

A test of migratory coupling in the salmon-trout predator-prey complex of a subarctic fjord

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Atlantic salmon (*Salmo salar*) smolts are vulnerable to predators during their seaward migration. To determine whether sea trout (*Salmo trutta*) exhibit a coupled migration to exploit the smolt run, we tracked Atlantic salmon smolts exiting the Vosso River in 2012 ($n = 40$) and 2013 ($n = 50$) as well as sea trout tagged in 2012 ($n = 40$) within an array of acoustic receivers. Spatial survival analysis was used to investigate patterns in smolt mortality, revealing no difference in survival between 2012 and 2013. In both years, losses were greatest in the rivers and their estuaries compared with the inner and outer fjord areas. Sea trout were predominantly detected in the area used by smolts in autumn, after the spring smolt run concluded and coinciding with the spawning migration of sea trout. High rates of smolt mortality merit further investigation to resolve low smolt survival in this region.

Introduction

Migration connects habitats by rapidly conveying matter, energy, and pathogens across boundaries. Seasonal pulses of nutrients brought by migratory animals may therefore represent important resources to many consumers (Furey *et al.* 2018). The phenomenon of migratory coupling is observed when consumers, such as predators, make migratory movements to exploit another migrating species (Furey *et al.* 2018). Pacific salmon migrations yield classic examples of migratory coupling with predators such as salmon sharks (*Lamna ditropis*), bull trout (*Salvelinus confluentus*) and brown bears (*Ursus arctos*) that exhibit synchronous movements to

exploit the seasonal migrations of this important prey species (Hulbert *et al.* 2001, Schindler *et al.* 2013, Furey *et al.* 2016). For many migratory species, however, the relationship between migrants and their predators are poorly understood and more research is needed to reveal examples of migratory coupling in other predator-prey systems.

Understanding the behaviour of predators is critical to developing management approaches that account for predator-prey dynamics in ecosystems. Experiments with electronic tags have revealed instances in which tagged prey have been consumed by predators, such as Atlantic salmon (*Salmo salar*) smolts eaten by striped bass (*Morone saxatilis*; Gibson *et al.* 2015) and



Fig. 1. Photographs of predation events by *Salmo trutta*. **Top:** a smolt removed from the stomach of a trout captured in Lake Evanger in the Vosso River. **Middle:** a trout captured in a marine net and a smolt removed from the stomach. **Bottom:** a brown trout captured with many smolts in the stomach.

sockeye salmon (*Oncorhynchus nerka*) smolts consumed by bull trout (Furey *et al.* 2016). Electronic tagging is well suited to investigating the extent of migratory coupling in these systems by tagging predators and prey and observing how predator and prey habitat use coincide in space and time.

Outmigration of Atlantic salmon smolts through rivers, estuaries and to the open ocean rapidly transports energy and matter across boundaries, which represent nutrient transfer from freshwater to the marine environment. During the springtime migration of smolts out from rivers, birds, mammals and other fishes are observed consuming smolts (Larsson 1985, Hvidsten and Møkkelgjerd 1987, Heggenes and Borgstrøm 1988, Hvidsten and Lund 1988, Kennedy *et al.* 2018, Nelson *et al.* 2018). Congeneric brown trout (*Salmo trutta*) spawn in the same rivers as Atlantic salmon and some will migrate to the sea where they predominantly remain in coastal areas within the fjord to feed and grow before returning to their natal river to spawn

after months or years at sea (Klemetsen *et al.* 2003, Thorstad *et al.* 2016). While residing in both freshwater and the marine environment, sea trout have been observed to feed on outmigrating Atlantic salmon smolts (Fig. 1). Whether this represents seasonal specialization indicative of migratory coupling or whether this is opportunistic generalist feeding is uncertain. Therefore, better knowledge of migratory coupling of sea trout to salmon smolt migration would add significant insight into the dynamics between these two migratory congeners.

The Vosso River was once a major salmon-producing river in Norway that collapsed in the 1980s with ongoing efforts focused on recovery of the wild stock. Wild smolts are supplemented annually with hatchery-reared fish as part of recovery efforts. Predation of both hatchery and wild smolts originating from the Vosso River by brown trout (Fig. 1) could represent a bottleneck that hinders reestablishment of the population, particularly if trout specialize on smolts during the migration. Observations confirm that sea trout consume Atlantic salmon smolts, but diet analyses by Davidsen *et al.* (2017) did not suggest Atlantic salmon to be an important component of the sea trout diet in fjords of central Norway (e.g., Rauma, Trondheimsfjord). Nonetheless, details of sea trout behaviour during the salmon smolt run are needed to determine whether their behaviour responds to a transient increase in availability of this seasonally available prey species, which would indicate migratory coupling.

To investigate possible migratory coupling in Atlantic salmon smolts migrating from the Vosso River, we tracked sea trout movement and smolt migrations using acoustic telemetry. Receivers were placed in the estuary, inner fjord and outer fjord to detect spatial dynamics of sea trout and migrations out of the fjord by salmon in 2012 and 2013. Spatiotemporal distributions of sea trout and Atlantic salmon smolts were resolved by kernel density calculations to test the extent of overlap in the distribution of the predator with the prey species. We hypothesized that sea trout movements correspond to the salmon smolt migration and predicted that when smolts were present (i.e., during their seaward migration), the degree of spatial overlap between sea trout

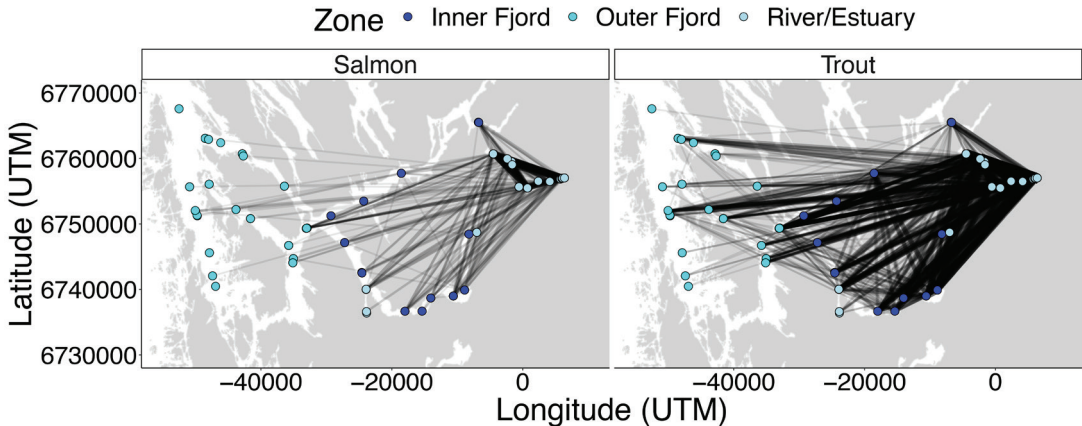


Fig. 2. Network map of sea trout (*Salmo trutta*) and Atlantic salmon smolt (*Salmo salar*) detections in the Vosso River and estuary and the Osterfjord, Western Norway. Receivers were situated in estuaries, in the inner Osterfjord (> -30000 UTM) and outer fjord (< -30000 UTM). Movements between receivers are illustrated by lines connecting receiver with thicker lines representing more frequent movements in between.

and Atlantic salmon smolt distributions would be highest, indicating that sea trout were behaviourally coupled to the smolt migration.

Methods

Atlantic salmon smolts and sea trout were studied in the Osterfjord in western Norway. The Osterfjord is located north of the city of Bergen and the Vosso River discharges at the distal end of the fjord. Other salmon- and trout-producing rivers in the fjord include Arnaelva, Daleelva, Ekso, Modalen and Loneelva. Whereas Atlantic salmon migrate out from freshwater as smolts, traveling through the fjord and to the open ocean to feed and grow, sea trout remain predominantly in coastal areas to feed and may make more frequent back-and-forth movements within the fjord and between the marine and freshwater environments (Eldøy *et al.* 2015). Sea trout has been observed to prey upon Atlantic salmon smolts in this system (Fig. 1).

Tagging of sea trout

To investigate predator aggregation around the Atlantic salmon smolt run, an acoustic telemetry array was established in the Osterfjord to track the habitat use and migration of both sea

trout and Atlantic salmon. The array consisted of receivers at 37 locations (38 in 2013) in rivers and their estuaries, the inner Osterfjord and outer fjord beyond the islands (Fig. 2). Detections were recorded between 24 April 2012 and 20 December 2013. From 24 May to 17 June 2012, we selected 40 sea trout (52.7 ± 11.2 cm) and instrumented each with an acoustic transmitter, one of which was never detected. Cultivated Atlantic salmon smolts were tagged in the Vosso River fish hatchery on 21 May 2012 ($n = 40$, length = 16.9 ± 0.4 cm) and on 21 May 2013 ($n = 50$, length = 16.8 ± 0.4 cm).

Two models of acoustic transmitters (VEMCO Ltd, Canada) were used to track sea trout during the study: the V13-1L ($n = 27$, $13 \text{ mm} \times 36 \text{ mm}$, mass in air = 11 g, battery life ~ 1117 days) and V13P-1L ($n = 11$, $13 \text{ mm} \times 48 \text{ mm}$, mass in air = 13 g, battery life ~ 727 days). Prior to tagging, fish were anesthetized with a combination of MS-222 and Benzocaine. The fish were then placed in a stable position on top of a wet cloth. Water was applied to the eyes and gills to avoid desiccation. Length and weight were measured while the fish was anesthetized. A small incision (3–4 cm in length) was made in the lower part of the body cavity, carefully avoiding puncture of any internal organs. The tag was rinsed in a solution of alcohol, disinfected water and an antibacterial solution before insertion through the incision.

The wound was closed using sutures (4-0 nylon, Ethicon) and a tissue adhesive (Braun Histoacryl). The fish recovered from surgery in a large bucket of water and were released when they re-oriented and resumed a normal rate of gill ventilation and pectoral fin movement. No fish died following capture, during surgery, or during recovery. Upon release, each individual swam away and none lingered at the release site. The surgery protocol was approved as described above by the Norwegian National Animal Research Authority (ID 4141) with provisions for reporting of adverse events — but no welfare issues were encountered.

Production and tagging of hatchery salmon smolt

Smolts were produced in Lake Evanger, a lake within the Vosso River, in a custom-made small net-pen. This method allows for production of 1-year old smolts, which grow to an average size of ~12–14 cm before release in mid- or late May. Size V7 tags were surgically implanted into the abdomen of the smolt. Minimum size for tagging was 16.2 cm. The fish was anesthetized with a combination of Benzocaine and MS-222 in 2012 and with 2-phenoxyethanol in 2013 before surgery. A small ventral incision was used to place the tag into the cavity of the fish and sutured together with surgical glue (only suture was applied in 2013) to close the wound. Fish were then released in a holding pen to recover before being released. The national animal welfare committee (FOTS, ID 5185) approved the study protocols with a human endpoint of euthanasia if any fish exhibited abnormal behaviour following tagging, but this did not occur. Forty fish were tagged and released in 2012 and 50 fish were tagged and released in 2013. In both years, fish were released together with a large group of cultivated fish (30 000) in the inlet of the river on 21 May. The date is just after the median date of the migration of wild smolt in the river. The size of the tagged cultivated smolts ranged from 16.2–17.9 cm (average: 16.8 cm, SD: 0.39). There were no differences in size of tagged fish in 2012 (avg. 16.9 cm) and 2013 (avg. 16.8 cm).

Data on smolt migration have been previously presented in Vollset *et al.* (2016).

Data Analysis

Behaviour within the receiver array was quantified using spatial and temporal metrics describing individual movements. We were specifically interested in factors affecting the survival of smolts along their migration, factors contributing to the patterns of space use by sea trout and indicators of migratory coupling.

Smolt Movement

To determine what factors contributed to the survival of the smolts, we implemented spatial survival analysis. Capitalizing on the west–east orientation of the river and fjord, we used the longitude as a spatial axis along which to ascertain survival (in lieu of time, which is normally used in survival analysis). We took the maximum longitude from the point of origin that a smolt was detected as an indication of how far it migrated. Those making it to the outer fjord were considered survivors (event = 0), while those that did not were considered mortalities (event = 1). For the survival analysis, the survival object was therefore a combination of the minimum longitude and its fate (whether it made it to the outer fjord or not) as a function of body length and release year. Survival analysis was implemented with the *cph* function in the *rms* package (Harrell 2018).

Sea Trout Movement

To determine whether sea trout movements were affected by body length or condition factor, we used linear regression with the *lm* function in R ver. 3.6.1 (R Core Team 2019). Two analyses were conducted with different dependent variables: one with the maximum distance moved from release (by maximum longitude); and one by individual kernel density (95%), calculated with the *kde* function in the *ks* package (Duong 2019). The condition factor was derived using

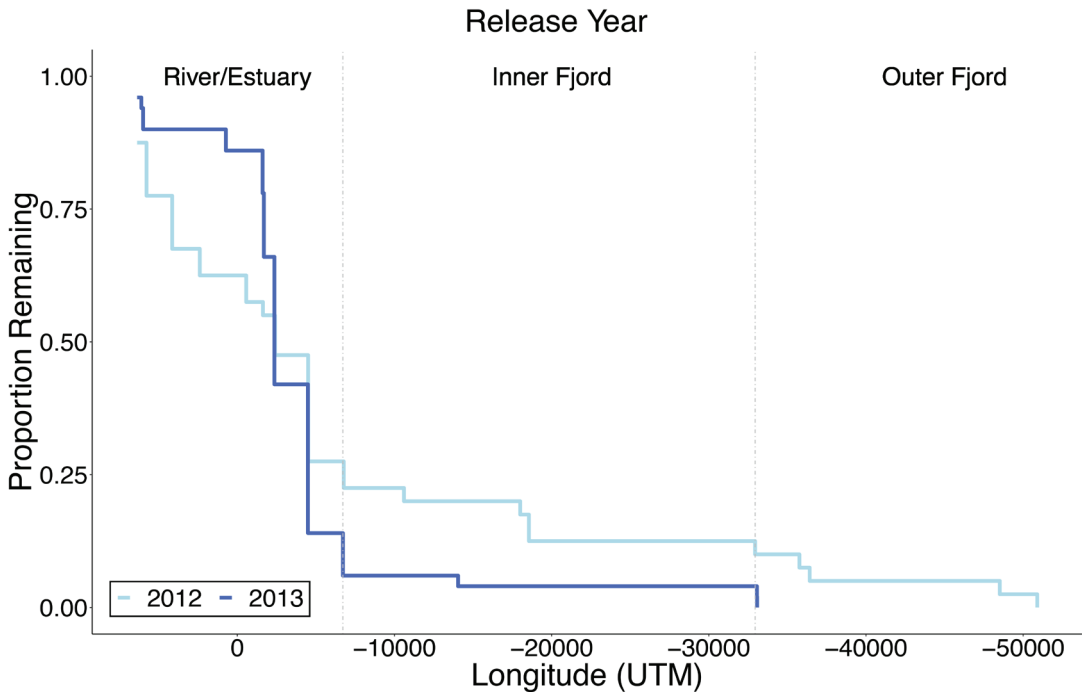


Fig. 3. Location (longitude) of final transmission by smolts tagged in 2012 ($n = 40$) and 2013 ($n = 50$) originating from the Vosso River. Vertical lines generally separate zones into the river and estuary area of the Vosso River, inner Osterfjord and outer fjord. Note that the x-axis is reversed (longitude going the wrong direction) for ease of interpretation.

Fulton's K : $K = 100 \times \text{weight} / (\text{length})^3$ as in Eldøy *et al.* (2015).

Migratory Coupling

To investigate migratory coupling, we computed a spatiotemporal kernel density estimate for salmon and sea trout using longitude and day of the year to compare the overlap between the two species with the *kde* function in the *ks* package. The area was measured with the *gArea* function in *rgeos* package and overlap was determined using the *gIntersection* function (Bivand and Rundel 2018). Using individual ranges as replicates, the spatiotemporal range was measured for each fish and the area of the range was compared between salmon and trout using a statistical t-test with the *t.test* function.

Finally, we measured the spatial area of 95% usage by kernel smoothing using the *kde* function. Detections were filtered to one per day per

individual per receiver. The range was generated for Atlantic salmon and compared to the sea trout polygons for each month by computing the area of overlap using the *gIntersection* and *gArea* functions. A t-test was implemented to compare the proportion of overlap of sea trout range during May and June and beyond (April, July–October) the typical smolt run timing with the 95% smolt kernel density area with the *t.test* function. Figures were drawn with *ggplot2* (Wickham 2016).

Results

Sea trout (mean 370 ± 219 d) were detected for longer periods than Atlantic salmon ($t = -9.50$, $p < 0.01$). Detection periods (i.e., time between the first and last detection in the array) were not different for salmon released in 2012 (35 ± 42 d) compared with 2013 (32 ± 35 d, $t = 0.38$, $p = 0.71$). Seven of the 90 smolts (8%)

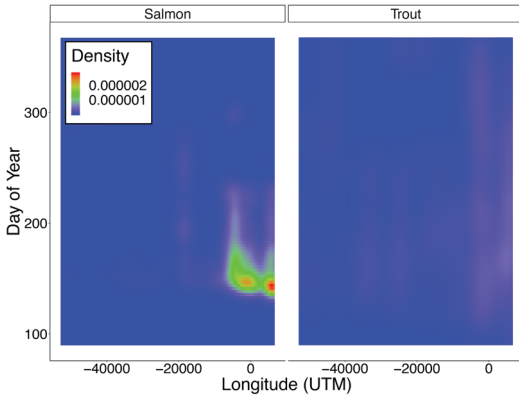


Fig. 4. Density map of Atlantic salmon smolt (*Salmo salar*) and sea trout (*Salmo trutta*) predators in the Vosso River and estuary and Osterfjord area of western Norway. Density is a function of the longitude individuals were tracked at (because the river and fjords have a west–east axis, this provides an index of the seaward distance travelled) and day of the year. Colours indicate density of smolts in space and time whereas the trout distribution was more diffuse during the study.

released in 2012 and 2013 were detected on receivers in the outer fjord, suggesting they were survivors of the early marine migration. There was no significant relationship of length ($z = -0.17$, $p = 0.86$) or release year ($z = 1.47$, $p = 0.14$) with smolt survival to the outer fjord and most individuals disappeared prior to entering the fjord (Fig. 3).

Sea trout with a smaller condition factor upon tagging had a larger 95% kernel area (area was log transformed for normality of residuals, $t = -4.13$, $p < 0.01$). However, there was no influence of individual condition ($t = 1.17$, $p = 0.25$) or length ($t = 0.03$, $p = 0.97$) on the maximum distance travelled away from the Vosso River based on longitude. The spatiotemporal core area measured 6.20 units (dimensionless) for sea trout and 1.03 for salmon smolts with an overlap of 0.99 units (Fig. 4). When using individuals as replicates, there was a significant difference between the size of the spatiotemporal area of sea trout and salmon smolts ($t = -6.63$, $df = 37.11$, $p < 0.01$, seven salmon and one trout excluded for which kernel density could not be estimated). Collectively, sea trout occupied areas up to 106 km² in May and as little as 9.9 km² in December; their range overlapped most in areas

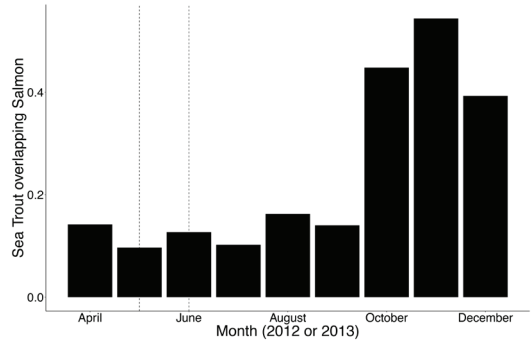


Fig. 5. Plot of the extent of the overlapping range (95% kernel density) of sea trout for each month with the overall range of Atlantic salmon smolts (note that the salmon range is not considered at the monthly scale), as a proportion. Vertical lines are used to reference the typical months of the smolt run from the river and through the fjord covered by receivers.

inhabited by salmon smolts in October (45%), November (54%) and December (39%). However, most smolt detections were in May, June and July, suggesting a mismatch between the timing of smolt and sea trout overlap (Appendix Fig. A1). Indeed, the smallest proportion of trout detections were on receivers in rivers and their estuaries in May, June, July and August (Fig. 5), corresponding to a higher incidence of habitat use in the Osterfjord and areas beyond. There was a near-significant difference suggesting that the temporal overlap of sea trout with the 95% area used by smolts could be higher at times beyond the smolt run compared with during the run ($t = 2.35$, $df = 6.51$, $p = 0.05$).

Discussion

Sea trout moved throughout rivers, estuaries, inner fjord and outer fjord areas around the Osterfjord with a high degree of spatial, but not temporal, overlap with Atlantic salmon smolts. There was evidence that sea trout movements were condition-dependent and that any predation of smolts was the result of generalist behaviour given that we did not find any evidence of aggregated behaviour during the smolt run. Although sea trout have been observed consuming Atlantic salmon smolts, their behaviour in the fjords was not indicative of migratory coupling. Despite

sea trout being found to occupy the same area as where we measured the Atlantic salmon smolts for their migration, they did so later in the year when the spring smolt migration would already have concluded and likely were using those areas near the river during the early phase of their spawning migration. This is important because it shows that sea trout use these areas and are not limited or excluded from them, but despite the seasonal influx of prey from smolts migrating out of the Vosso River, they spend time in other areas rather than focus on an area with many migrating smolts. Although there are other rivers in the area, the Vosso River is the largest and produces a large number of smolts both of wild and hatchery origin, which was why we predicted it would aggregate predators.

Mortality during the early marine migration can be high for Atlantic salmon (Thorstad *et al.* 2012). Indeed, we found that most smolts were lost prior to being detected in the inner Osterfjord, suggesting that they died during the early phase of migration through rivers and their estuaries. Birds and other fish species have been recorded preying salmon smolts in large numbers during the downriver migration, including gadids (Hedger *et al.* 2011, Vollset *et al.* 2016). Only a small percentage of the smolts that we released made it to the outer fjord (8%), which we interpreted as surviving the early marine migration. A comparison with other studies suggests 8% is a very small rate of survival; 75% of smolts successfully navigated the Altafjord from the rivermouth of Alta to the end of the fjord, 31% of smolts of different fjord origin made it out of the Hardangerfjord system and approximately 35% for wild and hatchery salmon smolts at 37 km through the Romsdalsfjord (Thorstad *et al.* 2007, Davidsen *et al.* 2009, Plantalech Manel-La *et al.* 2011). Vollset *et al.* (2016) also demonstrated that the likelihood of being registered outside the estuary was conditional on the migration speed of the individual and speculated that this could be because slower migrating individuals were more vulnerable to predators.

There were important differences in the seasonal distribution of sea trout in the Osterfjord. Sea trout may remain at sea during the winter, but many return to freshwater in the late summer and autumn to reproduce (Klemetsen *et*

al. 2003), which is consistent with our observations that the distribution of the sea trout population shifted towards the rivers and estuaries during this period. Our receivers were not active from January–March, so we do not have additional information about the habitat use during the winter months, but by springtime (beginning in April), sea trout were active in the marine environment. This usage of marine habitat in both the inner and outer fjords reflected a distinct difference from our hypothesis that sea trout would overlap in space and time with the migrating smolts. This finding was particularly clear given that the sea trout were released in an area overlapping the smolt run in 2012, so the observation that they were using marine areas immediately after release implied an active seaward movement during this period rather than lingering to exploit smolts. Eldøy *et al.* (2015) observed greater dispersal by sea trout with poorer condition and although we did not find that the condition factor was related to distance from the river changed, we did find that sea trout measured to have a poorer condition factor tended to inhabit a larger kernel density area. Together, this suggests that sea trout in poor condition were more active than those with a higher condition factor and may be taking more time and searching more for food to improve their condition and not remaining in a small area close to the river to exploit smolts. The results from this study thus confirms the result from Vollset *et al.* (2016), which inferred, based on trolling, that there were relatively low abundance of sea trout in the estuary during the smolt run. They suggested that this could be due to the generally poor status of the population of sea trout in the Vosso River. Nevertheless, even small sea trout populations could potentially inflict a large impact on the smolt population if they exhibit migratory coupling; yet, we found no evidence of this in our study. What we observed was the seasonal migration of trout from freshwater to use the marine area during the summer and the return migration to spawn in autumn, uncoupled from the smolt run in springtime. This corresponds to diet analyses showing that fish prey of sea trout were predominantly sandeel (*Ammodytes tobianus*), sprat (*Sprattus sprattus*), herring (*Clupea herengus*) in central Norway, comprising 18% of the diet (Davidsen *et al.* 2017) and in southern

Norway, where clupeids and gobiids, were the primary food source (Knutsen *et al.* 2003).

Predation is an important driver of smolt mortality of all anadromous species and predation on salmon smolts has been observed throughout literature on smolt behaviour. Healthy salmon populations provide an important nutrient subsidy to many species and predators have a role in migratory culling, which can be compensatory mortality of sick or weak individuals (e.g., Bradley and Altizer 2005). For example, Miller *et al.* (2014) found that predated sockeye salmon (*Oncorhynchus nerka*) smolts were more burdened by pathogens than surviving counterparts did. Populations with poor abundance such as that in the Vosso River may be more vulnerable to predation if predators do not reduce their rate of prey consumption in response to small population size (i.e., depensation; Liermann and Hilborn 2001). Kennedy *et al.* (2018) estimated smolt mortality in lakes, where an aggregation of pike (*Esox lucius*) was simultaneously tagged and tracked, was 31.2% per km compared with 2.4% per km in the river. In fjords, Atlantic cod (*Gadus morhua*) was tracked by Hedger *et al.* (2011), who suggested that some cod aggregated around river mouths during the smolt run and were using shallow depths at night, indicative of foraging on smolts. Vollset *et al.* (2016) also documented cod predation of the smolt at the end of the estuary in the Vosso River.

Recent approaches have yielded evidence of predation on salmon smolts by striped bass (*Morone saxatilis*; Gibson *et al.* 2015, Daniels *et al.* 2018). We attempted to summarize movement metrics for all our tagged fish and apply similar statistical learning algorithms to identify salmon smolts that had been eaten by predators based on their movement tracks, but the model performed poorly and was not included in this paper. Sensor tags have also been developed to directly ascertain information about tagged fish predation; although this tool would not provide direct information about the species of predator, it would add substantial value to confirm the fate of more tagged smolts (Halfyard *et al.* 2017).

It is important to take into consideration that the salmon used in this study was hatchery salmon smolt. Salmon smolts with a hatchery background behave differently and may be more susceptible to

predation (Hvidsen and Lund 1988, Aarestrup *et al.* 2014, Barlaup *et al.* 2018). More recent studies on smolt migration using wild fish in the Vosso River, however, indicate that migration time overlaps with the migration window of salmon smolts in this study and that mortality of wild fish is also high during the estuarine transition. In a synthesis, Thorstad *et al.* (2012) estimated median mortality in estuaries of 6.0% per km compared with mortality in rivers (2.3% per km) and in coastal areas (1.4% per km). The observation that so few smolts make it to the fjord reduced the sample size with which we could calculate spatial metrics, which could have negatively affected the kernel density estimates calculated for smolts. Nevertheless, this study provides relevant information to stakeholders working to restore Atlantic salmon in the Vosso River, indicating that sea trout movement does not respond strongly to the smolt migration by moving into areas more occupied by smolts.

Conclusions

Understanding the factors contributing to smolt mortality in the riverine and early marine phases of migration are critical to conservation. Sea trout predation could affect survival of smolts emigrating from the Vosso River, where low rates of survival are observed (Barlaup *et al.* 2018). Although our study does not rule out predation as an important mechanism, we did not find evidence that sea trout aggregated around the Vosso River during the smolt run, which would have been interpreted as evidence for migratory coupling and specialization on this seasonal pulse of nutrients (Furey *et al.* 2018). If the smolts were being eaten by mobile aquatic species such as salmonids, gadoids, or marine mammals, we would have expected to observe more movement of the tags within the array in the bodies of predators (e.g., Gibson *et al.* 2015, Daniels *et al.* 2017). Dead smolts would be expected to drift downriver and eventually settle on the bottom or be taken by a scavenger (Muhametsafina *et al.* 2015, Havn *et al.* 2017). A greater receiver coverage around the estuary could assist in making finer-scale observations of smolt migration through this critical area as well as novel tags equipped with predation sensors

(Halfyard *et al.* 2017). Further research is clearly needed to identify mechanisms contributing to the high mortality of salmon smolts observed in this study, but migratory coupling of sea trout and salmon smolt do not appear to be an important factor given the lack of an aggregative response revealed by tracking in this study (Vollset *et al.* 2016).

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References

- Aarestrup, K., Baktoft, H., Koed, A., del Villar-Guerra, D. & Thorstad, E. B. 2014. Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts. *Mar. Ecol. Prog. Ser.* 496: 197–206.
- Barlaup, B.T., Rund, H., Normann, E.S., Stranzl, S., Mahlum, S. & Vollset, K.W. 2018. Out of sync: monitoring the time of sea entry of wild and hatchery salmon *Salmo salar* smolt using floating passive-integrated transponder antennae. *J. Fish Biol.* 93: 455–464.
- Bivand, R. & Rundel, C. 2018. *rgeos: Interface to Geometry Engine — Open Source ('GEOS')*. R package ver. 0.4-2. Available at: <https://CRAN.R-project.org/package=rgeos>
- Bradley, C.A. & Altizer, S. 2005. Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. *Ecol. Lett.* 8: 290–300.
- Daniels, J., Chaput, G. & Carr, J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. *Can. J. Fish. Aquat. Sci.* 75: 1811–1822.
- Darimont, C.T., Reimchen, T.E. & Paquet, P.C. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. *Can. J. Zool.* 81: 349–353.
- Davidson, J.G., Rikardsen, A.H., Halttunen, E., Thorstad, E.B., Økland, F., Letcher, B.H., Skarøhamar, J. & Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *J. Fish Biol.* 75: 1700–1718.
- Duong, T. 2019. *ks: Kernel Smoothing*. R package ver. 1.11.4. Available at: <https://CRAN.R-project.org/package=ks>
- Eldøy, S.H., Davidson, J.G., Thorstad, E.B., Whoriskey, F., Aarestrup, K., Næsje, T.F., Rønning, L., Sjørnsen A.D., Rikardsen, A.H. & Arnekleiv, J.V. 2015. Marine migration and habitat use of anadromous brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* 72: 1366–1378.
- Furey, N.B., Armstrong, J.B., Beauchamp, D.A. & Hinch, S.G. 2018. Migratory coupling between predators and prey. *Nature Ecol. Evol.* 2: 1846.
- Furey, N.B., Hinch, S.G., Bass, A. L., Middleton, C.T., Minke-Martin, V. & Lotto, A.G. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *J. Anim. Ecol.* 85: 948–959.
- Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J. & Redden, A. M. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. *Can. J. Fish. Aquat. Sci.* 72: 728–741.
- Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F. & Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods Ecol. Evol.* 8: 1063–1071.
- Harrell, F.E. 2018. *rms: Regression Modeling Strategies*. R package ver. 5.1-2. Available at: <https://CRAN.R-project.org/package=rms>
- Havn, T.B., Økland, F., Teichert, M.A., Heermann, L., Borcherding, J., Sæther, S.A., Tambets, M., Diserud, O.H. & Thorstad, E. B. 2017. Movements of dead fish in rivers. *Anim. Biotelem.* 5: 7. <https://doi.org/10.1186/s40317-017-0122-2>
- Hedger, R.D., Uglem, I., Thorstad, E.B., Finstad, B., Chitenden, C.M., Arechavala-Lopez, P., Jensen, A.J., Nilsen, R. & Økland, F. 2011. Behaviour of Atlantic cod, a marine fish predator, during Atlantic salmon post-smolt migration. *ICES J. Mar. Sci.* 68: 2152–2162.
- Heggenes, J. & Borgstrom, R. 1988. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. *J. Fish Biol.* 33: 885–894.
- Holtgrieve, G.W. & Schindler, D.E. 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology.* 92: 373–385.
- Hulbert, L.B., Aires-da-Silva, A.M., Gallucci, V.F. & Rice, J.S. 2005. Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. *J. Fish Biol.* 67: 490–509.
- Hvidsten, N.A. & Lund, R.A. 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla, Norway. *J. Fish Biol.* 33: 121–126.
- Hvidsten, N.A. & Møkkelgjerd, P.I. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. *J. Fish Biol.* 30: 273–280.
- Kennedy, R.J., Rosell, R., Millane, M., Doherty, D. & Allen, M. 2018. Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. *J. Fish Biol.* 93: 134–137.
- Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish.* 12: 1–59.
- Knutsen, J.A., Knutsen, H., Gjøsæter, J. & Jonsson, B. 2001.

- Food of anadromous brown trout at sea. *J. Fish Biol.* 59: 533–543.
- Krumm, C.E., Conner, M.M., Hobbs, N.T., Hunter, D.O. & Miller, M.W. 2009. Mountain lions prey selectively on prion-infected mule deer. *Biol. Lett.* 6: 209–211.
- Larsson, P.O. 1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. *J. Fish Biol.* 26: 391–397.
- Liermann, M. & Hilborn, R. 2001. Depensation: evidence, models and implications. *Fish and Fisheries* 2: 33–58.
- Miller, K.M., Teffer, A., Tucker, S., Li, S., Schulze, A.D., Trudel, M., Juanes, F., Tabata, A., Kaukinen, K.H., Ginther, N.G., Ming, T.J., Cooke, S.J., Hipfner, J.M., Patterson, D.A. & Hinch, S.G. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. *Evol. Appl.* 7: 812–855.
- Muhametsafina, A., Midwood, J.D., Bliss, S.M., Stamplecoskie, K.M. & Cooke, S.J. 2014. The fate of dead fish tagged with biotelemetry transmitters in an urban stream. *Aquat. Ecol.* 48: 23–33.
- Naiman, R.J., Bilby, R. E., Schindler, D.E. & Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*. 5: 399–417.
- Nelson, B.W., Walters, C.J., Trites, A.W. & McAllister, M.K. 2018. Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* 76: 447–462.
- Packer, C., Holt, R. D., Hudson, P. J., Lafferty, K. D. & Dobson, A. P. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecol. Lett.* 6: 797–802.
- Plantalech Manel-la, N., Chittenden, C.M., Økland, F., Thorstad, E.B., Davidsen, J.G., Sivertsgård, R., McKinley, R.S. & Finstad, B. 2011. Does river of origin influence the early marine migratory performance of *Salmo salar*? *J. Fish Biol.* 78: 624–634.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Schindler, D.E., Armstrong, J.B., Bentley, K.T., Jankowski, K., Lisi, P.J. & Payne, L.X. 2013. Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biol. Lett.* 9: 20130048.
- Subalussy, A.L., Dutton, C.L., Rosi, E.J. & Post, D.M. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Nat. Acad. Sci.* 114: 7647–7652.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H. & Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *J. Fish Biol.* 81: 500–542.
- Thorstad, E.B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P.A. & McKinley, R.S. 2007. Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. In: Almeida P., Quintella B., Costa M. & Moore A. (eds.), *Developments in Fish Telemetry*, Springer, Dordrecht, pp. 99–107.
- Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kälås, S., Berg, M. & Finstad, B. 2016. Marine life of the sea trout. *Mar. Biol.* 163: 47.
- Vollset, K.W., Mahlum, S., Davidsen, J. G., Skoglund, H. & Barlaup, B.T. 2016. Interaction between migration behaviour and estuarine mortality in cultivated Atlantic salmon *Salmo salar* smolts. *J. Fish Biol.* 89: 1974–1990.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Appendix

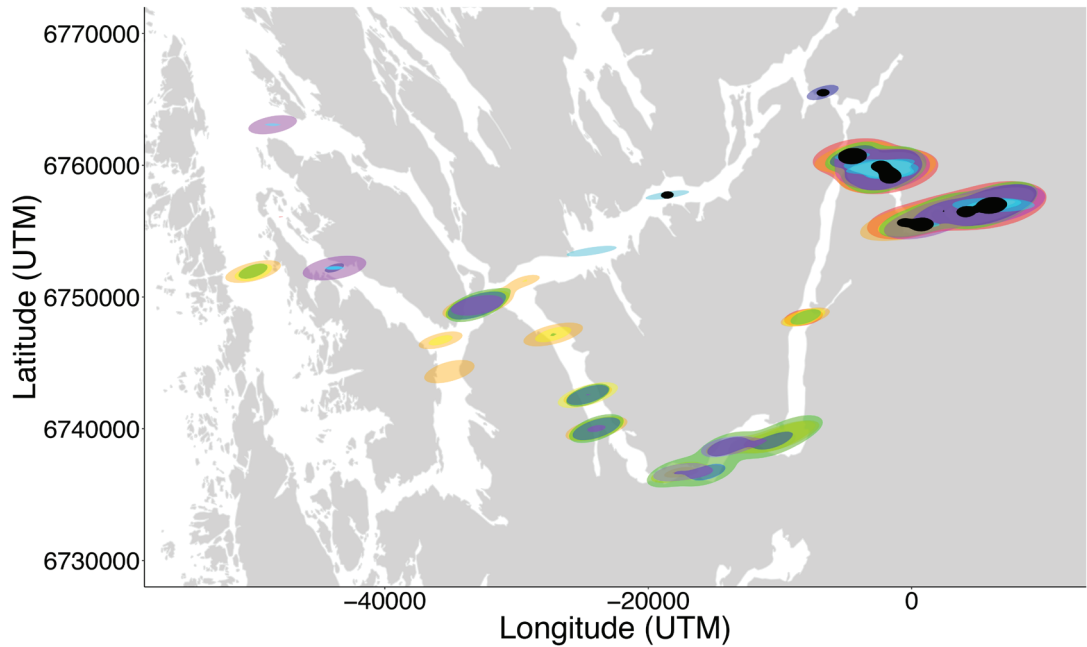


Fig. A1. Range polygons, 95%, for sea trout (*Salmo trutta*, colours for each month) and Atlantic salmon (*Salmo salar*, all months) in the Ostefjord, Norway. Overlap of the 95% range of trout with the salmon range was the highest in the autumn when sea trout were returning to estuarine areas to spawn, rather than in the spring when the salmon were actually there (refer to Fig. 5).