Riverine and near coastal migration performance of hatchery brown trout *Salmo trutta* L.

J. G. DAVIDSEN‡*, M. DAVERDIN‡, J. V. ARNEKLEIV‡, L. RØNNING‡, A. D. SJURSEN‡ AND J. I. KOKSVIK‡

‡*NTNU Museum, Norwegian University of Science and Technology, N-7491 Trondheim, Norway.*

Running headline: Migratory performance of brown trout smolts

*Author to whom correspondence should be addressed. Tel.: +47 924 64314;

email: jan.davidsen@ntnu.no

To study migration performance and return rates of hatchery brown trout *Salmo trutta* L. smolts the first 5 months after release, 50 fish in each year (L_F 158-288 mm) were in two subsequent years tagged with acoustic transmitters and recorded by automatic listening stations in the River Nidelva (Central Norway), its estuary and in the marine environment. More than half of the smolts became anadromous migrants (52% in 2011; 70% in 2012). The fish spent longer time in the estuary than in the marine environment and the results suggest that migratory behaviour of *S. trutta* smolts is not only restricted to be resident or anadrome/lacustrine, but that there is also an intermediary strategy of estuarine feeding. There were no differences in fork length or mass between groups of smolts with different migration patterns. Return rates from the sea within the first five months after release were in both years 16%. Median progression rate in the river was 0.090 L_F s^{-1} but decreased significantly as the smolts entered the estuary (0.015 L_F s^{-1}). The long residential time in the estuary may increase the risk of negative impacts from anthropogenic activities in estuaries such as boat harbours and industrial development, and special attention should be given to evaluate effects of such activities.

Key words: acoustic telemetry; compensatory hatchery program; migratory behaviour; mortality; sea trout; strategy.

INTRODUCTION

Brown trout *Salmo trutta* L. 1758 has two distinct life history strategies. One is a migration strategy where the individual accomplishes one or several migrations to feeding areas in fresh or marine waters, and the other is a resident strategy, where the fish remains in its native river during the entire life cycle (Jonsson & Jonsson, 2011). This phenomenon of population split into migratory and resident individuals is termed partial migration, and it is suggested that the strategy used by the individual fish is determined by metabolic rate and growth rate (Jonsson & Jonsson, 1993). This is supported by Forseth *et al*. (1999), who found that fast growing juvenile *S. trutta* shifted their niche earlier and at a smaller body size than slower growing individuals. The authors suggested that this difference in migratory behaviour was caused by maintenance of higher metabolic rates in fast growers which were energetically constrained at a younger age by limited food resources than slow growers.

As a compensation measure to the decreases in many *S. trutta* populations in watersheds influenced by hydropower regimes, hatchery smolts are released annually into some of these rivers. The intention is often to support the sea run part of the population, aiming at producing fish that undergo one or several marine feeding migrations and return to the river for spawning after a period in the sea. However, ranching and enhancement of populations of anadromous *S. trutta* may be problematic since the species is only partly migratory. In hatcheries, the juvenile feeding rate is higher than in the wild, and the propensity to residency may therefore increase in hatchery *S. trutta* (Jonsson, 1989). In earlier studies, it was observed that less than 50% of the released *S. trutta* smolts migrated to the sea, but it was also found that migration tendency increased with increasing fish length (Jonsson *et al.*, 1995; Ugedal *et al.*, 1998). The low tendency of seaward migration raised the question about the value of releasing hatchery smolts in order to enhance sea trout populations impacted by human activity (Ugedal *et al.*, 1998).

As a consequence of these concerns, Norwegian hatcheries have during the last decades increased food ratios, and the food quality has been improved in order to produce a larger and apparently better suited *S. trutta* smolt for release. However, new research (Serrano *et al.*, 2009; Larsson *et al.*, 2012) has indicated that this may give an undesirable effect, since larger smolts with a higher lipid content, according to the theory on partial migration, may become residents instead of migrating to the sea.

The aim of this work was to study riverine and near coastal migration performance and return rates after the first summer at sea of *S. trutta* smolts reared under a contemporary production regime. By using acoustic telemetry, detailed information about migration behaviour, the proportion of resident and anadromous migrants and the return rates from the sea during the first five months after release could be collected.

MATERIALS AND METHODS

Study area

The study was performed in the River Nidelva in Central Norway, which drains into the marine Trondheim Fjord. The accessible river stretch to anadromous *S. trutta* is 9 km (Fig. 1). In 2011, mean flow was 99 $m^3 s^{-1}$. The river is influenced by seven hydropower stations and consequently, the part of the river accessible for anadromous *S. trutta* is periodically affected by rapid and frequent alterations in the water discharge due to regulation for hydropower production (hydropeaking), with flows varying between 30 and 150 $m^3 s^{-1}$. The dominant fish species in the lower part of the river are Atlantic salmon *Salmo salar* L. 1758 and *S. trutta*.

The lower part of the river channels through the central part of Trondheim, which is the third largest city in Norway. The river mouth and estuary (zone 2, Fig. 1) are heavily modified with residential properties and industrial development next to the river banks and boat harbours in the river channel. The same area constitutes the transition zone between the marine and freshwater habitat with relatively large environmental fluctuations caused by tides, variable weather situations and daily changes in the freshwater outlet caused by hydropeaking. The tidal cycle (2–3 m difference between water level at low and high water) influences the water level in the River Nidelva up to array #3 (Fig. 1), however sea water rarely extends further upstream than the first two km (half way between array #2 and array #3). Zone 2 was in this study defined as the estuary. The Trondheim fjord is a long (126 km) and wide fjord with a maximal depth of max 617 m. Salinity levels in zone 1 is generally above 30. There are only few islands, and consequently the littoral zone constitutes a relatively small area.

Fish origin

Fifty randomly chosen individuals of two-year-old hatchery *S. trutta* smolts were obtained for tagging in each of the study years (2011 and 2012) from the Lundamo hatchery located 23 km from the release site in the River Nidelva. The smolts were F1 progeny of 15 families of wild-captured anadromous *S. trutta* from the River Nidelva. The light regime in the hatchery followed the natural daylight periods and the water temperature was 1.5-5 °C (upwelling ground water). These are standard procedures used in several Norwegian hatcheries for producing a seawater-tolerant smolt at the time of the wild smolt migration. The physiological smoltification status was both years examined two weeks before release by sacrificing a subsample of the hatchery fish and analysing gill Na+,K+-ATPase activity (performed by Pharmaq Analytiq, Norway, www.hi.no), using the protocol of McCormick (1993).

Physiological smolt status

The gill Na+,K+-ATPase activity indicated that smolts were physiologically prepared for the seaward migration (Aarestrup *et al.*, 2000) at the time of release in both study years (2011: n =20, mean±S.D.=6.2±1.4 µmol ADP mg protein^{-1} h^{-1}, range 3.6–9.5; 2012: n=10, mean±S.D.=7.2±2.2 µmol ADP mg protein^{-1} h^{-1}, range 4.9–12.5).

Fish tagging and release

Prior to tagging, fork length (L_F) and mass (W) were measured to the nearest mm and g, respectively. The fish were significantly longer in 2011 (n=50, L_F±S.D. 223±27 mm, range 158–288 mm) than in 2012 (n=50, mean L_F±S.D. 199±12 mm, range 172–232 mm; student t-test, n=100, P<0.005). Mean mass was also higher in 2011 than in 2012 (n=50, mean W±S.D. 141±58 g, range 47–318 g) than in 2012 (n=50, mean W±S.D. 95±18 g, range 58–149 g; student t-test, n=100, P<0.005).

The fish were surgically implanted with an individually coded acoustic transmitter (2011: Thelma Biotel AS, Norway, www.thelmabiotel.com, model LP-7.3, 7.3 X 18.0 mm, mass in water:air of 1.2:1.9 g, nominal delay between pulses: 45 s, estimated tag life 165 days; 2012: Vemco Inc., Canada, www.vemco.com, model V7-4L, 7.0 X 22.5 mm, mass in water:air of 1.0:1.8 g, nominal delay: 45 s, estimated tag life 138 days). Before tagging, individuals were anaesthetised by 4 min immersion in an aqueous solution of 2-phenoxy ethanol (EC No 204-589-7; SIGMAChemical Co., USA; www.sigmaaldrich.com; 0.5 ml l^{-1}). The transmitter was inserted in the body cavity through a 1.0–1.5 cm incision on the ventral surface anterior to the pelvic girdle. The incision was closed using two independent monofilament sutures (RESORBA Wundversorgung GmbH & Co. KG, Germany; www.resorba.com; 5/0 Resolon). During surgery, the gills were continuously flushed with aerated water. Following recovery (5–10 minutes), the smolts were placed in a tank with freshwater. Two–four days after surgery, the tagged smolts were transported 35 min by car in a 1000 l tank with oxygenated water to the release site in the River Nidelva (Fig. 1, release date 2011: 18 May; 2012: 16 May). The tagged smolts were released together with a few hundred untagged hatchery smolts.

Tracking of tagged fish

Fish behaviour was monitored using 18 automatic listening stations (ALS, Vemco Inc., model VR2W) from 18 May – 15 October 2011 and 16 May – 15 October 2012 (Fig. 1). The ALSs in the river were deployed 1–3 m below surface, while the ALSs in the fjord were deployed 3–5 m below surface. Most of the ALSs were moored in arrays (A1-A3). The arrays were used to divide the study area into four zones (Z1-Z4). Z1 was the marine habitat in the fjord, Z2 was the estuary while Z3 and Z4 were the lower and upper parts of the river, respectively. Each ALS recorded the identity code from the transmitter and the time when tagged fish were within the detection range. The detection ranges were 100–400 m, and varied with environmental conditions such as wind, currents and haloclines. The receiver arrays were part of the Ocean Tracking Network www.oceantrackingnetwork.org. Manual tracking was performed along the river once every 1.5 month using a portable receiver with an omnidirectional hydrophone (Vemco Inc., model VR100) to detect if tagged *S. trutta* had passed some of the ALSs without being recorded.

Receiver performance

All fish recorded at any of the receiver sites downstream the release site had in all cases been recorded by the previous arrays. This indicates that all tagged fish were recorded when passing the three receiver arrays. This is supported by the results from manual tracking. The two outermost receivers did not cover the entire distance across the fjord, so the number of fish recorded at this site is a minimum estimate. However, during the main period of the seaward migration in 2012 (Mai – June), five additional receivers were deployed across the fjord, forming a full array also at this site. All fish recorded by the additional receivers were also recorded by one of the two original receivers deployed near shore at this outermost site. *S. trutta* post-smolts often move back and forth along the littoral zone (Jonsson & Jonsson, 2011). Such behaviour may explain why all individuals entering the marine habitat were recorded by the two near-shore receivers.

Data analysis

Results from the first two days after release were excluded from statistical analyses to reduce the risk of including adverse behaviour induced by handling and tagging stress (Pottinger, 2010). Hatchery smolts that were tracked for more than 48 days were divided into four groups according to their behaviour: A) River feeding individuals, which never entered the estuary; B) estuarine feeders, which entered the estuary but never entered the fjord; C) estuarine/marine feeders, which entered the fjord for a total period of less than a week, but mainly stayed in the estuary; D) marine feeders, which spent more than one week in the fjord.

Cumulative dwelling time was estimated week-by-week by summarising the proportion of time each fish spent in the different zones. Fish not detected during a week were supposed to be in the zone where it was last detected until next detection. Since detection efficiency in the fjord was not 100%, registrations of fish in zone 1 and 2 were combined in the analyses of the cumulative dwelling time. Due to a low number of individual fish detected during the last part of the study period, cumulative dwelling time was only estimated for the first eleven weeks after release.

Progression rate was estimated as individual body lengths (L_F) per second by assuming the fish had moved the shortest distance between the ALS sites, thus giving minimum estimates (Thorstad *et al.*, 2004). Only fish that migrated as far as to zone 1 were used in this analysis. Differences in progression rates between zone 1, 2 and 3 were tested as unbalanced unreplicated repeated measurements by fitting a linear mixed model using the restricted maximum likelihood (REML) method. The progression rates were ln-transformed. Zones 1-4 (Fig. 1) were used as fixed effects and individual fish id as random effects. The resulting zone term in the fitted model was then tested with a maximum likelihood (ML) ratio test against the null model (with exclusion of the zones as fixed effects). The model was validated by visual inspection of the model residuals. The package “lme4” (Bates & Maechler, 2010) was used in the software program R 2.12 (www.r-project.org).

RESULTS

Habitat use and individual migration strategies

In total, 83% of the *S. trutta* smolts entered the estuary and/or marine habitat (Fig. 2) and four to five weeks after release (both years) a higher proportion was registered in the estuary and/or marine habitat than in the river. Based on individual means, it was found that the fish spent 45% (2011) and 50% (2012) of the first eleven weeks after release in areas with saline waters (i.e. estuary or marine habitat).

The smolts displayed a large individual variation in migration patterns. Fourteen of the 100 tagged fish migrated into the fjord and were never registered again. Of the remaining fish, 58 individuals (67%) were tracked for more than 48 days. Of these, 13 individuals (22%) were categorised as river feeders, 16 (28%) as estuarine feeders, 15 (26%) as estuarine/marine feeders and 14 (24%) as marine feeders (Table I). There was no difference in body length at release among the four groups (ANOVA, d.f=54, P=0.86), or between estuarine feeders and marine feeders (ANOVA, d.f=28, P=0.39,). Similarly, there were no differences in body mass among the four groups (ANOVA, d.f=54, P=0.65), or between estuarine feeders and marine feeders (ANOVA, d.f=28, P=0.26,).

Migration performance, return rates and rate of progression

None of the smolts were recorded upstream of the release site. A total of 97 smolts were registered in zone 3 (Fig. 1 & 2) and 61 smolts (61%) were registered at one or several occasions in zone 1 (marine habitat). Thirty eight of the individuals recorded in the marine habitat (38%) returned to the estuary (zone 2, Fig. 3) and 16 smolts (16%) continued migrating upstream into the river at return (zone 3). Only smolts that returned within the 5 months battery life of the acoustic tag could be registered.

Only 18 smolts (36%) in 2011 and 25 smolts in 2012 (50%) were still recorded 11 weeks after release. The last registration of a fish was most often (37%) in zone 2 (Fig. 3).

Downstream progression rate (Fig. 4) was faster in zone 3 (median 0.090 L_F s^{-1}) than in zone 2 (median 0.015 L_F s^{-1}) and zone 1 (median 0.016 L_F s^{-1}; Linear mixed-effects model: n=235, P<0.001).

DISCUSSION

Habitat use and individual migration strategies

The estuary seemed to be an important habitat during summer for the hatchery *S. trutta* smolts tracked in this study. Anadromous brown trout are usually not found offshore in the Atlantic Ocean, but feed chiefly in estuaries and shallow waters close to shore (Jonsson & Jonsson, 2011). *Salmo trutta* are well known to display a large plasticity in life history strategies (Jonsson & Jonsson, 2011). Results in the present study suggest that migratory behaviour of *S. trutta* smolts is not only restricted to be resident or anadrome/lacustrine, but that there is also an intermediary strategy of estuarine feeding. Chernitsky *el al.* (1995) hypothesized that in northern Russia, estuarine feeding and longer marine migrations may be alternative life history tactics in anadromous *S. trutta*. However, there is little knowledge about such a migratory dichotomy from other areas. An extensive estuarine feeding may be caused by better feeding options in the estuary than in the marine area. In the river Nidelva, the estuary is long and with extensive littoral areas, while the marine Trondheim fjord is wide, deep and only with few islands, so productive littoral zones are here a limited resource.

It has been suggested that larger smolts are more willing to migrate (Ugedal *et al.*, 1998). However, there was no difference in body length or mass between groups of smolts with different migration strategies in the present study, and those categorised as fjord feeders were not larger than others. Further, strontium analyses of scales from adult *S. trutta* caught in the lower part of the River Nidelva (Koksvik & Steinnes, 2005) indicated that the majority of these fish had migrated mainly to the estuarine habitat.

The smolts exhibited a large individual variation in their migration behaviour in the present study. A similar result was found in a study of *S. trutta* smolts in western Scotland, where pronounced individual differences in habitat use were observed (Middlemas *et al.*, 2009). The underlying cause for this large individual variation is unknown, but may be explained by e.g. differences in sea water tolerance, growth rates, body size or feeding behaviour.

Migration performance and return rates

In this study, a large proportion (52% in 2011; 70% in 2012) of the hatchery *S. trutta* smolts migrated to the marine habitat. Further, 76% (2011) and 90% (2012) of the smolts were registered in the estuary. Hence, a large proportion of the released *S. trutta* smolts moved to areas with saline waters and can consequently be characterised as anadromous migrants.

The results differ from studies conducted in other Norwegian fjords 20–30 years ago. At that time, Jonsson *et al.* (1995) found that 23–53% (average 34%) of hatchery *S. trutta* released in the River Akerselva, southern Norway, became sea-run migratory after release. Similarly, Ugedal *et al.* (1998) observed that only 34% of hatchery *S. trutta* released into the River Halselva in northern Norway migrated downstream to the river mouth. However, larger proportions of migratory *S. trutta* were recorded in two newer studies of hatchery fish released in the River Klarälven (Lans *et al.*, 2011) and the River Sävarån (Larsson *et al.*, 2012) in Sweden. In both studies, 45-50% of the *S. trutta* smolts reared under modern standard hatchery conditions migrated to the river mouth.

In the current study, 16% of the tagged fish returned to the river after the first summer in the sea both study years. Jonsson and Jonsson (2009) found that on average 15% of wild *S. trutta* leaving the River Imsa in May survived the marine migration in the years 1976-2005. Our results are thus similar to what Jonsson and Jonsson (2009) found, however, annual variation may influence the sea survival.

Due to the relatively short lifetime of the batteries in the acoustic tags used in this study (five months), only return rates after the first summer migration were estimated. Since *S. trutta* in the River Nidelva normally migrate to sea 2-4 times (A. D. Sjursen, pers. com.) before first maturation, it cannot be concluded from this study that releases of hatchery trout in this river actually contributed to the spawning population. Genetic analyses of *S. trutta* in Limfjorden in Denmark (Ruzzante *et al.*, 2004), suggested that hatchery *S. trutta* that became anadromous experienced high mortality at sea and were largely absent among the mature individuals and therefore unlikely to contribute significantly to the local gene pool.

The high number of fish lost in the river during the first eleven weeks of the study period (64% 2011; 50% 2012) may be due to predatory birds or mammals bringing the smolts out of the river, malfunctioning transmitters, or the smolts moving or drifting to a place where the detection efficiency was low (like rapids and other places with high current speeds) (Davidsen *et al.*, 2009). Further, the fourteen individuals that were last time detected in the fjord may have been predated during their marine migration or they may have returned to the river after the study period ended (five months after release). New research have found that adult sea trout in central and northern Norway are able to overwinter in marine waters (Davidsen *et al*., unpublished results; Jensen & Rikardsen, 2008, 2012), however no such information exist for post-smolts.

Progression rates

Progression rates decreased as the smolt entered the area with brackish water (zone 2) in both study years. A similar pattern was observed in a study of hatchery sea trout released into the River Sävarån in Sweden (Serrano *et al.*, 2009). The decreased progression rates may be related to feeding in the estuary. Another reason may be that the smolts needed time for acclimation to sea water. However, analyses of gill Na^+,K^+-ATPase activity indicated that the smolts were physiologically prepared for the seaward migration at the time of release. *Salmo trutta* smolts are thought to be particularly vulnerable to predation during the transition between fresh and sea water (Dieperink *et al.*, 2001), but the long residential time in the estuary observed in the present study, may indicate that the gain is (or has been) higher than the risk. A consequence of the long residential time in the estuary is an increased risk of being influenced by building of boat harbours, boat traffic, industrial development, local pollution, gravel extraction and other physical developments along the coastline that are often concentrated in estuaries. There is need for evaluating the effects of anthropogenic activities in estuaries and near coastal areas and whether they may have any negative impact on *S. trutta* feeding behaviour or survival rates.

In conclusion, a large proportion of the tagged individuals migrated to the estuary or fjord and were consequently categorised as anadromous migrants. The progression rate decreased significantly as the smolts entered the estuary. The estuary area seemed to be an important habitat during the entire summer. The return rates from the marine habitat were 16% both years. However, it cannot be concluded from the present study to which extent the sea-run hatchery fish actually survived to maturation and contributed to the spawning population and local gene pool. Longer-term studies are needed to address this issue.

T. Weiseth and the staff at Lundamo hatchery are thanked for providing hatchery fish and for practical help during fish tagging and release. Thanks to G. Kjærstad for practical help in the field and to H. Urke at Norwegian Institute for Water Research for loan of acoustic receivers in 2011. Comments from E. B. Thorstad and two anonymous referees helped to improve the manuscript. This study was financed by NTNU Museum. The experimental procedures concur with the national ethical requirements and were approved by the Norwegian National Animal Research Authority.

REFERENCES

Aarestrup, K., Nielsen, C. & Madsen, S. S. (2000). Relationship between gill Na+,K+-ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2086-2095.doi:10.1139/cjfas-57-10-2086

Chernitsky, A. G., Zabruskov, G. V., Ermolaev, V. V. & Shkurko, D. S. (1995). Life history of trout, *Salmo trutta* L., in the Varsina River estuary, (The Barents Sea). *Nordic Journal of Freshwater Research* **71**, 183-189

Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., Skarðhamar, J. & Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon (*Salmo salar*) post-smolts: effects of environmental factors. *Journal of Fish Biology* **75**, 1700-1718.doi: 10.1111/j.1095-8649.2009.02423.x

Dieperink, C., Pedersen, S. & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish* **10**, 177-183

Forseth, T., Næsje, T., Jonsson, B. & Hårsaker, K. (1999). Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* **68**, 783-793

Jensen, J. L. A. & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic charr Salvelinus alpinus and brown trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810-1818

Jensen, J. L. A. & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology* **81**, 735-749

Jonsson, B. (1989). Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshwater Biology* **21**, 71-86

Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348-365

Jonsson, B. & Jonsson, N. (2009). Migratory timing, marine survival and growth of anadromous trout *Salmo trutta* in the River Imsa, Norway. *Journal of Fish Biology* **74**, 621-638.doi: 10.1111/j.1095-8649.2008.02152.x

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout - Habitat as a template for life histories*. 708 p. New York: Springer.

Jonsson, N., Jonsson, B., Aass, P. & Hansen, L. P. (1995). Brown trout *Salmo trutta* released to support recreational fishing in a Norwegian fjord. *Journal of Fish Biology* **46**, 70-84

Koksvik, J. I. & Steinnes, E. (2005). Strontium content of scales as a marker for distinguishing between sea trout and brown trout. *Hydrobiologia* **544**, 51-54

Lans, L., Greenberg, L. A., Karlsson, J., Calles, O., Schmitz, M. & Bergman, E. (2011). The effects of ration size on migration by hatchery-raised Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Ecology of Freshwater Fish* **4**, 548-557.doi:10.1111/j.1600-0633.2011.00503.x

Larsson, S., Serrano, I. & Eriksson, L.-O. (2012). Effects of muscle lipid concentration on wild and hatchery brown trout (*Salmo trutta*) smolt migration. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 1-12.doi:10.1139/F2011-128

McCormick, S. D. (1993). Methods for nonlethal gill biopsy and measurement of Na+, K+ -ATPase activity. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 656-658

Middlemas, S. J., Stewart, D. C., Mackay, S. & Armstrong, J. D. (2009). Habitat use and dispersal of post-smolt sea trout *Salmo trutta* in a Scottish sea loch system. *Journal of Fish Biology* **74**, 639-651

Pottinger, T. G. (2010). A multivariate comparison of the stress response in three salmonid and three cyprinid species: evidence for inter-family differences. *Journal of Fish Biology* **76**, 601-621.doi:10.1111/j.1095-8649.2009.02516.x

Ruzzante, D. E., Hansen, M. M., Meldrup, D. & Ebert, K. (2004). Stocking impact and migration pattern in an anadromous brown trout (*Salmo trutta*) complex: where have all the stocked spawning sea trout gone? *Molecular Ecology* **13**, 1433-1445.10.1111/j.1365-294X.2004.2004.02162.x

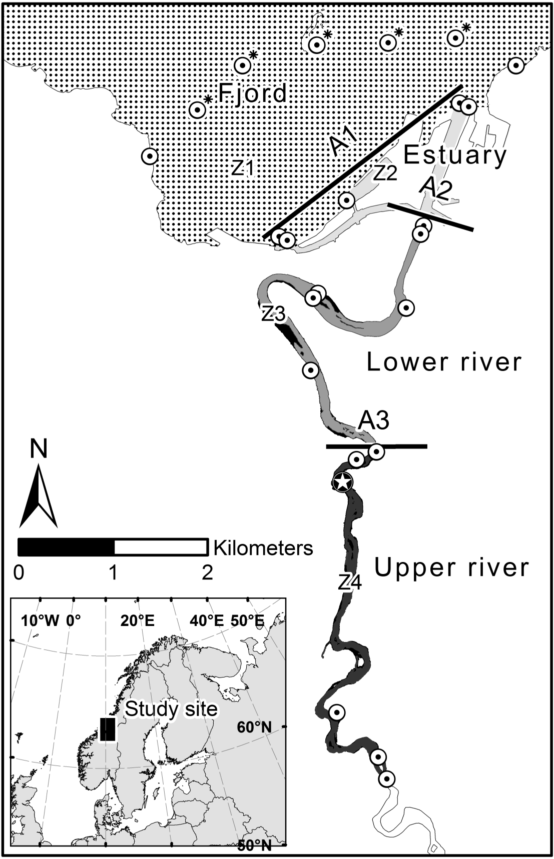
Serrano, I., Larsson, S. & Eriksson, L.-O. (2009). Migration performance of wild and hatchery sea trout (*Salmo trutta* L.) smolts—Implications for compensatory hatchery programs. *Fisheries Research* **99**, 210-215

Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P. A. & McKinley, R. S. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes* **71**, 305-311.doi:10.1007/s10641-004-1264-7

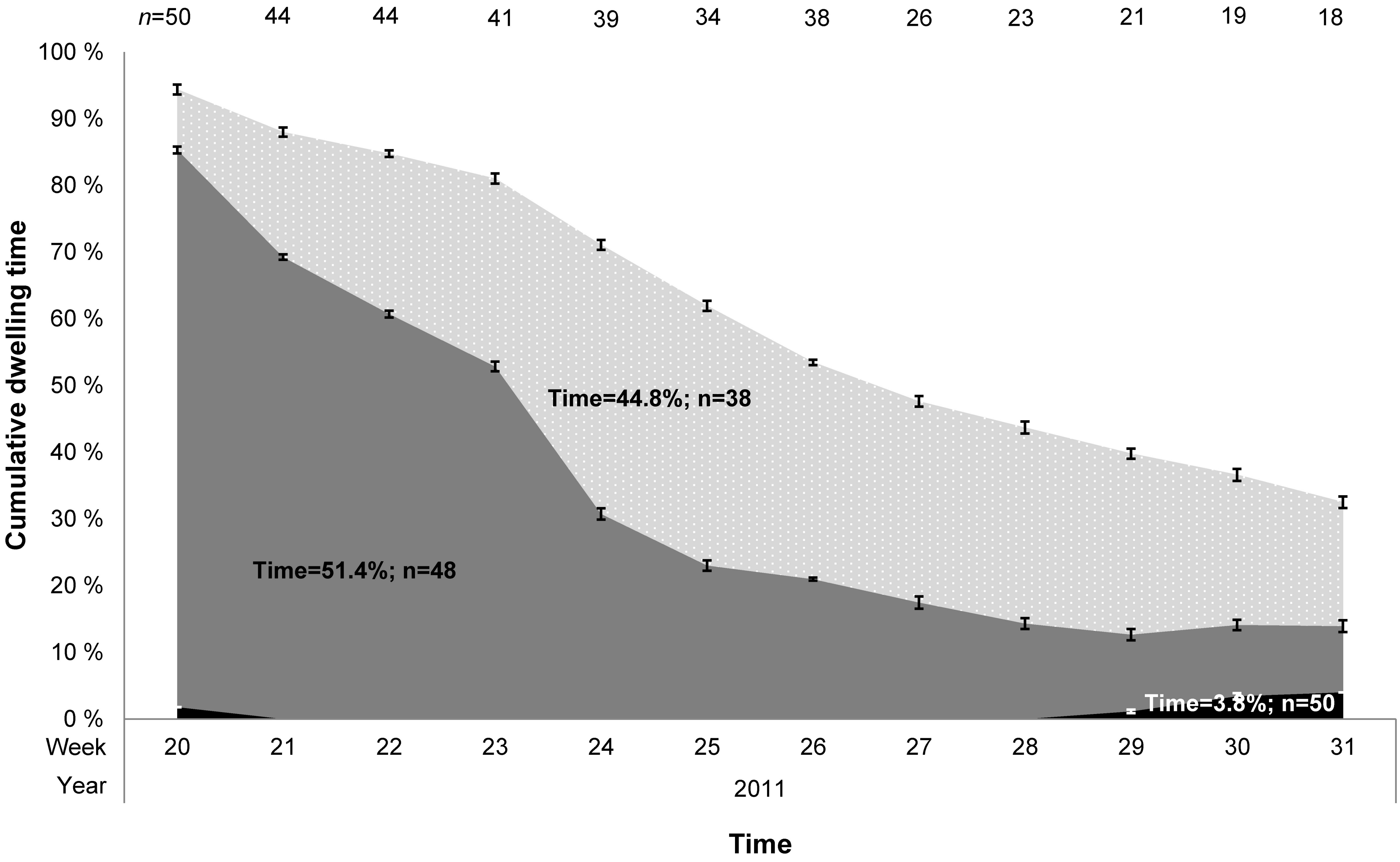
Ugedal, O., Finstad, B., Damsgård, B. & Mortensen, A. (1998). Seawater tolerance and downstream migration in hatchery-reared and wild brown trout. *Aquaculture* **168**, 395-405

ELECTRONIC REFERENCES

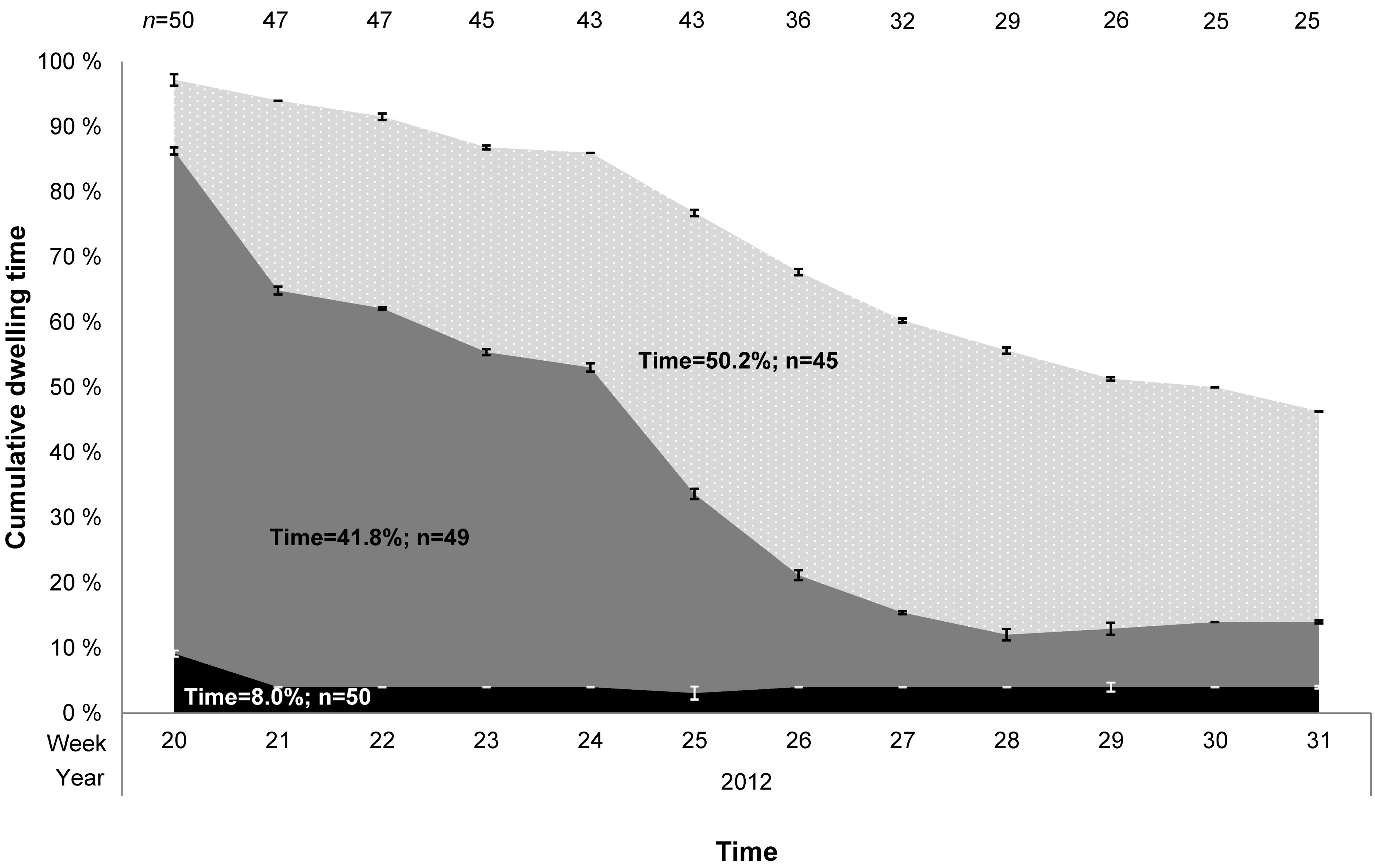
Bates, D. & Maechler, M. (2010). Package "lme4". Reference manual for the package. Available at http://cran.r-project.org/web/packages/lme4/lme4.pdf. (last accessed 04 March 2013).



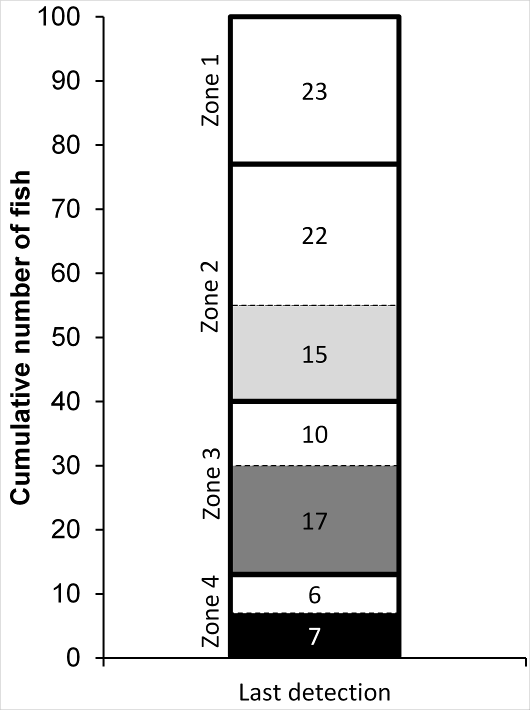
Fjord
A1
Z1
Z2
Estuary
A2
Z3
Lower river
A3
N
Kilometers
0
1
2
Upper river
Z4
10°W 0°
20°E
40°E 50°E
Study site
60°N
50°N



n=50
44
44
41
39
34
38
26
23
21
19
18
100 %
90 %
80 %
70 %
60 %
50 %
40 %
30 %
20 %
10 %
0 %
Cumulative dwelling time
Time=44.8%; n=38
Time=51.4%; n=48
Time=3.8%; n=50
Week
20
21
22
23
24
25
26
27
28
29
30
31
Year
2011
Time



n=50
47
47
45
43
43
36
32
29
26
25
25
100 %
90 %
80 %
70 %
60 %
50 %
40 %
30 %
20 %
10 %
0 %
Cumulative dwelling time
Time=50.2%; n=45
Time=41.8%; n=49
Time=8.0%; n=50
Week
20
21
22
23
24
25
26
27
28
29
30
31
Year
2012
Time


Cumulative number of fish
100
90
80
70
60
50
40
30
20
10
0
Zone 1
Zone 2
Zone 3
Zone 4
23
22
15
10
17
6
7
Last detection

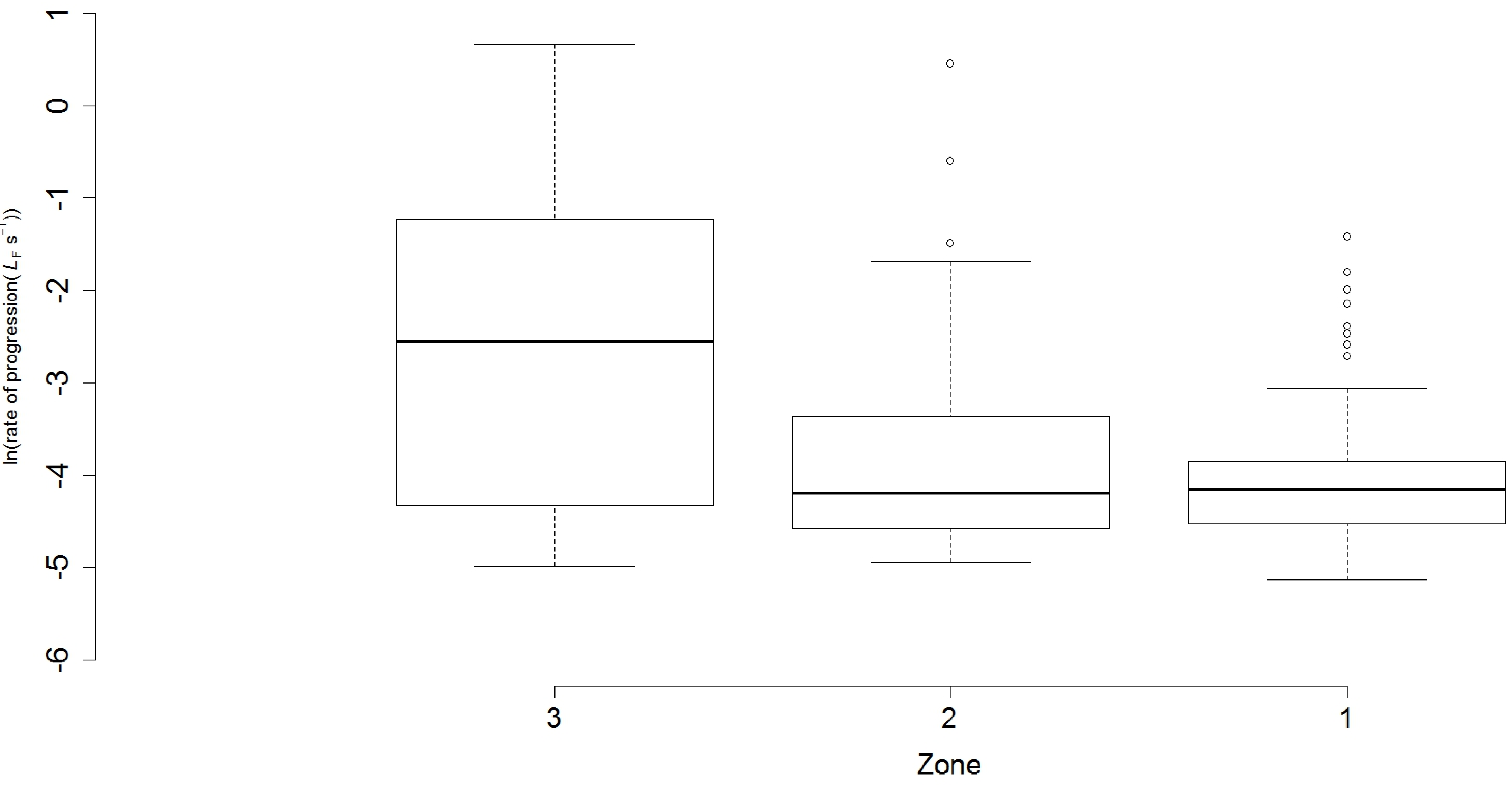

ln(rate of progression(L_F s^-1))
1
0
-1
-2
-3
-4
-5
-6
3
2
1
Zone

Figure captions

Figure 1: The lower part of the River Nidelva and the inner part of the Trondheim Fjord showing the release site (star) and acoustic receivers (circles). A1-A3 indicate the arrays of automatic listening stations and Z1-Z4 the zones in the study area. * indicates that the receiver was only operative Mai – June 2012.

Figure 2a&b: Seasonal variation in habitat use of hatchery brown trout *Salmo trutta* L. smolts released into the River Nidelva in 2011 and 2012, respectively. Black colour refers to zone 4, dark grey colour to zone 3 and light grey colour with dots to zone 2 and 1 (combined; see map Fig. 1). *n* indicates the number of fish registered in each zone and the per cent proportion of time spent in each habitat.

Figure 3: Habitat distribution of the last detection of hatchery brown trout *Salmo trutta* L. smolts equipped with acoustic transmitters and released into the River Nidelva in 2011 and 2012. Each section of the bar shows the proportion of fish that had their last registration within each zone (Z1-Z4, see map Fig. 1). The sections representing zone 2-4 are divided into two parts, where the white part shows the number of fish that had been registered in the fjord before they returned to the zone where they were last detected.

Figure 4: Progression rates of hatchery brown trout *Salmo trutta* L. smolts in the lower part of the River Nidelva (Z3), the estuary (Z2) and the marine habitat (Z1). The box-and-whisker plots show the median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers).

Table I: Downstream migrating hatchery *Salmo trutta* L. smolts divided into four groups according to their migration pattern. River feeding individuals never entered the estuary, estuarine feeders never entered the fjord, estuarine/fjord feeders entered the fjord for a period less than a week and stayed mainly in the estuary, and marine feeders spent more than one week in the fjord.

	n (proportion)	Length (mm) Mean±S.D.	Length (mm) range	Mass (g) Mean±S.D.	Mass (g) range
River feeders	13 (22%)	207±18	183-240	108±29	75-180
Estuarine feeders	16 (28%)	206±19	179-255	108±32	69-189
Estuarine/marine feeders	15 (26%)	207±27	171-281	111±54	58-285
Marine feeders	14 (24%)	215±27	182-272	127±55	73-257