

Changes in swimming depths of Atlantic salmon
***Salmo salar* post-smolts relative to light intensity**

J. G. Davidsen§*, N. Plantalech Manel-la†, F. Økland‡, O. H. Diserud‡, E. B. Thorstad‡, B. Finstad‡, R. Sivertsgård‡, R. S. McKinley† & A. H. Rikardsen§

§ Norwegian College of Fishery Science, University of Tromsø, NO-9037 Tromsø, Norway

† The University of British Columbia, Centre for Aquaculture and Environmental Research,
4160 Marine Drive West Vancouver, BC V7V 1N6, Canada

‡ Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

Running headline: Swimming depth in relation to light intensity

* Author to whom correspondence should be addressed. Tel.: +47 776 46960; fax +47 776 46020

email: jan.davidsen@nfh.uit.no

Eight hatchery-reared Atlantic salmon *Salmo salar* post-smolts, implanted with acoustic depth sensing transmitters and manually tracked for 5-12 h in the Hardangerfjord (Norway), spent most of their time (49-99%) at 1-3 m depth during the day, whereas four of seven fish tracked were found close (<0.5 m) to the surface at night, with a strong negative cross-correlation between general swimming depth and surface light intensity. Hence, the actual swimming depth of post-smolts during their early marine migration may depend on the light conditions, although the individual variation in vertical movement pattern was large. No cross-correlations were found between light intensity and swimming depth during daytime periods with rapid changes in light intensity, indicating that other factors than light intensity were important in initiating the irregular dives that were recorded down to 6.5 m depth.

Key words: acoustic telemetry; behaviour, salmonid; vertical movement.

The period of sea entry and the first weeks of the marine life of the Atlantic salmon *Salmo salar* L. is considered as a critical period for their survival, and thus the total production of this species (Montevecchi *et al.*, 2002; Rikardsen *et al.*, 2004). Several studies have shown that post-smolts are exposed to high predation immediately after sea entry (Reitan *et al.*, 1987; Hvidsten & Lund, 1988; Dieperink *et al.*, 2002). Hence, the predation risk is expected to have a strong selective effect on the behaviour of fjord migrating post-smolts (Solomon, 1982). Several studies in riverine systems have indicated that the smolts alter their behaviour according to the light regime. Typically, smolts have been shown to move deeper in the water column during the day than during the night (Thorpe & Morgan, 1978; Youngson *et al.*, 1983; Hansen & Jonsson, 1985; Aarestrup *et al.*, 2002), which is probably a strategy to minimize predation risk from avian predators (Solomon, 1982). It has also been observed that *S. salar* smolts in rivers may react to rapid decreases in light intensity during the day by immediately diving deeper (Davidsen *et al.*, 2005). These observations were interpreted as anti-predator behaviour, since a sudden decrease in light intensity may indicate the vicinity of an avian predator. It is not known, however, if outward-migrating smolts maintain this behaviour after entering the marine environment. Earlier studies indicated that fjord migrating *S. salar* post-smolts migrate through the whole fjord system at swimming speeds up to 1.8 body lengths s⁻¹ (Finstad *et al.*, 2005). The post-smolts tend to swim near the surface at a median depth of 2m (Døving *et al.*, 1985; J. Sturlaugsson & K. Thorisson, unpubl. data). Although spending most of their time close to the surface, post-smolts have been observed to make regular rapid changes in the swimming depth (Westerberg, 1982; Reddin *et al.*, 2006). Little information exists, however, on how environmental factors, such as light intensity, influence the swimming depth and migration route in the early marine phase (Moore *et al.*, 2000). The objective of this study was to examine how changes in light intensity affect the swimming behaviour of fjord migrating *S. salar* post-smolts.

The study was performed in 2006 in the Eidfjord (60° 28' N; 7° 04' E), which is the innermost part of the 150 km long Hardangerfjord in south-western Norway. The mean and maximum depths of the Eidfjord are approximately 150 m and 600 m, respectively. A freshwater input exists throughout the year with a maximum in June and July. During the study period, there was a halocline at 1-2 meters depth, but no defined thermocline was observed. The salinity varied from 18-26 above and 22-28 below the halocline. Surface water temperature varied from 7-12 °C. The fish used were 2 year-old hatchery-reared smolts from the Statkraft Energy AS hatchery in Eidfjord (n = 8, mean total length, L_T , 319 mm, range 277-395 mm, mean mass 239 g, range 221-291 g), with wild parents of the River Lærdal stock. The light regime in the hatchery was controlled with an on-off switch with no dimming of light, and windows were covered by black plastics. The hatchery fish were exposed to 8L:16D cycles from 15 December 2005 to 28 February 2006, after which they were exposed to 24 h light until 17 April. From 17 April, the light regime was adjusted to follow the natural daylight periods including the periods of dusk and dawn to ensure that the smolts were adjusted to natural daylight periods before release. In addition, the smolts were also gradually introduced to the actual salinity level (25) of the fjord system. Water temperature in the hatchery was 6.5-7.0 °C (ground water). A seawater challenge test (Blackburn & Clarke, 1987) performed on 9 April revealed mean plasma chloride levels of 146.4 mM at a temperature of 7 °C, indicating that smolts were ready to be released into sea water (Sigholt and Finstad, 1990). The production regimes described above are standard procedures used at several hatcheries in Norway for producing a seawater-tolerant smolt at the time of the wild smolt migrations.

The smolts were tagged with acoustic depth transmitters (Thelma AS, Trondheim, Norway; ADT-9-short, diameter of 9 mm, length of 34 mm, and mass in water/air of 3.3/5.3 g). Before surgery, individuals were anaesthetised using a 3-min immersion in an aqueous solution of 2-

phenoxy ethanol (EC No 204-589-7, Sigma Chemical Co., Evanston, IL, USA, 0.5 ml l⁻¹). The transmitter was inserted through a 13 mm incision on the ventral surface posterior to the pelvic girdle. The transmitter was subsequently pushed gently forward into the body cavity. The incision was closed using two independent silk sutures (4.0 Ethicon; Ethicon Inc., Somerville, NJ, U.S.A.). Following surgery, the smolts were placed in a saltwater tank for 1-4 days and maintained under natural light conditions. Tagged individuals were transported to the outlet of the River Eio in Eidfjord and released over a 20 day period (Table I). According to the natural behaviour of migrating smolts, each tagged smolt was released together with 10-15 untagged hatchery-reared smolts. Tagged smolts were tracked manually from a boat using an acoustic receiver (VR60, Vemco, Halifax, Nova Scotia, Canada). Depth was continuously decoded based on the time delay between two successive acoustic pulses. A delay of 1000 ms corresponded to the surface, increasing 100 ms m⁻¹ below the sea surface. On average, one depth measurement was recorded every 4 s. The positions of the fish were fixed every 10 min after release using a GPS receiver. Individual fish were followed 5-12 h (mean 11 h, Table I). Light intensity at the sea surface was automatically recorded every 15 s (every min on 10 and 11 May; every 5 s on 15 May) by an LI-200 pyranometer sensor (precision \pm 5%) (LI-COR Corp., Lincoln, NE, U.S.A.) connected to a LI 400 data acquisition unit positioned on the top of the boat. Depth transmitters (precision \pm 0.3 m) were calibrated (conditions: 25 °C, 1000 hpa) by the manufacturer. Depth measurements recorded were corrected to atmospheric pressure at the study site during tracking events. Recorded signals were also corrected for extraneous noise (*e.g.* boat traffic) by eliminating values with a vertical velocity >1 m s⁻¹ and values indicating a swimming depth of >0.3 m above the sea surface. As a result, 0.07% of the data collected for individual fish was deleted.

The relationship between light intensities at the sea surface and the smolts' swimming depths were evaluated using the cross-correlation (CC) function (Wei, 1994). The CC function correlates one time series with an increasingly delayed version of another series. Only the CC for lag = 0 are presented here since no delay in smolt response to variations in light intensity was assured. To obtain time series for swimming depths and light intensities that were suitable for a cross-correlation analysis, the series were interpolated to a second-wise scale. If the time difference between two consecutive depth registrations was >30 s, no interpolation was done, so all the swimming depth series became "broken" at irregular intervals. On average, the swimming depth data for each fish consisted of 18 sub-series. Rapid changes in the light intensity were defined as all light intensities >700 W m⁻² that dropped >200 W m⁻² within 15 s. The nocturnal period was defined as the time when light intensity was constantly <100 W m⁻², corresponding to the sunset on days with a clear sky. All statistical analyses were performed with the free statistical software R (<http://www.r-project.org>).

In general, the swimming depth of the tagged post-smolt ranged from 0-6.5 m (range of individual averages: 0.5-2.3 m) and the light intensities from 0-1338 W m⁻² (range of individual averages: 82-602 W m⁻²) (Table I). The results showed large individual variation between light intensity and swimming depths. Four smolts (1, 4, 6 and 7) showed a strong negative cross correlation [CC= (-0.64) – (-0.75)] between general swimming depth and light intensity during day and night (Table I and Fig. 1), indicating individuals were swimming deeper at higher light intensities during day and closer to the surface during night. In contrast, three other individuals (3, 5 and 8) did not reflect a similar behaviour [CC = (-0.09) – (0.11)], but stayed at 2-3 m depth during the entire tracking period. Smolt number 2 was only followed during the day. When only data collected during the day were included in the analyses, only three of eight smolts (1, 4 and 7) showed a relatively strong CC [(CC= (-0.42) – (-0.63)] between light intensity and general

swimming depth (Table I). During the day, all post-smolts spent from 49-99% of their time at 1-3 m depth. When light intensities exceeded $200\text{-}300\text{ W m}^{-2}$, all the fish typically stayed deeper than 0.5 m from the surface (Fig 1). The definition of rapid changes in the light intensity was only observed in two of the days (15 May and 26 May). The CC between light intensity and swimming depth during the periods of rapid changes in light intensity these two days were very weak (CC = 0.041 and -0.024).

As far as is known, the present study is the first to examine the early marine migration behaviour of *S. salar* post-smolts relative to light intensity. Similar to other studies, tagged post smolts swam between 1-3 m (Døving *et al.*, 1985; J. Sturlaugsson & K. Thorisson, unpubl. data). But, the results indicated that the actual swimming depth of post-smolts during their early marine migration appeared to be influenced by light conditions, as more than half of the fish were swimming closer to the surface during the night than during higher day light intensities, with a strong negative cross correlation between general swimming depth and surface light intensity. The more shallow swimming depth during the night than during the day has been observed for out-migrating smolts in rivers (Hesthagen & Garnås, 1986; Hvidsten & Johnsen, 1997). The opposite behaviour has also been reported (Davidsen *et al.*, 2005), but these observations were made in a river above the polar circle with midnight sun conditions and only a negligible difference in light between day and night. Several authors have shown that predation on post-smolts, from fishes and birds, is a constant threat during the seaward migration and directly influences the behaviour of migrating post-smolts (Reitan *et al.*, 1987; Feltham, 1995; Mather, 1998). Lacroix *et al.* (2004) reported that smolts tended to move out of estuaries at night thereby minimising avian and other fish predation. It is likely that the vertical behaviour of the fish observed in this study may be due to a trade-off between avoidance of predators coming from above (birds) and below (fishes). In addition, varying the use of the water column by post-smolts

may also result in other advantages. Swimming close to the surface may be a help for migrating post-smolts during navigation (Flamarique & Hawryshyn, 1993), and avoiding deeper layers with higher levels of salinity in the initial phase of the post-smolt stage may reduce osmoregulatory demands. The observed change in the swimming depth between 3-5 meters during the day and closer to the surface during the night could possibly be a trade-off between the combined benefits provided by these two water layers. Feeding opportunities may also affect the vertical behaviour of the post-smolts. Fjord-migrating post-smolts in Western Norway, however, mainly feed on crustaceans (Rikardsen *et al.*, 2004), which exhibit a daily vertical migration from close to the surface during the night and down to 50-400 m depth during the day (Gorsky *et al.*, 2000). The vertical migrations of post-smolts as observed in the present study can, therefore, not alone be explained by the smolts following the vertical migration patterns of their food items.

In the present study, three out of the seven fish with night recordings did not show any correlation between swimming depth and the light regime. These three post-smolts were released in days with a much larger variation in light intensity than for the other four smolts (fish number 3, 5 and 8; Fig. 1). The larger variation was due to changing cloud cover on these days. If the post-smolt interprets rapid changes in the light regime as a predator approaching from above, days with a frequent variation in light intensity may stress the post-smolt to the point that it does not respond by varying depth preferences. Handeland *et al.* (1996) showed that too frequent reactions to predators in osmotically stressed fish might result in increased lactate accumulation in the muscles, with negative consequences for later attacks and the osmoregulatory capacity. As a result, it can be speculated that post-smolts may moderate the responses to changes in the light regime and avoid coming closer to the surface during the evening.

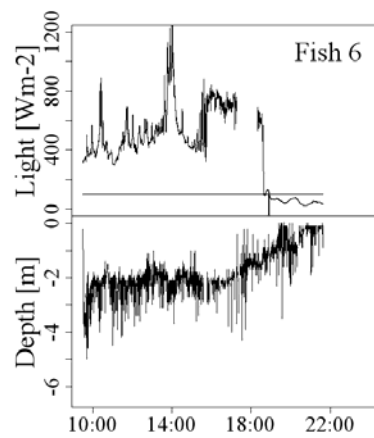
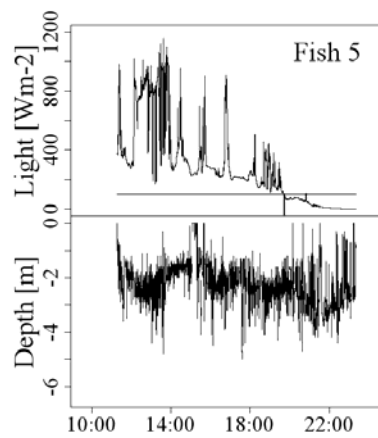
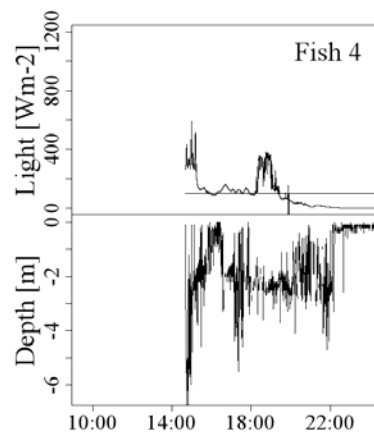
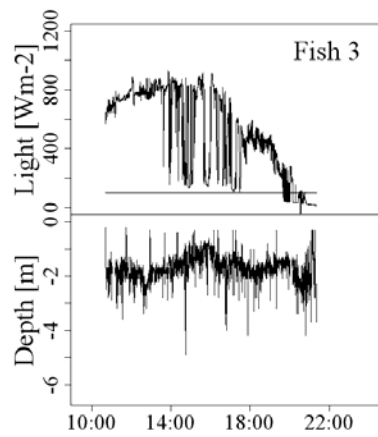
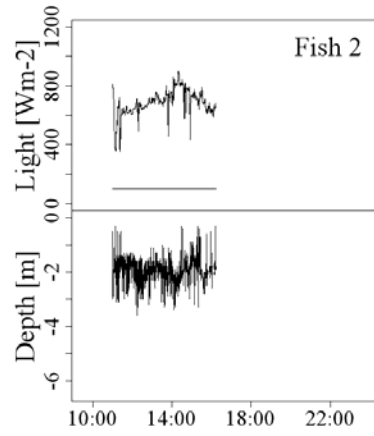
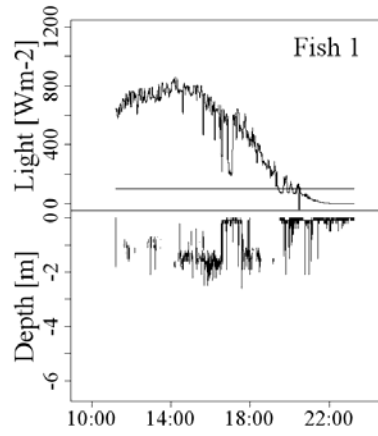
Independent from the light regime the *S. salar* often changed the swimming depth for shorter periods (1-5 min) (Fig 1), indicating that other factors than light intensity were important in setting the irregular dives. Such diving behaviour has been interpreted by other authors as exploratory searches for small-scale differences (<1 m) in the horizontal layers of water (Døving & Stabell, 2003; Rikardsen *et al.*, 2007) or as prey search (Reddin *et al.*, 2006). The exploratory behaviour of smolts may also represent a cost effective strategy to locate and exploit the most favourable outgoing current. The exact causes of the dives of the post-smolt, however, are not yet known.

This study was performed using hatchery-reared post-smolts, and an important question is whether the results are representative also for wild post-smolts. The hatchery-reared post-smolts had been adjusted to the natural light regime prior to release, to ensure that the observed behaviour was not a result of smolts being adapted to an artificial light regime in the hatchery that was different from the light regime during the study. Previous studies have shown that hatchery-reared and wild post-smolts did not differ in their migration behaviour during the seaward migration (Økland *et al.*, 2006; Thorstad *et al.*, 2007), indicating that results from hatchery-reared smolts during this migration stage may be representative also for wild post-smolts, despite different previous experiences in the wild and hatchery environment. The vertical behaviour, however, has not specifically been compared because wild post-smolts were too small for the current generation of acoustic transmitters. The increase in depth relative to increased light levels, and reluctance to expose themselves during daylight, appears to be a shared characteristic among different life stages of wild and farmed *S. salar* (Hvidsten & Johnsen, 1997; Fernö *et al.*, 1999; Thorstad *et al.*, 2008). Thorstad *et al.* (2008) suggested that such anti predator behaviour may be a basic instinct throughout all life stages. Hatchery fish have also been observed to swim deeper

in the tanks when the light is turned on (Hansen, 1998), thereby reflecting a similar behaviour to wild fish.

In conclusion, the present study showed that the swimming depth of the *S. salar* post-smolts may depend on the differences in light intensity between day and night. This behaviour may be a trade-off response between searching for prey, navigating, avoiding osmoregulatory problems and decreasing the predation risk from predators attacking from above or below.

This study was possible due to financial support from the Fishery and Aquaculture Industry Research Fund, NSERC – Canada, the Norwegian Research Council, the Norwegian Institute for Nature Research and the Norwegian College of Fishery Science. The staff at the Statkraft Energy AS hatchery in Simadalen is thanked for extensive help during the fieldwork and two anonymous referees for comments to an earlier draft of the manuscript. The experimental procedures used conform to local ethical requirements and were approved by the Norwegian National Animal Research Authority.



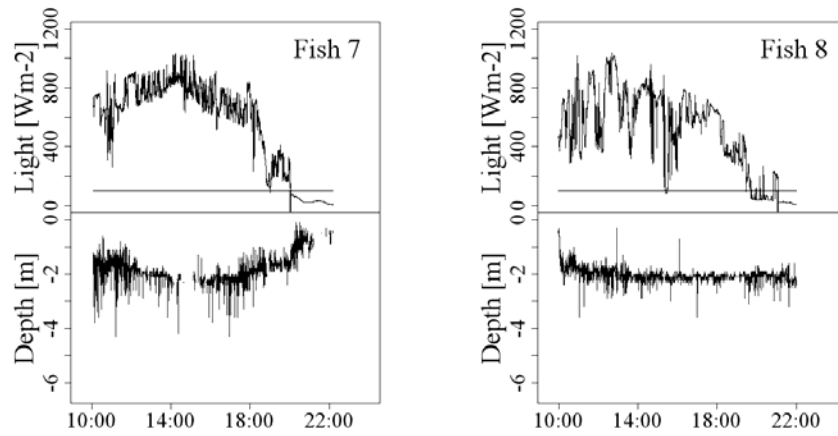


FIG. 1. Light intensity (—, 100 W m^{-2} level, the value used to separate the day and night periods) and swimming depth recorded during manual tracking of eight acoustically tagged post-smolt *Salmo salar* in the Hardangerfjord. For fish 4, the light and depth profiles are only shown until 2400 hours. It was tracked until 0243 hours, but stayed at the same depth after 2230 hours.

Table I: Release date, time period of tracking, swimming depths and surface light intensities for individual post-smolt *Salmo salar* equipped with acoustic transmitters and manually tracked in the Hardangerfjord in 2006. Cross correlations (CC) between swimming depth and light intensity are also given, both for analyses of day and night data combined, and for data collected during the day only (fish number 2 was only tracked during the day). All cross-correlations, except fish number 8 - day only, were significant ($P < 0.05$). This significance, also for the weaker cross-correlations, is caused by the high number of observations in each time series, so even if a cross-correlations, is caused by the high number of observations in each time series, so even if a cross-correlation is statistically significant it does not have to be biologically relevant. (N/A, not available)

| Fish numbers | Release date | Time period the fish was tracked | | Depth, maximum/minimum (mean) (m) | Light during day and night, maximum/minimum (mean) ($W m^{-2}$) | | CC day and night | CC day only |
|--------------|--------------|----------------------------------|------------------------------|-----------------------------------|---|--|------------------|-------------|
| | | Time period | the fish was tracked (hours) | | Light during day and night, maximum/minimum (mean) ($W m^{-2}$) | Light during day only, maximum/minimum (mean) ($W m^{-2}$) | | |
| 1 | 10 May | 1410–2315 | -2.6/0 (-0.5) | 858/0 (409) | 858/66 (550) | -0.75 | -0.63 | |
| 2 | 11 May | 1100–1600 | -3.6/-0.3 (-2.0) | 901/309 (602) | 901/309 (687) | N/A | -0.19 | |
| 3 | 15 May | 1041–2121 | -4.9/-0.2 (-1.7) | 934/15 (513) | 934/31 (549) | -0.09 | -0.17 | |
| 4 | 20 May | 1440–0243 | -6.5/0 (-1.5) | 593/0 (82) | 593/57 (171) | -0.64 | -0.50 | |
| 5 | 26 May | 1117–2321 | -5.0/0 (-2.3) | 1160/0 (301) | 1160/90 (426) | 0.11 | -0.14 | |
| 6 | 28 May | 0930–2139 | -5.0/0 (-1.8) | 1338/0 (350) | 1338/92 (512) | -0.69 | -0.12 | |
| 7 | 29 May | 1004–2211 | -4.3/-0.1 (-1.8) | 1036/0 (502) | 1036/87 (663) | -0.72 | -0.42 | |
| 8 | 30 May | 0959–2201 | -3.6/-0.3 (-2.0) | 1038/0 (448) | 1038/31 (523) | 0.06 | 0 13 | |

References

- Aarestrup, K., Nielsen, C. & Koed, A. (2002). Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia* **483**, 95-102.
- Blackburn, J. & Clarke, C. W. (1987). Revised procedure for the 24 hour seawater challenge test to measure seawater adaptability of juvenile salmonids. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1515**, 1-39.
- Dauidsen, J., Svenning, M. A., Orell, P., Yoccoz, N., Dempson, J. B., Niemela, E., Klemetsen, A., Lamberg, A. & Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research* **74**, 210-222.
- Dieperink, C., Bak, B. D., Pedersen, L. F., Pedersen, M. I. & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology* **61**, 848-852.
- Døving, K. B., Westergård, H. & Johnsen, P. B. (1985). Role of olfaction in the behavioural and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1658-1667.
- Døving, K. B. & Stabell, O. B. (2003). Trails in open waters: Sensory cues in salmon migration. In *Sensory Processing in Aquatic Environments* (Collin, S. P. & Marshall, N. J., eds.), pp. 39-52. New York: Springer-Verlag.
- Feltham, M. J. (1995). Consumption of Atlantic salmon smolts and parr by goosanders - Estimates from doubly-labelled water measurements of captive birds released on 2 Scottish rivers. *Journal of Fish Biology* **46**, 273-281.
- Fernö, A., Huse, I., Juell, J. E. & Bjordal, A. (1999). Vertical distribution of Atlantic salmon (*Salmo salar* L.) in net pens; trade-off between surface light avoidance and food attraction. *Aquaculture* **132**, 285-296.

- Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A. & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild sea trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology* **66**, 86-96.
- Flamarique, I. N. & Hawryshyn, C. W. (1993). Spectral characteristics of salmonid migratory routes from southern Vancouver-Island (British-Columbia). *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1706-1716.
- Gorsky, G., Flood, P. R., Youngbluth, M., Picheral, M. & Grisoni, J.-M. (2000). Zooplankton Distribution in Four Western Norwegian Fjords. *Estuarine, Coastal and Shelf Science* **50**, 000-000.
- Handeland, S. O., Jarvi, T., Ferno, A. & Stefansson, S. O. (1996). Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2673-2680.
- Hansen, L. P. & Jonsson, B. (1985). Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the river Imsa, Norway. *Aquaculture* **45**, 237-248.
- Hansen, T. (1998). *Oppdrett av laksesmolt*. Norway: Landbruksforlaget (in Norwegian).
- Hesthagen, T. & Garnås, E. (1986). Migration of Atlantic salmon smolts in River Orkla of central Norway in relation to management of a hydroelectric station. *North American Journal of Fisheries Management* **6**, 376-382.
- Hvidsten, N. A. & Johnsen, B. O. (1997). Screening of descending Atlantic Salmon (*Salmo salar* L.) smolts from a hydropower intake in the river Orkla, Norway. *Nordic Journal of Freshwater Research* **73**, 44-49.
- Hvidsten, N. A. & Lund, R. (1988). Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla, Norway. *Journal of Fish Biology* **33**, 121-126.

- Lacroix, G. L., McCurdy, P. & Knox, D. (2004). Migration of Atlantic salmon post-smolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society* **133**, 1455-1471.
- Mather, M. E. (1998). The role of context-specific predation in understanding patterns exhibited by anadromous salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 232-246.
- Montevecchi, W. A., Cairns, D. K. & Myers, R. A. (2002). Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 602-612.
- Moore, A., Lacroix, G. L. & Sturlaugsson, J. (2000). Tracking Atlantic salmon post-smolts in the sea. In *The ocean life of Atlantic salmon: environmental and biological factors influencing survival* (Mills, D. D., ed.), pp. 49-64. Oxford: Fishing News books.
- Økland, F., Thorstad, E. B., Finstad, B., Sivertsgård, R., Plantalech, N., Jepsen, N. & McKinley, R. S. (2006). Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration. *Fisheries Management and Ecology* **13**, 271-274.
- Reddin, D. G., Downton, P. & Friedland, K. D. (2006). Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life. *Fishery Bulletin* **104**, 415-128.
- Reitan, O., Hvidsten, N. A. & Hansen, L. P. (1987). Bird predation on hatchery reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. *Fauna Norvegica Ser. A* **8**, 35-38.
- Rikardsen, A. H., Haugland, M., Bjorn, P. A., Finstad, B., Knudsen, R., Dempson, J. B., Holst, J. C., Hvidsten, N. A. & Holm, M. (2004). Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of Fish Biology* **64**, 1655-1679.
- Rikardsen, A. H., Diserud, O. H., Elliott, J. N., Dempson, J. D., Sturlaugsson, J. & Jensen, A. J. (2007) The marine temperature and depth preferences of Arctic charr and sea trout, as recorded by data storage tags. *Fishery Oceanography* **16:5**, 436-447.

- Sigholt, T. & Finstad, B. (1990). Effect of low temperature on sea-water tolerance in Atlantic salmon (*Salmo salar*) smolts. *Aquaculture* **84**, 167-172.
- Solomon, D. J. (1982). Smolt migration in Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.). In *Salmon and Trout Migratory Behaviour Symposium* (Brannon, E. L. & Salo, E. O., eds.), pp. 196-203. Seattle: University of Washington.
- Thorpe, J. E. & Morgan, R. I. G. (1978). Periodicity in Atlantic salmon *Salmo salar* L. smolt migration. *Journal of Fish Biology* **12**, 541-548.
- 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. *Hydrobiologia* **582**, 99-107.
- Thorstad, E. B., Økland, F., Aarestrup, K. & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, doi: 10.1007/s11160-007-9076-4.
- Wei, W. W. S. (1994). *Time Series Analysis – Univariate and Multivariate methods*. Redwood City: Addison-Wesley.
- Westerberg, H. (1982). Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.) – II. Swimming depth and temperature stratification. *Report of the Institute of Freshwater Research Drottningholm* **60**, 102-120.
- Youngson, A. F., Buck, R. J. G., Simpson, T. H. & Hay, D. W. (1983). The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: Environmental release of migration. *Journal of Fish Biology* **23**, 625-639.