.015	39	48	9	100
$S(Seas, = 1)p(F * Z)\psi(F * Z)$	2030.354	63.074	0	0	1958.666	35	41	1	88
$S(disp(L), res(1))p(F * Z)\psi(F * Z)$	2031.326	64.047	0	0	1963.826	33	39	1	87
$S(M + L, = 1)p(F * Z)\psi(Z * F * Temp * Prec) = 1$	2032.300	65.021	0	0	1854.411	84	104	1	82
$S(F * Z, = 1)p(Z)\psi(F * Z)$	2036.504	69.225	0	0	1975.262	30	31	1	100
$S(Seas * L, = 1)p(F * Z)\psi(F * Z)$	2039.995	72.715	0	0	1966.209	36	45	1	82
$S(F * Z, = 1)identityp(F * Z)\psi(F * Z)$	2042.806	75.527	0	0	1950.015	45	48	3	100
$S(M + L, = 1)identityp(F * Z)\psi(F * Z)$	2044.154	76.875	0	0	1861.777	86	104	1	84
$S(M, = 1)p(F * Z)\psi(F * Z)$	2047.714	80.434	0	0	1867.582	85	104	1	83
$S(F * Z)p(F * Z)\psi(F * Z)$	2049.193	81.914	0	0	1950.015	48	48	0	100
$S(disp(Z * L), res(1))p(F * Z)\psi(F * Z)$	2052.792	85.513	0	0	1979.006	36	43	1	86
$S(Seas, = 1)p(F * Z)\psi(Z * F * Temp * Prec) = 1$	2056.906	89.627	0	0	1997.746	29	35	1	86
$S(F * Z)p(F * Z)\psi(F * Z)$	2056.984	89.705	0	0	1883.571	82	90	1	92
$S(Seas * L, = 1)p(F * Z)\psi(Z * F * Temp * Prec) = 1$	2058.992	91.713	0	0	1881.103	84	92	1	92
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L + Temp + Prec), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L) = 1$	2061.234	93.954	0	0	1881.102	85	94	1	91
$S(M(Wsp) + L * Seas(su = fa), = 1)p(In(F * L), No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L) = 1$	2062.405	95.126	0	0	1855.120	97	90	2	110
$S(F * Z, = 1)disp(F * Z)\psi(Z)$	2068.658	101.379	0	0	1886.281	86	92	2	96
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z)\psi(Z)$	2068.711	101.431	0	0	2038.393	15	30	9	80
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z)\psi(Z * F * Temp * Prec) = 1$	2074.075	106.796	0	0	1898.425	83	90	1	93
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z, No\&Ou = 1)\psi(Z * F * Temp * Prec + F * L) = 1$	2077.546	110.267	0	0	1897.414	85	91	6	100
$S(Zaine = 11)p(F * Z)\psi(F * Z)$	2078.458	111.179	0	0	1998.363	39	40	1	100
$S(F * Z, = 1)p(F * Z)\psi(L * Seas)for sok2$	2082.430	115.151	0	0	1959.611	59	72	0	82
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z, Nor = 1)\psi(Z * F * Temp * Prec + Z * L) = 1$	2083.155	115.875	0	0	1896.277	88	93	2	97
$S(Z)p(F * Z)\psi(F * Z)$	2085.193	117.913	0	0	2005.097	39	39	0	100
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z, Nor = 1)\psi(Z * F * Temp * Prec + L) = 1$	2091.578	124.299	0	0	1920.398	81	88	6	99
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z, Ou\¬ak = 1)\psi(Z * F * Temp * Prec) = 1$	2092.671	125.392	0	0	1923.721	80	90	6	96
$S(M(Wsp) + L * Seas(su = fa), = 1)p(F * Z, Nor = 1)\psi(Z * F * Temp * Prec * L) = 1$	2098.524	131.245	0	0	1893.519	96	111	2	88
$S(F)p(F * Z)\psi(F * Z)$	2099.882	132.603	0	0	2017.678	40	40	0	100
$S(M(Wsp) + L * Seas(su\&fa), = 1)p(F * Z)\psi(Z * F * Temp * Prec) = 1$	2112.042	144.763	0	0	1934.153	84	96	1	89
$S(F * Z, = 1)p(Z, No\&lonc)\psi(F * Z)$	2663.111	695.832	0	0	2603.951	29	38	9	100
$S(F * Z, = 1)p(F)\psi(F * Z)$	2787.956	820.677	0	0	2724.631	31	40	9	100



Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway