DTU Library

Testing three common stocking methods: Differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (Salmo salar)

Birnie-Gauvin, Kim; Larsen, Martin Hage; Thomassen, Søren T.; Aarestrup, Kim

Published in:
Aquaculture

Link to article, DOI:
10.1016/j.aquaculture.2017.10.021

Publication date:
2018

Document Version
Version created as part of publication process; publisher's layout; not normally made publicly available

Accepted Manuscript

Testing three common stocking methods: Differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (Salmo salar)

Kim Birnie-Gauvin, Martin H. Larsen, Søren T. Thomassen, Kim Aarestrup

PII: S0044-8486(17)31820-3
DOI: doi:10.1016/j.aquaculture.2017.10.021
Reference: AQUA 632875

To appear in: *aquaculture*

Received date: 11 September 2017
Revised date: 12 October 2017
Accepted date: 16 October 2017

Please cite this article as: Kim Birnie-Gauvin, Martin H. Larsen, Søren T. Thomassen, Kim Aarestrup , Testing three common stocking methods: Differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (Salmo salar). The address for the corresponding author was captured as affiliation for all authors. Please check if appropriate. Aqua(2017), doi:10.1016/j.aquaculture.2017.10.021

Testing three common stocking methods: differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (*Salmo salar*)

In prep for Aquaculture

Kim Birnie-Gauvin[1], Martin H. Larsen[1,2], Søren T. Thomassen[2], Kim Aarestrup[1]

[1] DTU AQUA, National Institute of Aquatic Resources, Section for Freshwater Fisheries Ecology, Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark

[2] Danish Centre for Wild Salmon, Brusgårdsvej 15, DK-8960, Randers SØ, Denmark.

Author for correspondence: K. Birnie-Gauvin, kbir@aqua.dtu.dk

Highlights

- We compare the outcome of three common stocking practices for two populations of Atlantic salmon by evaluating smolt output from these practices and the potential effects of inherited traits on probability and timing of migration.
- We find that releasing half-year old fish belonging to the upper modal group of their year class is the most profitable stocking practice, given the higher migration propensity and lower rearing cost.
- We also find that fish from different populations migrate at different a time, indicating that inherited traits, which likely reflect local adaptations, influence migration timing.

Abstract

The influence of three common stocking practices for two strains (Ätran and Burrishoole) of hatchery-reared Atlantic salmon, *Salmo salar*, on smolt size, migration probability and migration timing were investigated *in situ*. Using a common garden experiment, fish from these populations were released as fry, half-year olds and one-year olds. Our results indicate that fish released at the fry and half-year stage produce smaller smolts, and migrate later in the year than their counterparts released at one-year of age, for both the Ätran and the Burrishoole populations. While fry had the lowest probability of migration, half-year old releases had greater migration rates than one-year olds of the same strain. Additionally, Ätran fish tended to migrate earlier in the year than Burrishoole fish of the same age. Our findings highlight the variability that exists among individuals and populations due to inherited factors, and emphasize the importance of considering age of fish and time spent in the hatchery when stocking populations in the wild to maximize smolt output.

Keywords: age-class, Atlantic salmon, migration, phenology, population, stocking

Introduction

The Atlantic salmon (*Salmo salar*) is an anadromous salmonid species, which has undergone severe decline, reaching historical lows in many rivers of Europe (Verspoor et al. 2007; Freyhof and Brooks 2011). This decline is largely due to hydroelectric development, habitat degradation, overfishing, pollution and climate change (Friedland 1998; Armstrong et al. 1998). Given its important value for recreational and commercial fisheries (Pinfold 2011), stocking of hatchery-reared Atlantic salmon has become a common practice to maintain population size, though success is ambiguous (Thorpe 1998). Currently, approximately 5.5 million smolts are released annually (along with an unknown number of fish released at earlier stages), but despite these efforts, Atlantic salmon populations continue to decline (ICES 2007).

The success of stocking is highly dependent on the survival of stocked fish, which is thought to be related to the condition of fish at the time of release, genetic background and on environmental conditions in rivers, estuaries and coastal environments (McCormick et al. 1998). Recently, efforts have been invested to develop optimal stocking strategies (Aprahamian et al. 2004), and while many studies have evaluated survival in relation to environmental factors and body condition, few studies have compared the rate of migration and migration timing of two or more stocked populations within the same river in a common garden scenario (i.e., effects of population differences on migration of fish exposed to the same environmental conditions; but see Nielsen et al. 2001). In fact, populations may differ in their ability to survive (Orciari et al. 1994) due to intra- and interspecific competition (Kennedy and Strange 1986) and ability to cope with environmental changes (e.g., changes in temperature, Kallio-Nyberg et al. 2004).

Salmon display variability within and among populations in terms of age at maturity (Jonsson et al. 1991), length of stay in freshwater (Randall et al. 1987) and use of habitat

(Heggenes et al. 1999). For example, the population of Northeast Brook (Newfoundland, Canada) is dominated by individuals that spend one year at sea, while the River Tana (Teno, Finland) population is dominated by individuals which spend 3 to 5 years at sea (Erkinaro et al. 1997; O'Connell et al. 2001). The age (Metcalfe et al. 1988) and size (Økland et al. 1993) of smolts may also vary. Smolts have been observed to migrate anywhere between 1 and 9 years of age (Robitaille et al. 1986; Jonsson and L'Abée-Lund 1993; Økland et al 1993; Klemetsen et al. 2003). The variability in salmon life-histories may reflect local adaptations within populations (Saunders and Schom 1985), and which maximize survival for individuals within these populations (Garcia de Leaniz et al. 2007). In other words, inherited traits from different populations may play a key role in an individual's ability to survive and migrate.

Our objective was to study the outcomes of three common stocking practices: (1) release of fry, (2) release of upper modal group of half-year olds in the fall, and (3) release of lower modal group of one-year olds in the early summer. Furthermore, to better understand the importance of inherited traits from population differences in hatchery-reared fish, growth, probability of migration and migration timing of stocked salmon was evaluated in River Lilleaa, Denmark. We released two strains of Atlantic salmon (Ätran from Sweden and Burrishoole from Ireland). Using this approach allows to ask questions on population and stocking differences that we otherwise would not be able to answer given that both populations are exposed to the same environmental conditions.

Material and Methods

Study location

River Lilleaa is located in eastern Jutland, Denmark. It is a tributary to River Gudenaa, which connects to the Randers Fjord before entering the Kattegat Sea (Figure 1). It was chosen as our study location because it is not home to a natural salmon population (i.e., our released salmon were the only salmon present; Figure 1). Two traps were set up: a wolf trap in the river channel as it runs parallel to the fish farm and a fyke net trap at the inlet channel of the fish farm. The traps spanned the entire width river, thus the majority of downstream-moving fish is expected to be caught.

Salmon populations

Hatchery salmon of different age classes (fry, half-year olds, and one-year olds) were obtained from two geographically distinct populations. The Ätran population is original to Sweden and the Burrishoole population from Ireland. The fish were reared in a hatchery (Danish Centre for Wild Salmon, Randers, Denmark). Respective groups of fish classes were reared in indoor tanks under identical conditions (i.e., at equal densities, in the same recycled water and fed from the same food source). All fish were first-generation offspring of salmon caught in their river of origin. To ensure genetic diversity, eggs and milt from over 100 adults were used for each population.

Release, recapture and migration of fish

Fry (n = 8700), half-year olds (n = 2479) and one-year olds (n = 1085) from the Ätran population, and half-year olds (n = 2649) and one year-olds (n = 892) from the Burrishoole population were transported from the hatchery to River Lilleaa. Before release, a subsample (N = 100) of fish from each age class except fry was randomly selected to be measured for total body length (±0.5cm). All fish, except the fry stage, were additionally fin clipped (pelvic fin) and tagged with coded nose wire tags in a specific manner to be associated to the proper age class and population. Specifically, half-year olds were not wire-tagged, but one year olds were; Ätran fish had the left pelvic fin clipped, while Burrishoole fish had the right pelvic fin clipped. All fish, including fry, had the adipose fin clipped. Fry were released on June 22, 1999. Half-year olds were released on October 21, 1999, and one-year olds were released on June 29, 1999. One-year olds were released this late in the year to try and minimize the number of individuals migrating in 1999. Both fry and half-year olds originated from the 1998-1999 parent cohort, while one-year olds originated from the 1997-1998 parent cohort. Upon capture in the traps, one-year old releases were of age 2, while fry and half-year old releases were of age 1. It is important to note that fish released as half-year olds represented the upper mode of their year class (the largest fish are selected), as is done in common stocking practices, in order to maximize the likelihood that they will migrate as one-year olds. One-year olds likely represented the lower mode of their year class because fish that had smoltified were released before. Hence, one-year olds were not smolts at their time of release. This method is currently part of the standard stocking approach used in Denmark and many regions of Europe.

Between March 1 and May 31, 2000, the two traps were emptied daily to determine if fish released the previous year had been captured (Figure 1). Fish captured at the traps were considered to be migrating smolts. Every day, at recapture, a subsample of fish was randomly selected to be measured for length (±0.5cm). See Table 1 for a summary of the release and recapture data. All procedures were carried out in accordance with the Danish Animal Experiments Inspectorate.

Statistical analysis

To investigate differences in length between the stocking types at release and at recapture, two separate generalized linear models (GLMs) with Gaussian distribution and identity link function were used:

$$Length_i = \alpha + \beta \times Stocking\ type_i + \varepsilon_i$$

$$\varepsilon_i \sim N(0,\sigma^2)$$

Where α is the intercept, β is the slope, and ε_i is normally distributed noise with mean 0 and variance σ^2. Stocking $type_i$ was included as dependent variable in the model and included only half-year olds and one-year olds from the Ätran population and the Burrishoole population. Fry from the Ätran population were not measured before release and were therefore omitted from this analysis. Subsequently, we used a Tukey contrast test to assess significant differences in length among stocking types at recapture.

The probability of migration among stocking types was evaluated using a GLM with binomial distribution (yes = migrate, no = not migrate) and logit link function:

$$Migration_i \sim B(1, \pi_i)$$

$$E(Migration_i) = \pi_i$$

$$var(Migration_i) = \pi_i \times (1- \pi_i)$$

$$Logit\ (\pi_i) = \alpha + \beta \times Stocking\ type_i + \varepsilon_i$$

Where $Migration_i$ is assumed to follow a binomial distribution with probability π_i, α is the intercept, β is the slope, and ε_i is residual variation. Stocking $type_i$ was included as dependent variable in the model and included all groups of released fish, that is, fry, half-year olds, and one-year olds of the Ätran population as well as half-year olds and one-year olds from the Burrishoole population. Tukey contrast test was subsequently performed to determine differences in migration probability among stocking types.

Lastly, we investigated differences in migration timing among stocking types using a Kruskal-Wallis test, given the lack of normality and equal variance in the data. Following the Kruskal-Wallis test, Dunn’s *post hoc* test with Bonferroni adjustment was used to determine differences in migration timing among stocking types. Here, migration time was defined as day of the calendar year.

All statistical analyses were performed using R 3.1.2 (R Development Core Team, 2014). Tukey contrast tests were conducted using the “glht” function in the “multcomp” package (Hothorn et al. 2008). Dunn’s test was performed using the “dunn.test” package (Dinno, 2017).

Results

In total, 186 fish released as fry, 640 fish released as half-year old and 163 fish released as one-year olds from the Ätran population, as well as 766 fish released as half-year olds and 145 fish released as one-year olds from the Burrishoole population were captured in the traps (Table 1). Lengths did not differ among stocking types at release (GLM, F = 0.20, df = 3, $P = 0.890$, Figure 2A), but differed at time of recapture in the trap (GLM, F = 130.3, df = 4, $P < 0.0001$, Figure 2B). Tukey contrast test revealed that the average length of all stocking types differed from one another ($P < 0.001$), except for Ätran and Burrishoole one-year olds ($P = 0.064$). The smallest fish at recapture were Ätran fry, followed by Ätran half-year olds, which were subsequently followed by Burrishoole half-year olds. The largest fish at recapture were one-year olds of both populations.

Probability of migration differed among stocking types (GLM, LRT = 2085.6, df = 4, $P < 0.0001$, Figure 3). Tukey contrast test showed a difference in migration propensity among all stocking types ($p < 0.001$), such that Ätran fry had the lowest propensity. One-year olds had an intermediate migration propensity, with no difference between Ätran and Burrishoole fish ($P = 0.941$). Finally, half-year olds had the highest probability of migration, but did not differ between Ätran and Burrishoole fish ($P = 0.089$).

Timing of migration differed among stocking types (Kruskal-Wallis test, $\chi^2 = 944.32$, df = 4, $P < 0.0001$, Figure 4), except for Burrishoole one-year olds and Ätran fry (Dunn's test, $P = 1.0$). We note that half-year old stocks generally migrated later than their one-year old counterparts and that Ätran half-year and one-year olds migrated earlier than their Burrishoole counterparts (Figure 5). More specifically, Ätran one-year olds migrated first, followed by Ätran half-year olds, Ätran fry/Burrishoole one-year olds, and Burrishoole half-year olds.

Discussion

Stocking approach

Individuals that vary in their year of migration may differ physiologically and behaviourally. For example, fish may vary in their dominance status, efficiency at detecting/processing food and their ability to enter marine environments successfully (Metcalfe et al. 1989; Jonsson and Jonsson 2006). Thus, depending on the age-at-release, fish may have a greater probability of migrating to sea, and/or be more prepared to migrate. A recent study investigated how size varied with age at seaward migration in *Salmo salar* and found that the probability of migrating to marine environments increased with size within each age-group (Jonsson et al. 2016). Previous stocking experiments showed that releasing fish at a younger age yields smaller smolt output due to mortality being generally greater when fish resided in rivers longer (Jokikokko and Jutila 2004). These conclusions were drawn from experiments where younger fish are released *before* older fish. Our study differs in that younger fish were released *after* older fish. Our results are therefore in agreement with previous findings in that the age class which spent the least amount of time in freshwater produced the largest smolt output. Half-year old released fish of both Ätran and Burrishoole populations had a greater probability of migration than their older counterparts, than fry and one-year olds, likely because shorter time spent in freshwater lowers natural mortality.

In hatchery fish, size is positively correlated with age at smolting, and thus older fish may yield a more favorable migrating class than younger fish because their size reduces potential predatory species and may increase the probability of smoltifying (Jonsson and Jonsson 2006). However, in the present study, fish of half- and one-year of age had similar lengths at release despite the age difference (due to upper and lower mode selections), suggesting that age-at-release or growth rate differences, and not size-at-release, were the driving factors for a greater proportion of half-year olds migrating. Fish stocked as fry had the lowest migration rate. The data for this age class are more complicated to interpret however, because it is likely that a significant number of individuals migrated the following year (in spring 2001), while no trapping was performed. Fry are also likely to be subjected to the highest predation pressure given their size and the dominance of brown trout (*Salmo trutta*) of several age classes in River Lilleå.

Longer time spent in a hatchery generally reduces post-release survival and migration rate due to increased stress and behavioural modifications sustained in the hatchery (i.e., decreased sheltering behaviour and predator avoidance; Johnsson et al. 2014), supporting our finding that half-year olds had a greater probability of migration than one-year olds. It is likely that one-year olds were maladapted to a wild environment given that they spent approximately 8 more months in the hatchery before being released. As such, it is possible that these fish suffered greater rates of predation due to their inability to avoid predators and find shelter (Johnsson et al. 2014) or experienced changes in morphology and physiology which may alter their survival and growth in nature (Sheehan et al. 2005; Jonsson and Jonsson 2006). It is important to note here that fish released as half-year olds and one-year olds were selected based on their size, and consequently, these fish were selected based on their growth rates. An alternative hypothesis is therefore that fish released as half-year olds, which potentially have higher growth rates, may be more dominant or risk-taking and better able to acquire food. While this link has not been found in Atlantic salmon, it has been found in a near relative, the brown trout (*Salmo trutta*) (Sundström and Johnsson 2001; Sundström et al. 2004; Riley et al. 2005). However, these fish were smaller at recapture than one-year olds, therefore suggesting that age and behaviour, not growth rate, are more likely the major proximate causes for migration in hatchery-reared fish. Furthermore, at the time of release for half-year olds (October), half-year olds were likely smaller than one-year olds, which were released 4 months before. These findings have important implications for salmon stocking and management. Half-year old fish are cheaper to produce (due to shorter time spent in the hatchery). Given that they appear to produce higher relative smolt numbers, the upper modal group of half-year olds may be the most profitable group to use for stocking. Additionally, shorter time spent in a hatchery environment will likely reduce other potential negative effects sustained during rearing (Jonsson et al. 2014). This approach may however entrain other consequences such as reducing the stock's capacity to respond to environmental change by reducing the variation in migration timing of the hatchery population. Future studies should consider releasing entire year classes at different ages to avoid the confounding growth rate factor.

The causes for differences in migration propensity are wide ranging and complex, including variation in environmental and physical factors as well as food availability/competition (Fjellheim and Johnsen 2001). Having been in the wild for longer, fry and one-year old releases likely suffered greater competition for food items, or were exposed to lower food availability than in the hatchery, and thus may have migrated to avoid these conditions (Olsson et al. 2006). This hypothesis also supports the finding that fry were on average smaller at recapture than half- and one-year-old released fish. One-year olds were however larger than half-year olds at recapture, likely because they had an additional 4 months in the river prior to the release of half-year olds, despite belonging to a group with lower growth rates. In fact, recent studies suggest that growth rate under hatchery conditions are not necessarily reflected in growth rates under natural conditions, and thus fish belonging to a lower growth rate group may have higher growth rates in the wild, and vice versa (Saikkonen et al. 2011; Vesamägi et al. 2016). Fry had the lowest recapture rate, suggesting that release at this age significantly diminishes survival, likely due to high competition for food, or high levels of predation (Whalen and LaBar 1998). This may be amplified in River Lilleå, where brown trout (*Salmo trutta*) are the dominant species. In general, fish released at a younger age tended to migrate later than one-year olds of the same population. Given their smaller size, it is possible that these fish delayed their migration in order to reach sufficient size and energy reserves which may increase their odds of successful migration (Bohlin et al. 1996; Jonsson et al. 2016).

Population effect

Individuals of the same species can compete for resources differently (Gross 1985; Caro and Bateson 1986). They can acquire flexible behavioural strategies (Arak 1988), or compete using a single strategy which may be a direct consequence of a particular developmental route (Gross and Charnov 1980). Stocked fish can also vary in their vulnerability to challenges related to environmental factors, competition and predation depending on their strain, maturity and available habitat in the wild (Orciari et al. 1994; Fjellheim and Johnsen 2001). Our results reflect these differences among different strains: Ätran fish tended to migrate earlier than Burrishoole fish for both half-year old and one-year old fish. A similar study by Aarestrup et al. (1999) using salmon released as smolts found that Ätran smolts tended to migrate earlier than Burrishoole fish, and attributed those findings to differences in inherited migratory behaviour. Genetic differences appear to play a significant role in the timing of gill enzyme development, which seems to reach higher levels earlier in Ätran fish, thus matching migration patterns (Nielsen et al. 2001). Our results support the hypothesis that migration timing is population-specific which reflect local adaptations.

Conclusion

Based on the present results, smolts size, rate of migration, and migration timing appear to be influenced by stocking practices and inherited traits. Our findings indicate that stocking the upper modal group of half-year old Atlantic salmon (*S. salar*) may be the most profitable stocking practice. These fish had a greater probability of migration (potentially due to age-at-release or higher growth rate or shorter time spent in freshwater) and are cheaper to produce (less time spent in hatchery). The present findings also suggest that differences in migratory behaviour (measured as timing of downstream migration) are likely to be inherited, reflecting local adaptations of native populations. We therefore recommend strain, age-at-release and growth rate at release be important considerations during fish stocking and management of related fisheries. The best stocking approach may differ depending on the specific objective at hand, and thus the weight of each of these considerations may vary. Our findings also highlight the need for more studies on behavioural and physiological differences among populations in order to better understand their influence on life-histories and population dynamics.

Acknowledgments

This study was funded by the Danish net and rod fish licenses.

Author Contributions

Field work: K.A. and S.T.T. Data analysis: M.H.L. and K.B.G. Data interpretation: K.B.G., M.H.L and K.A. Writing: K.B.G. Editing: K.B.G., M.H.L., S.T.T. and K.A.

References

Aarestrup, K., Jepsen, N., Rasmussen, G. and Okland, F. (1999). Movements of two strains of radio tagged Altlantic salmon, Salmo salar L., smolts through a reservoir. *Fisheries Management and Ecology*, 6, 97-107.

Arak, A. (1988). Callers and satellites in the natterjack toad: evolutionary stable decision rules. *Animal behaviour*, 36, 416-432.

Aprahamian, M.W., Barnard, S., Farooqi, M.A. (2004). Survival of stocked Atlantic salmon and coarse fish and an evaluation of costs. *Fisheries Management and Ecology*, 11, 153-163.

Armstrong, J.D., Grant, J.W.A., Forsgren, H.L., Fausch, K.D., DeGraaf, R.M., Fleming, I.A., Prowse, T.D., Schlosser, I.J. (1998). The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 303-311.

Bohlin, T., Dellefors, C., Faremo, U. (1996). Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *Journal of Fish Biology*, 49,157-164.

Caro, T.M., Bateson, P. (1986). Organization and ontogeny of alternative tactics. *Animal Behaviour*, 34, 1483-1499.

Dinno, A. (2017). Dunn's test of multiple comparisons using rank sums. Available at https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf

Erkinaro, J., Dempson, J.B., Julkunen, M., Niemelã, E. (1997). Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. *Journal of Fish Biology*, 51, 1174-1185.

Fjellheim, A., Johnsen, B.O. (2001). Experiences from stocking salmonid fry and fingerlings in Norway. *Nordic Journal of Freshwater Research*, 75, 20-36.

Forseth, T., Hurley, M.A., Jensen, A.J., Elliott, J.M. (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology*, 46, 173-186.

Freyhof, J., Brooks, E. 2011. European Red List of Freshwater Fishes. Luxembourg: Publications Office of the European Union.

Friedland, K.D. (1998). Ocean climate influences on critical Atlantic salmon (*Salmon salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 119-130.

Garcia de Leaniz, C., Fleming, I.A., Einum, S., Verspoor, E., Jordan, W.C., Consuegra, S., Aubin-Horth, N., Lajus, D., Letcher, B.H., Youngson, A.F., Webb, J., Vøllestad, L.A., Villanueva, B., Ferguson, A., Quinn, T.P. (2007). A critical review of inherited adaptive variation in Atlantic salmon. *Biological Reviews*, 66, 289-304.

Gross, M.R. (1985). Disruptive selection for alternative life histories in bluegill sunfish. *Nature*, 313, 47-49.

Gross, M.R., Charnov, E.L. (1980). Alternative male life histories in blue gill sunfish. *Proceedings of the National Academy of Sciences USA*, 77, 6937-6940.

Heggenes, J., Baglinière, J.L., Cunjak, R.A. (1999). Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. *Ecology of Freshwater Fish*, 8, 1-21.

Hothorn, T., Bretz, F., Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.

Hvidsten, N.A., Heggberget, T.G., Jensen, A.J. (1998). Sea water temperatures at Atlantic salmon smolt entrance. *Nordic Journal of Freshwater Research*, 74, 79-86.

ICES. (2007). *Report of the Baltic Salmon and Trout Working Groups (WGBAST)*. ICEAS 2007/ACFM, 12, pp.225.

Jokikokko, E., Jutila, E. (2004). Divergence in smolt production from the stocking of 1-summer-old and 1-year-old Atlantic salmon parr. *Journal of Applied Ichthyology*, 20, 511-519.

Johnsson, J.I., Brockmark, S., Näslund, J. (2014). Environmental effects on behavioural development consequences for fitness of captive-reared fishes in the wild. *Journal of Fish Biology*, 85, 1946-1971.

Jonsson, N., Hansen, L.P., Jonsson, B. (1991). Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *Journal of Animal Ecology*, 60, 937-947.

Jonsson, B., L'Abée-Lund, J.H. (1993). Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology*, 43, 1–16.

Jonsson, B., Jonsson, N. (2006). Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *ICES Journal of Marine Science*, 63, 1162-1181.

Jonsson, B., Jonsson, M., Jonsson, N. (2016). Optimal size at seaward migration in anadromous salmonid. *Marine Ecology Progress Series*, 559, 193-200.

Kallio-Nyberg, I., Jutila, E., Saloniemi, I., Jokikokko, E. (2004). Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simokoji River in the Baltic Sea. *Journal of Fish Biology*, 65, 122-134.

Kennedy, G.J.A., Strange, C.D. (1986). The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream. *Journal of Fish Biology*, 28, 479-489.

McCormick, S.D., Hansen, L.P., Quinn, T.P., Saunders, R.L. (1998). Movement, migration, and smelting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 77-92.

Metcalfe, N.B., Huntingford, F.A., Graham, W.D., Thorpe, J.E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London B*, 236, 7-19.

Nielsen, C., Holdensgaard, G., Petersen, H.C., Björnsson, B.T., Madsen, S.S. (2001). Genetic differences in physiology, growth hormone levels and migratory behaviour of Atlantic salmon smolts. *Journal of Fish Biology*, 59, 28-44,

O'Connell, M.F., Walsh, A., Cochrane, N.M. (2001). Status of Atlantic salmon (*Salmo salar* L.) in Middle Brooke (SFA 5), Northeast Brook, Trepassey (SF9), and Northeast River, Placentia (SFA 10), Newfoundland, in 2000. Canadian Stock Assessment Secretariat Research Document 2001/042, pp.89.

Økland, F., Jonsson, B., Jensen, A.J., Hansen, L.P. (1993). Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? *Journal of Fish Biology*, 42, 541-550.

Olsson, I. C., Greenberg, L. A., Bergman, E., Wysujack, K. (2006). Environmentally induced migration: the importance of food. *Ecology Letters*, 9, 645-651.

Orciari, R.D., Leonard, G.H., Mysling, D.J., Schluntz, E.C. (1994). Survival, growth, and smolt production of Atlantic salmon stocked as fry in a southern New England stream. *North American Journal of Fisheries Management*, 14, 588-606.

Pinfold, G. (2011) Economic value of wild Atlantic salmon. Atlantic Salmon Federation, Canada.

R Development Core Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randall, R.G., Healey, M.C., Dempson, J.B. (1987). Variability in length of freshwater residence of salmon, trout, and char. *American Fisheries Society Symposium*, 1, 27-41.

Riley, S. C., Tatara, C. P., Scheurer, J. A. (2005). Aggression and feeding of hatchery-reared and naturally reared steelhead (Oncorhynchus mykiss) fry in a laboratory flume and a comparison with observations in natural streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1400-1409.

Russell, I.C. (1994). Salmon stocking in north-east England – some factors affecting return rates. In: Rehabilitation of freshwater fisheries. Cowx, I.G. Ed. Hull International Fisheries Insitute, University of Hull, UK, pp. 255-267.

Saikkonen, A., Kekäläinen, J., Piironen, J. (2011). Rapid growth of Atlantic salmon juveniles in captivity may indicate poor performance in nature. *Biological Conservation*, 144, 2320-2327.

Salminen, M., Alapassi, T., Ikonen, E. (2007). The importance of stocking age in the enhancement of River Kymijoki salmon (*Salmo salar*). *Journal of Applied Ichthyology*, 23, 46-52.

Saunders, R.L., Schom, C.B. (1985). Importance of the variation in life history parameters of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 615-618.

Sheehan, T.F., Kocik, J.F., Cadrin, S.X., Legault, C.M., Atkinson, E., Bengtson, D. (2005). Marine growth and morphometrics for three populations of Atlantic salmon from eastern Maine, USA. *Transactions of the American Fisheries Society*, 134, 775-788.

Sundström, L.F., Johnsson, J.I. (2001). Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal Behaviour*, 61, 249-255.

Sundström, L.F, Peterssen, E., Höjesjö, J., Johnsson, J.I., Järvi, T. (2004). Hatchery selection promotes boldness in newly hatchery brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, 15, 192-198.

Thorpe, J.E. (1998). Salmonid life-history evolution as a constraint on marine sock enhancement. *Bulletin of Marine Science*, 62, 465-475.

Vasemägi, A., Kahar, S., Ozerov, M.Y. (2016). Genes that affect Atlantic salmon growth in hatchery do not have the same effect in the wild. *Functional Ecology*, 30, 1687-1698.

Verspoor, E., Stradmeyer, L. Nielsen, J.L. (2007). The Atlantic Salmon. Genetics, Conservation and Management. Blackwell Publishing, Oxford, UK.

Whalen, K.G., LaBar, G.W. (1998). Survival and growth of unfed and fed Atlantic salmon fry stocked in a Vermont tributary of the Connecticut River. *North American Journal of Fish Management*, 19, 931-935.

Table 1. Release and recapture data. Average length of both Ätran and Burrishoole stocking types at time of release and recapture. All values presented are mean ± SD, with number of individuals in brackets.

	Ätran			Burrishoole	
Stocking type	**Fry**	**Half-year old**	**One-year old**	**Half-year old**	**One-year old**
Number released	8700	2479	1085	2649	892
At release (cm)	-	10.4±1.3 (100)	10.4±1.5 (100)	10.5±1.6 (100)	10.5±1.6 (100)
At recapture (cm)	13.4±0.9 (163)	14.1±1.2 (651)	15.6±1.2 (161)	14.4±1.2 (410)	15.9±1.3 (122)
Proportion migrated (%)	2.1 (186)	25.8 (640)	15.0 (163)	28.9 (766)	16.3 (145)

Figure 1. River Lillea is situated in eastern Jutland, Denmark (A), and joins a large river system, River Gudenaa (B) as a large tributary. Red highlights on panel C represent locations where fish were released, and the red point where the traps were located.

Figure 2. Initial (A) and at recapture (B) lengths of stocked Ätran and Burrishoole salmon (*Salmo salar*). Median values are presented with box ends as the 25th and 75th percentiles, and whiskers as the 10th and 90th percentiles. Open data points represent outliers. Bars not sharing the same letter are significantly different from one another ($P < 0.05$). Note the different scales.

Figure 3. Probability of migration for Ätrans and Burrishoole salmon (*Salmo salar*) of different ages.

Figure 4. Migration timing of Ätran and Burrishoole salmon (*Salmo salar*) stocked as fry, half-year olds and one-year olds. Median values are presented with box ends as the 25th and 75th percentiles, and whiskers as the 10th and 90th percentiles. Open data points represent outliers. Bars not sharing the same letter are significantly different from one another ($P < 0.05$).

Figure 5. Daily numbers of stocked Ätran (A) and Burrishoole (B) salmon (*Salmo salar*) captured in the traps, and cumulative migration curve (C) of Ätran fry, half-year old and one-year old, as well as Burrishoole half-year old and one-year old stocked salmon (*Salmo salar*). Different colors denote different stocks.

Figure 1.

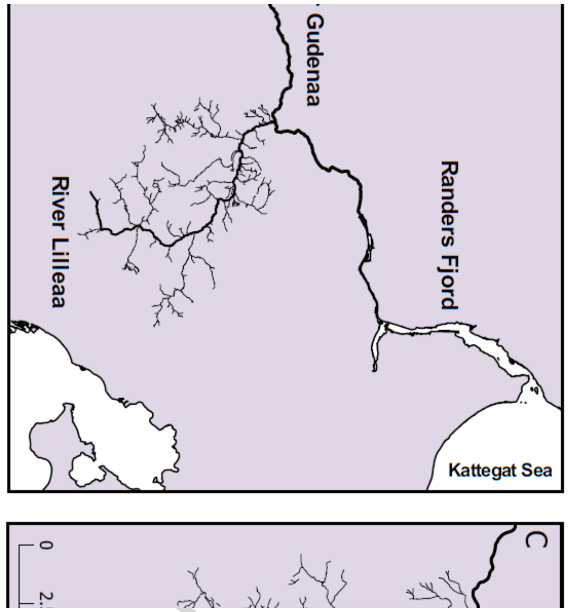


Figure 2.

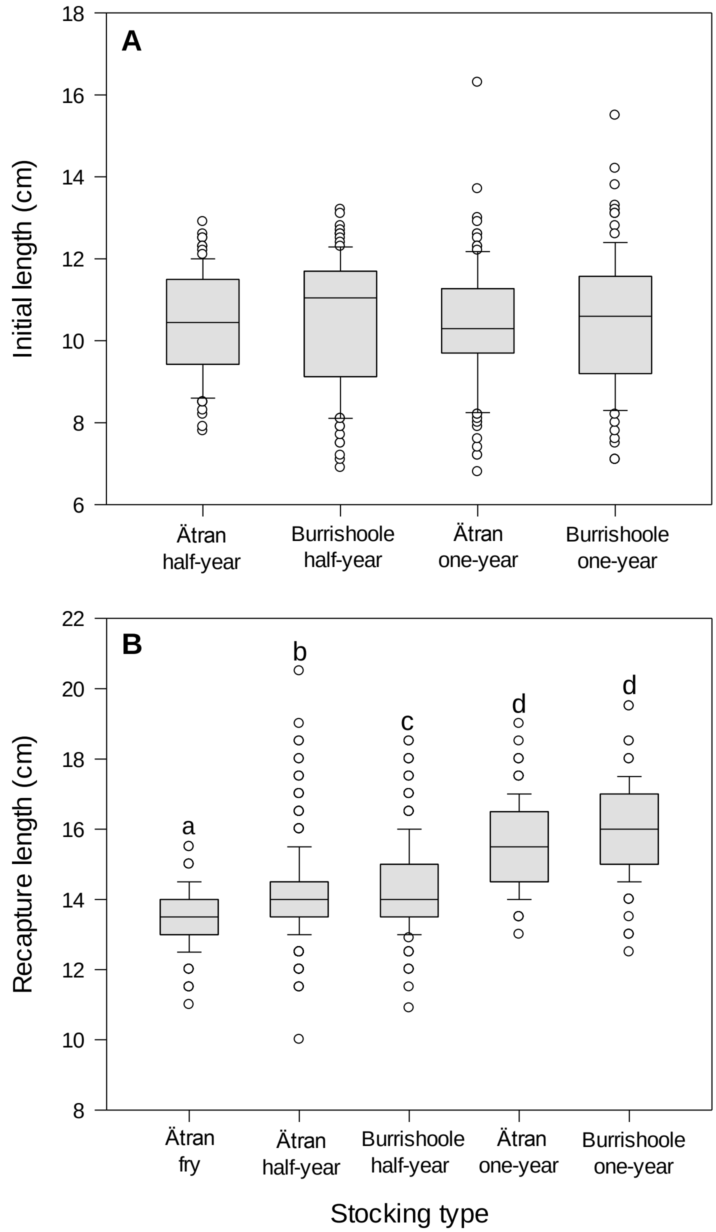
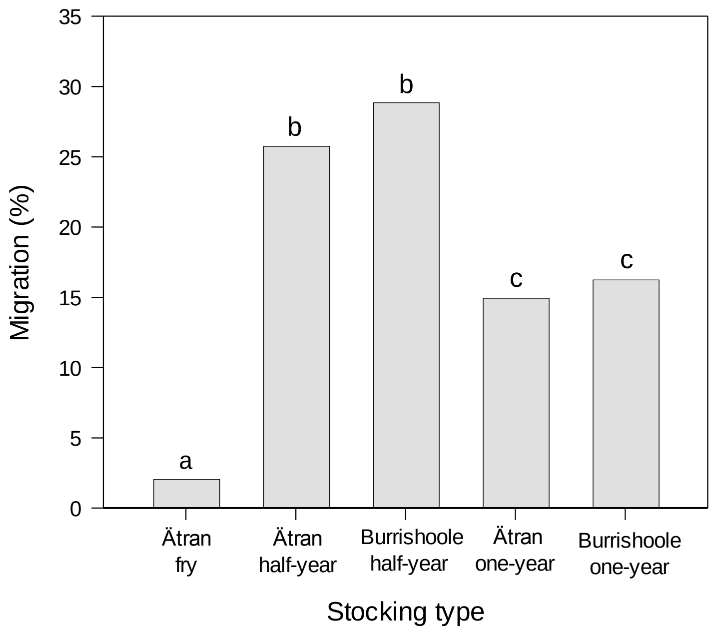

A
Initial length (cm)
18
16
14
12
10
8
6
Ätran half-year
Burrishoole half-year
Ätran one-year
Burrishoole one-year
B
Recapture length (cm)
22
20
18
16
14
12
10
8
a
b
c
d
d
Ätran fry
Ätran half-year
Burrishoole half-year
Ätran one-year
Burrishoole one-year
Stocking type

Figure 3.



Migration (%)
0
5
10
15
20
25
30
35
a
b
b
c
c
Ätran fry
Ätran half-year
Burrishoole half-year
Ätran one-year
Burrishoole one-year
Stocking type

Figure 4.

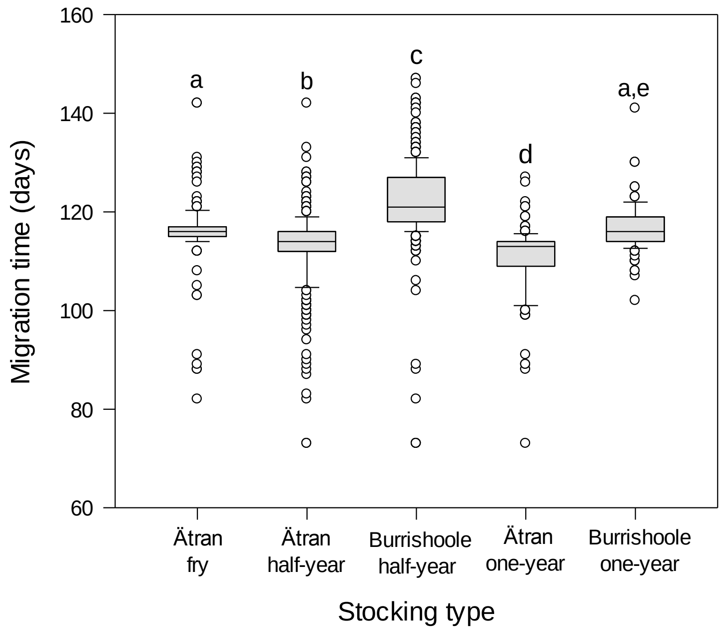
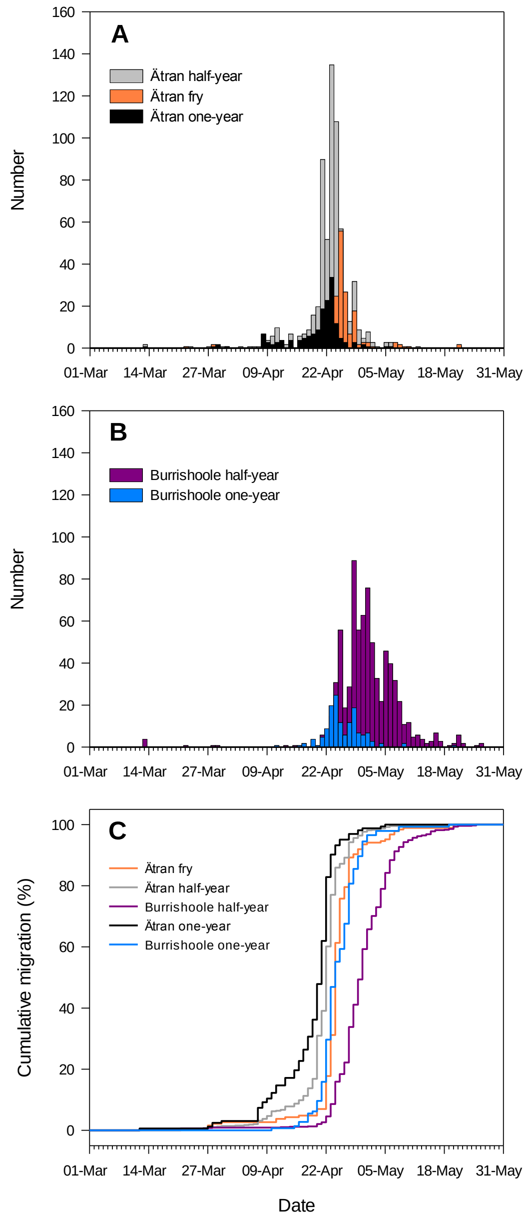

160
140
120
100
80
60
Migration time (days)
a
b
c
d
a,e
Ätran fry
Ätran half-year
Burrishoole half-year
Ätran one-year
Burrishoole one-year
Stocking type

Figure 5.


A
Ätran half-year
Ätran fry
Ätran one-year
Number
160
140
120
100
80
60
40
20
0
01-Mar
14-Mar
27-Mar
09-Apr
22-Apr
05-May
18-May
31-May
B
Burrishoole half-year
Burrishoole one-year
C
Ätran fry
Ätran half-year
Burrishoole half-year
Ätran one-year
Burrishoole one-year
Cumulative migration (%)
Date