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A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration

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The anadromous life cycle of Atlantic salmon *Salmo salar* involves long migrations to novel environments and challenging physiological transformations when moving between salt-free and salt-rich waters. In this article, (1) environmental factors affecting the migration behaviour and survival of smolts and post-smolts during the river, estuarine and early marine phases, (2) how behavioural patterns are linked to survival and (3) how anthropogenic factors affect migration and survival are synthesized and reviewed based on published literature. The timing of the smolt migration is important in determining marine survival. The timing varies among rivers, most likely as a consequence of local adaptations, to ensure sea entry during optimal periods. Smolts and post-smolts swim actively and fast during migration, but in areas with strong currents, their own movements may be overridden by current-induced transport. Progression rates during the early marine migration vary between 0.4 and 3.0 body lengths s⁻¹ relative to the ground. Reported mortality is 0.3–7.0% (median 2.3) km⁻¹ during downriver migration, 0.6–36% (median 6.0) km⁻¹ in estuaries and 0.3–3.4% (median 1.4) km⁻¹ in coastal areas. Estuaries and river mouths are the sites of the highest mortalities, with predation being a common cause. The mortality rates varied more among studies in estuaries than in rivers and marine areas, which probably reflects the huge variation among estuaries in their characteristics. Behaviour and survival during migration may also be affected by pollution, fish farming, sea lice *Lepeophtheirus salmonis*, hydropower development and other anthropogenic activities that may be directly lethal, delay migration or have indirect effects by inhibiting migration. Total mortality reported during early marine migration (up to 5–230 km from the river mouths) in the studies available to date varies between 8 and 71%. Hence, the early marine migration is a life stage with high mortalities, due to both natural and human influences. Factors affecting mortality during the smolt and post-smolt stages contribute to determine the abundance of spawner returns. With many *S. salar* populations in decline, increased mortality at these stages may considerably contribute to limit *S. salar* production, and the consequences of human-induced mortality at this stage may be severe. Development of management actions to increase survival and fitness at the smolt and post-smolt stages is crucial to re-establish or conserve wild populations.

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INTRODUCTION

In diadromous fishes, the migration between freshwater and the marine environment is seen as a strategy of adaptive value, with individuals utilizing the best suited habitat during different stages of the life cycle to increase individual fitness (Lucas & Baras, 2001). For many species, like the Atlantic salmon *Salmo salar* L. 1758, the diadromous life cycle involves long and complex migrations to novel environments and challenging physiological transformations when moving between salt-free and salt-rich waters.

Salmo salar is a species of biological, cultural and economic importance. The life cycle usually involves spawning in fresh water and an eventual migration to the sea where rapid growth due to rich food resources occurs (Klemetsen *et al.*, 2003). The life cycle, however, is considered plastic, and freshwater-resident individuals, and even exclusively freshwater resident populations, exist throughout the species' range.

Juveniles from anadromous populations can grow in fresh water for 1–8 years before they first migrate to sea in the spring or early summer. Once in the ocean they can spend ≥ 4 years feeding prior to returning for their first spawning, although 1–2 years is more typical (Klemetsen *et al.*, 2003). Prior to seaward migration, the fish undergo a preparatory smolting process involving morphological, biochemical, physiological and behavioural changes that preadapt them for life in high salinity water (Hoar, 1988; Høgåsen, 1998; Thorpe *et al.*, 1998; Finstad & Jonsson, 2001). The morphological changes include a slimmer body form and alterations in body colouration (darkened fins, dark back, white belly and silver sides) that help to conceal the fish in the pelagic environment. The key physiological challenge is posed by the need to control body salt levels in the ocean (Evans & Claiborne, 2006). Fully silver juvenile *S. salar* migrating towards the sea are termed smolts during the freshwater portion of their journey, and post-smolts as soon as they have entered the marine environment and until the end of the first winter in the sea (Allan & Ritter, 1977). The average total body length (L_T) of wild smolts is usually 10–20 cm, and they may weigh from 10 to 80 g (Thorstad *et al.*, 2011a).

Biologists have long believed that this freshwater–ocean transition phase was a critical phase in the life cycle of *S. salar*, and a time when they suffered a high mortality as the fish must struggle to cope with increased salinity, novel predators and new food types (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2011a). Evidence for this has been limited as, until recently, available sampling techniques (mainly passive traps, electrofishing and mark–recapture studies) did not allow documentation of the cost to *S. salar* during this stage of the migration. The development of telemetry methods over the past two decades has considerably expanded the knowledge of the smolt migration within rivers and during the early marine phase and of the factors affecting movements and survival.

During the past few centuries, wild *S. salar* populations have declined dramatically (Parrish *et al.*, 1998; WWF, 2001). More recently, overall marine survival (smolts out from rivers *v.* numbers of adults returning to spawn) and in some cases, growth have precipitously declined for unknown reasons (ICES, 2011). It is possible that the decline of *S. salar* is related to significant population-limiting bottlenecks during post-smolt migration, but evidence for this has not yet been compiled and systematically reviewed. In truth, the time-consuming and lengthy migration of the species means that factors acting over long periods and broad geographic scales may all contribute, both cumulatively and synergistically, to the currently depressed

populations. For the protection of existing populations and to guide supportive rearing programmes, an increased understanding of mortality causes and migration patterns at all phases of the life cycle is needed.

In this article (1) environmental factors affecting the migration behaviour and survival of smolts and post-smolts during the river phase, estuarine phase and early marine phase in fjords and coastal areas, (2) how behaviour patterns are linked to survival during these migration phases and (3) how various anthropogenic factors affect the smolt and post-smolt migration behaviour and the survival of *S. salar* are synthesized and reviewed. The extent to which these factors may act as population-limiting mechanisms determining the abundance of *S. salar* populations is considered, management recommendations are outlined and useful directions for future research are identified. The review is based on published literature, and it may serve as a knowledge base for scientists, managers and policy makers.

MIGRATION BEHAVIOUR DURING SMOLT AND INITIAL POST-SMOLT MIGRATION

In this section, behavioural patterns and migration speeds of smolts and post-smolts during the river, estuarine and early marine phases in fjords and coastal areas, as well as how these are affected by environmental factors, are synthesized and discussed.

RIVER PHASE

Adaptation to a life in high salinity water: smoltification

Whether a parr will smoltify and migrate to sea, or alternatively delay smoltification or mature in fresh water, is based on the individual growth rate and the energetic status in late summer and autumn the year before (Metcalfe *et al.*, 1989; Thorpe *et al.*, 1998; Rikardsen *et al.*, 2004a). Individuals that emigrate from fresh water to the sea maintain a high growth rate in late summer and early autumn the year before compared with non-emigrating fish. Individuals that remain freshwater resident usually arrest growth in autumn and allocate and store surplus energy as lipids instead of building proteins. A high lipid level in autumn combined with a low rate of change of lipid during winter is associated with maturation the following summer, without emigration from fresh water (*i.e.* mature male parr).

The final initiation of the smolting process is influenced by photoperiod (increased day length) and water temperature (McCormick & Saunders, 1987; McCormick *et al.*, 1998). During smoltification, juveniles undergo significant changes in their morphology, physiology and behaviour that adapt them to their subsequent life in the sea (McCormick & Saunders, 1987). The physiological changes include modifications of plasma ion concentrations (*e.g.* chloride Cl^- and sodium Na^+) and increases in gill Na^+K^+ ATPase activity (Hoar, 1988; Boeuf, 1994; Strand *et al.*, 2011), thyroid hormones (Iwata, 1995; Hutchison & Iwata, 1998), growth hormone (GH), cortisol and insulin-like growth factor-I (Hoar, 1988; Sakamoto *et al.*, 1995).

Environmental triggers to initiate smolt migration

When smolts are physiologically prepared, an environmental trigger is usually required to initiate downstream migration (McCormick *et al.*, 1998; Riley *et al.*,

2002). The environmental factors cuing downstream migration are mainly water discharge and water temperature. Each of these factors, however, may be of varying importance, and they may stimulate migration in different ways in different populations (Antonsson & Gudjonsson, 2002; Carlsen *et al.*, 2004; Davidsen *et al.*, 2005; Jutila *et al.*, 2005). In some rivers, the smolt migration may be initiated solely by changes in water temperature, whereas in other rivers, increased water discharge during the spring spate may be more important (Jonsson & Ruud-Hansen, 1985; Hvidsten *et al.*, 1995). Cumulative temperature experienced by the smolts over time may also determine the timing of downstream migration (Zydlewski *et al.*, 2005). In addition, social cues, such as presence of other migrants in the river, may stimulate migration (Hansen & Jonsson, 1985; Hvidsten *et al.*, 1995).

Timing and duration of smolt migration

With a few exceptions, smolt migration takes place during spring and early summer. The timing of the migration has an important role in determining smolt survival in the marine environment (McCormick *et al.*, 1998). It is believed that smolts use environmental cues in the rivers that may predict favourable ocean conditions to initiate downstream migration (Hvidsten *et al.*, 1998, 2009). For instance, smolts from Norwegian rivers enter the sea at different times of the season, but even though downriver migration is triggered by different environmental factors, the different populations appear to be adapted to enter the sea when the sea temperature reaches 8° C (Hvidsten *et al.*, 1998, 2009). This implies that smolts from southern populations migrate earlier than smolts from northern populations, where the sea temperature reaches the preferable levels later in the season. Similarly, the smolt runs in Icelandic rivers coincide with a narrow range in sea surface temperatures (SST) in spite of a wide range in emigration time (Antonsson & Gudjonsson, 2002). Preference for specific ocean temperatures could be explained by increased smolt mortality due to low salinity tolerance at low sea temperatures (Sigholt & Finstad, 1990). Increased survival at higher temperatures may also be linked to match–mismatch scenarios with increased prey availability and growth-mediated survival (Rikardsen & Dempson, 2011), perhaps in combination with increased swimming performance that enhances predator avoidance at higher temperatures (Hvidsten *et al.*, 2009). Hence, the timing of the smolt run may be adapted through natural selection to meet the most optimal environmental conditions in the sea. This hypothesis is supported by the finding that post-smolt survival is higher at water temperatures of 8–10° C when the smolts enter the sea in the North Atlantic Ocean, compared with temperatures of 5–7° C (Friedland, 1998; Friedland *et al.*, 2000; Hvidsten *et al.*, 2009). Similarly, for *S. salar* from the Simojoki River in the northern Gulf of Bothnia (63° 37' N; 25° 03' E), the SST that optimize survival range from 9 to 12° C during the smolt migration, with lower survival in colder or warmer years (Jutila *et al.*, 2005). In southern parts of the distribution range of *S. salar*, with generally higher sea temperatures, the optimal survival may be at other temperatures, but run timing may still be adapted so that smolts enter the sea during periods with favourable environmental conditions.

In general, the smolt migration extends over a three to seven-week period during April to July, with the earliest timing in southern populations (Veselov *et al.*, 1998; Antonsson & Gudjonsson, 2002; Stewart *et al.*, 2006; McGinnity *et al.*, 2007; Orell *et al.*, 2007). The majority of individuals belonging to a population, however, may migrate within a relatively short period (1–2 weeks). The duration of the main run

may be shorter in years when the onset of the smolt run is delayed (Juttila *et al.*, 2005). A synchronous migration is expected if the optimal period for seawater entry is brief, but synchronous migration may also reflect an antipredator behaviour to increase survival through confusion effects and predator swamping (Finstad & Jonsson, 2001). Within a given catchment, smolts from upper tributaries may initiate migration earlier than those from lower tributaries, which results in a synchronized sea entry for smolts from within the entire catchment (Stewart *et al.*, 2006). Smolts often migrate downstream in groups, or shoals (Hvidsten *et al.*, 1995; Riley, 2007), and it has even been suggested that smolts may migrate in kin-structured groups (Olsen *et al.*, 2004).

Diurnal migration pattern within rivers

The riverine migration usually takes place during the night, but towards the end of the migration period, it may take place during both night and day (Hansen & Jonsson, 1985; Hvidsten *et al.*, 1995; Moore *et al.*, 1995, 1998; Ibbotson *et al.*, 2006; Koed *et al.*, 2006). This diel migration pattern seems linked to water temperature, with predominantly nocturnal migration occurring at temperatures up to *c.* 12°C, and an increasing proportion of the population migrating during daytime at higher temperatures (Veselov *et al.*, 1998; Ibbotson *et al.*, 2006). Nocturnal migration at low temperatures is thought to be an adaptive behaviour to avoid predation by visual predators. Daytime migration using visual cues, however, may in other respects be advantageous for the smolts, and daytime migration may be safer at higher water temperatures when smolt escape responses are faster, and also may be because of the silver coloured body. Hence, whether a diurnal or nocturnal migration is the overall most advantageous strategy may depend on water temperature, in combination with water depth and river size. Water discharge and turbidity may also affect the optimal migration time. At high latitudes with 24 h daylight, smolts may migrate at all times of the day (Carlsen *et al.*, 2004; Davidsen *et al.*, 2005).

Movement pattern during within-river migration

The downstream migration of smolts was previously believed to be a passive displacement in river currents, but several studies have now documented that active migration occurs, with smolts swimming faster than the current (Fängstam, 1993; Davidsen *et al.*, 2005; Svendsen *et al.*, 2007). Smolts may swim with their head pointing downstream or may turn against the current and orient their head upstream when, for instance, entering accelerating flow fields in riffles or at weirs (Hansen & Jonsson, 1985; Haro *et al.*, 1998; Davidsen *et al.*, 2005). Turning against the current may reduce damage to the fish and provide a better opportunity for controlled movements in strong currents. The net ground speed of downriver migration is a combination of each smolts' own movements and water velocity. Ground speeds may vary considerably, with reported speeds of 0.2 to 60 km day⁻¹ (Ruggles, 1980; Aarestrup *et al.*, 2002). Martin *et al.* (2009) reported that migration over a 16 km long river stretch took between 0.4 and 3.5 days (mean 1.3 days) for individual smolts. Similarly, Davidsen *et al.* (2009) reported that migration over an 11 km long river stretch took between 0.3 and 55 days (mean 4.7 days), and Thorstad *et al.* (2011b) reported that migration over a 9 km long river stretch took between 0.1 and 46.0 days (median 1.0 days). Spicer *et al.* (1995) reported migration speeds of 3.7 km day⁻¹ (range 0.5–15.7) over river stretches longer than 5 km. The downstream migration

speed appears to be slower in small streams than in large rivers (Ruggles, 1980). Little is known of the overall downstream movement patterns of smolts, *i.e.* whether they have a fast and continuous migration from upper reaches of rivers to the estuary or whether they perform a stepwise migration with breaks along the river. Strand *et al.* (2011), however, have shown that early descending smolts with low gill $\text{Na}^+\text{K}^+\text{ATPase}$ activity may delay their final sea entry and spend some time in the lower part of the river, thereby synchronizing their final sea entry with later arriving smolts. It has been observed that smolts may actively feed during the seaward migration (Garnås & Hvidsten, 1985; Jutila & Jokikokko, 2008), but it is not known how widespread this is and to what extent it affects the migration pattern.

Migrating smolts often utilize the middle part of the river channel with the highest water velocity, and they appear to avoid being caught in backwaters and sloughs (Hansen & Jonsson, 1985; Davidsen *et al.*, 2005; Svendsen *et al.*, 2007). They often migrate in near-surface waters, but occupation of the deepest half of the water column has also been recorded (Hesthagen & Garnås, 1986; Hvidsten & Johnsen, 1997; Davidsen *et al.*, 2005; Svendsen *et al.*, 2007). Differences in migration depth may be an adaptation to avoid local predators (predators hunting in near-surface waters *v.* those catching their prey close to the bottom) or an adaptation to use the part of the water channel with the highest water velocities (Davidsen *et al.*, 2005). On average, the highest discharge in an open channel occurs from the surface to *c.* one-third of the depth of the channel and near the thalweg (centre line) (Coutant & Whitney, 2000). It has also been observed that smolts seek actively to avoid predators and typical predator habitats (Bakshtanskiy *et al.*, 1980).

In many catchments, smolts have to pass through lakes during their migration. Smolts are able to swim actively and fast through lakes [up to 15.6 km day^{-1} (Bourgeois & O'Connell, 1988)], although migration at very low speeds has also been recorded (Thorpe *et al.*, 1981; Hansen *et al.*, 1984). There are few published studies, however, of smolt migration through natural lakes, and little is known on the migration patterns and mechanisms in such habitats. More is known about migration through man-made reservoirs.

Autumn migration

Downstream movement of *S. salar* parr during the autumn has been recorded in populations in both North America and Europe (Youngson *et al.*, 1983; Cunjak & Chadwick, 1989; Riley *et al.*, 2002), a phenomenon also termed autumn smolt migration. Studies on the River Frome, a chalk stream in southern England, U.K. ($50^\circ 41' \text{ N}$; $02^\circ 05' \text{ W}$) have demonstrated that a substantial proportion of the population migrate downstream during the autumn with the peak movement occurring during October and November (*c.* 27% of the spring smolt run, in absolute terms; Pinder *et al.*, 2007). The ecological drivers for autumn migrations of *S. salar* are unknown (Riley *et al.*, 2008), although a number of mechanisms have been proposed. These include displacement of subordinates by dominant fish (Bjornn, 1971; Mason, 1976), the requirement for juveniles to migrate to more suitable freshwater habitats (Riddell & Leggett, 1981; Huntingford *et al.*, 1992; Riley *et al.*, 2008) or the requirement for mature male parr to locate mature female adults in order to maximize reproductive success. In some cases, the autumn migrations have also been associated with elevated stream discharge (Youngson *et al.*, 1983). Such movements can be composed of predominantly precocious male parr (Buck & Youngson,

1982) or alternatively of fish of both sexes (Riley *et al.*, 2008). Recent studies on the River Frome have indicated that the autumn migrants, including those that subsequently move to and reside within the tidal reaches of the river during the winter months, are not physiologically adapted to permit permanent, or early, entry into the marine environment (Riley *et al.*, 2008). It has been shown, however, that some parr that migrate downstream in the autumn survive and subsequently contribute to the adult stock (Riley *et al.*, 2009). Frequency histograms of seasonal downstream parr movements in the U.K. suggest a dual peak in the autumn and winter migration, the first occurring in early autumn, the second later during the spawning season for the river system in question (Riley *et al.*, 2002; Pinder *et al.*, 2007; Riley, 2007). Although there is often no information from these studies on the sex composition of the migrants, it is speculated that the later migration may involve mature male parr and be related to reproductive activity. These fish are often older than those migrating during the autumn (Riley, 2007). The extent to which the timing and relative magnitude of these migrations might vary between rivers or over time is unclear.

ESTUARY PHASE

Salmo salar smolts emigrate rapidly from the freshwater environment and into the sea generally using an ebbing tide within the estuary (Moore *et al.*, 1992, 1995, 1996, 1998; Lacroix *et al.*, 2004). The migration of *S. salar* smolts through the upper sections of estuaries is often passive during the hours of darkness but with some degree of orientation that maintain the smolts in the upper water column and within the main current (Moore *et al.*, 1995). This passive orientation is often discontinued through the lower estuary and migration here is indicative of active directed swimming. There is evidence of a selective ebb-tide transport component to the movement through the estuary with the smolts moving within the upper water column and in the fastest moving section of the water channel (Moore *et al.*, 1995; Lacroix *et al.*, 2004). The migration from fresh water through the estuary and into the marine environment is predominantly nocturnal during the early part of the smolt run. During the latter part of the season, a significant proportion of the smolts switch to migration during both day and night. During the migration, there is no apparent period of acclimation required to adjust to saltwater osmotic and ionic conditions (Moore *et al.*, 1998; Lacroix *et al.*, 2005). *Salmo salar* smolts are considered to have physiologically adapted to the marine environment while still in fresh water (Hoar, 1988) and a requirement to move to saline conditions may be the principal physiological mechanism initiating smolt emigration (Moore *et al.*, 1995). Predation on seaward migrating smolts can be a major mortality factor (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006), and the fast and nocturnal migration through estuaries may serve to reduce the predation risk.

EARLY MARINE PHASE

As soon as *S. salar* end their juvenile life in the river and enter the marine environment, they are termed as post-smolts. With the recent development in telemetry methods with smaller acoustic transmitters and more suitable, cheaper and robust automatic receivers, a range of studies on *S. salar* behaviour and survival during the early marine phase in fjords and bays have been carried out during the past 10 years,

both in the north-west and north-east Atlantic Ocean and in the Baltic Sea. These studies have greatly expanded the knowledge regarding this life phase of *S. salar*.

The movement patterns during the first phase of the coastal migration are complex, with some post-smolts taking a direct route towards the sea and others moving in different directions over short spatial and temporal scales (Økland *et al.*, 2006; Hedger *et al.*, 2008). The migration, however, is an active process, with an overall seaward vector. Progression rates vary among sites, years and groups of fish (Table I). For instance, in the Bay of Fundy, Canada, travel rates varied between $<10 \text{ km day}^{-1}$ and $>30 \text{ km day}^{-1}$ among different populations and release groups, and the residence period in the 230 km long bay may thus be >1 month (Lacroix, 2008). Similarly, Kocik *et al.* (2009) found median travel rates of wild post-smolts of $17\text{--}24 \text{ km day}^{-1}$ in the Narraguagus Bay, U.S.A. In Norwegian fjords (which are up to 200 km long), most fish may spend from <1 week and up to 4 weeks before they enter the open ocean (Table I). Migration speeds over the ground varied between 0.4 and 1.2 body lengths s^{-1} in most studies performed in coastal areas, although it was up to 3.0 fork length (L_F) s^{-1} in one study (studies covering stretches of 3 km to >230 km; Table I). Large post-smolts swim faster in the sea than small post-smolts. This may explain the faster migration rates of larger hatchery-reared post-smolts compared to smaller wild post-smolts (Thorstad *et al.*, 2007; Lacroix, 2008). Individual variation in the post-smolt travel rates is generally large.

Progression rates calculated from straight-line transit times between distant points may not reflect true swimming speeds, as post-smolts do not always take the shortest possible route. Further, migration speeds relative to the ground depends not only on the active movement of the post-smolts but also on the movements of the water currents, which are induced primarily by tidal, wind and freshwater runoff forcing (Thorstad *et al.*, 2004). Several studies have shown that smolt migration within the coastal environment can involve active directed swimming at speeds in excess of the prevailing water currents (Moore *et al.*, 1995; Lacroix & McCurdy, 1996; Thorstad *et al.*, 2004; Hedger *et al.*, 2008; Martin *et al.*, 2009). When corrected for the movement of the water, a true post-smolt swimming speed of $1.2 L_T \text{ s}^{-1}$ was calculated over 10 min periods, further supporting the occurrence of active movement of the post-smolts during migration (Økland *et al.*, 2006). A laboratory study has shown that swimming speeds during smolt migration may be *c.* 2.3 body lengths s^{-1} (Fängstam, 1993). Further, smolts tested in the laboratory could maintain average sustained swim speeds (*i.e.* swim speeds that they should be able to maintain for >200 min) of $4.4 L_F \text{ s}^{-1}$ (Booth, 1998). In summary, the movement speed of a post-smolt over the ground is the product of both speed and direction of own movements and of the water current. In areas with low water currents, the outward progression rate will mainly be the result of the post-smolt's own swimming speed and direction, while in areas with strong currents, these may override the fish movements.

There have been few studies exploring the diurnal movement pattern during coastal migration, but Hedger *et al.* (2008) found that swimming speed was greater during daytime than at night and suggested that this pattern was consistent with post-smolts migrating offshore nocturnally and using daytime for prey detection and predator avoidance. Dempson *et al.* (2011) found that slightly more movements occurred during the night than day.

Post-smolts usually swim close to the surface during the early marine migration (1–3 m depth), but make irregular dives down to 6.5 m depth (LaBar *et al.*, 1978;

TABLE I. Progression rates of *Salmo salar* post-smolts tagged with acoustic transmitters in coastal areas. Study site, the distance over which the migration was recorded (from the river mouth and in most studies for some distance in the ocean), migration duration (*i.e.* the time spent passing this stretch), the corresponding migration speeds over the ground (where available), fish origin and the source reference are given. Duration and speed are given as average values, with the range in parentheses if available

Site	Country	Distance (km)	Migration duration (days)	Migration speed	Fish origin	Reference
Bay d'Espoir Fjord	Canada	50	40 (maximum 56)	—	Wild	Dempson <i>et al.</i> (2011)
Bay of Fundy	Canada	>230	26 and 35 ^a	0.4 and 0.5 L_T s ^{-1b}	Hatchery	Lacroix (2008)
Bay of Fundy	Canada	120–175	11–25 ^b	0.5–1.2 L_F s ^{-1b}	Wild and hatchery	Lacroix (2008)
Bay of Fundy	Canada	<100	3–18	0.9–2.0 L_F s ⁻¹	Wild and hatchery	Lacroix (2008)
Gaspé Bay	Canada	10	0.45 and 0.96 (0.1–2.1) ^d	8.9 and 18.5 cm s ⁻¹	Wild	Hedger <i>et al.</i> (2008)
York Estuary	Canada	9	1.9 (0.3–4.2)	—	Wild	Martin <i>et al.</i> (2009)
Passamaquoddy Bay	Canada	23–35	2–6 (maximum 12)	—	Wild and hatchery	Lacroix <i>et al.</i> (2004)
Northern Baltic Sea	Finland	3	0.4 (0.05–0.5)	1.74 L_T s ⁻¹	Wild	Hyvärinen <i>et al.</i> (2006) ^c
Northern Baltic Sea	Finland	3	0.4 (0.2–0.5)	0.43 L_T s ⁻¹	Hatchery	Hyvärinen <i>et al.</i> (2006) ^c
Ellidaar Estuary	Iceland	3	21	0.2 L s ⁻¹	Wild and hatchery	Gudjonsson <i>et al.</i> (2005)
Alta Fjord	Norway	31	1.5 (0.5–6.9)	3.0 f L_F s ⁻¹	Wild	Davidson <i>et al.</i> (2009)
Hardanger Fjord	Norway	167	15 and 18 (7–26) ^a	0.63 km h ⁻¹	Hatchery	Plantalech Manel-la <i>et al.</i> (2011)
Romsdal Fjord	Norway	48	2.7 (1.7–6.9)	0.69 L_T s ⁻¹	Hatchery	Finstad <i>et al.</i> (2005)
Romsdal Fjord	Norway	80	6.3 (maximum 8.6)	0.45 L_T s ⁻¹	Hatchery	Sivertsgård <i>et al.</i> (2007)
Romsdal Fjord	Norway	37	19 (1.5–62)	0.56 L_T s ⁻¹ (0.04–1.89)	Wild	Thorstad <i>et al.</i> (2007)
Romsdal Fjord	Norway	37	7 (1.1–28)	0.77 L_T s ⁻¹ (0.08–1.85)	Hatchery	Thorstad <i>et al.</i> (2007)
Romsdal Fjord	Norway	37	3.3 (0.9–7.4)	—	Hatchery	Thorstad <i>et al.</i> (2012)

L_T , total length; L_F , fork length.

^aRecording of two different stocks.

^bEstimated values from figures shown in publication.

^cBased on manual tracking from boat.

^dRecording in two different years.

Davidson *et al.*, 2008; Plantalech Manel-la *et al.*, 2009). They have been shown to swim closer to the surface at night (0–0.5 m) than during the day (McCleave, 1978; Reddin *et al.*, 2006; Davidson *et al.*, 2008). Various factors such as predation risk (avian predators from above and fish predators from below), orientation mechanisms and feeding may alone or in combination affect depth choice in marine environments. Smolts may also prefer to swim at depths providing the most efficient energy use either for movements or physiological processes. For instance, in a cold Norwegian fjord (7–12° C), the migrating smolts appeared to choose the warmest water layer available (Plantalech Manel-la *et al.*, 2009). In this fjord, with a thin freshwater layer near the surface and a saltwater layer below, the smolts did not show a preference for specific salinity concentrations and were frequently alternating between layers of different salinities, with a mean salinity of 19 at the migration depth (Plantalech Manel-la *et al.*, 2009). In sum, the vertical distribution of post-smolts may be a trade-off between the combined benefits and disadvantages of the different depth layers and their characteristics.

Once post-smolts leave the coastal area, little is known of their migration to ocean feeding grounds. *Salmo salar* are distributed over large areas of the Atlantic Ocean and undertake long sea migrations. Post-smolts have the capacity to rapidly travel over long distances, as tagged individuals recaptured in the Faroe–Shetland Channel had covered 713–874 km during the 38–51 days after they were released in rivers as smolts, corresponding to a minimum progression rate of 14–21 km day⁻¹ (Shelton *et al.*, 1997). Similar recapture data have shown minimum progression rates of between 6 and 26 km day⁻¹ (Holm *et al.*, 2003).

Orientation

Salmo salar migrate from rivers to distant ocean feeding areas and possess an intriguing ability to find their way back to their home river. In general, *S. salar* return to their home river with a high precision (Harden Jones, 1968; Stasko *et al.*, 1973), although a small percentage of the population stray to other rivers (usually <3–6%; Stabell, 1984; Jonsson *et al.*, 2003). Imprinting is thought to be the mechanism by which juvenile *S. salar*, similar to other fish species (Hasler, 1966), memorize olfactory cues and other characteristics of their natal stream for recognition as returning adults (Harden Jones, 1968). The capability of homing is probably based on sequential learning of cues during the downstream and outward migration (Hansen *et al.*, 1993). The imprinting seems to become fixed and was not overridden by a new learning process at the post-spawning stage in a transplantation experiment (Hansen & Jonsson, 1994). Limited experimental evidence exists regarding the sensory mechanisms and cues used during migrations. A diverse array of cues has been proposed, ranging from celestial and magnetic compasses to infrasound patterns in the ocean (Moore *et al.*, 1990; Sand & Karlsen, 2000), but the exact mechanisms are not known.

Post-smolts are novices that must find their way to feeding grounds through unknown waters and new environments. Several studies have suggested that water current is the major orientation factor in the seaward post-smolt migration from the river mouths (LaBar *et al.*, 1978; Lacroix & McCurdy, 1996; Moore *et al.*, 2000). This may be the case in coastal areas with strong outward moving currents, but not in other areas with complex current patterns or weaker currents, where post-smolts must swim actively and use other cues to find the direction towards the open

ocean. In studies of detailed post-smolt movements in a fjord with weak currents, the direction of movement over the ground was dependent on the actual movement of the fish and not on the water current (Thorstad *et al.*, 2004; Økland *et al.*, 2006). A lack of highly directional movements did not indicate precise navigation of the wild post-smolts, although the highest frequency of movements was out of the fjord, resulting in a net seaward movement. The smolts swam *c.* twice the distance of the shortest route from the river mouth. Water currents were not systematically used as an orientation cue, as the actual movements were random compared to the direction of the water current (Thorstad *et al.*, 2004; Økland *et al.*, 2006).

It might be questioned to which extent a fish that is in a large body of moving water is actually able to sense the current direction. If however there are different water layers with different current speeds and directions, it might be possible to sense and use this information through vertical movements crossing these layers. This possibility is supported by several studies which have reported that post-smolts frequently move up and down in the upper few metres of the water column (Plantalech Manel-la *et al.*, 2009). Døving *et al.* (1985) proposed that such diving behaviour was linked to different odour characteristics of the different hydrographic layers, and that the olfactory sense was used for orientation in near-shore regions. If the post-smolts actively use tidal stream transport for the outward migration, this also implies the use of different water depths, as they must follow the outward moving tide but occupy low-current parts of the water column during the inward moving tide. Such active vertical behaviour related to the tide, however, has never been documented for *S. salar* post-smolts.

Swimming towards increasing salinities may also be a way of orientating from the rivers to ocean areas. In support of this, Hedger *et al.* (2008) found that exposure to more saline waters increased swimming speeds. Similarly, Martin *et al.* (2009) found that even small increases in salinity in an estuary induced a shift in the behaviour of the post-smolts to an increasingly active and seaward-oriented migration. In general, post-smolts increase their migration speed as they move from the river towards the ocean (Moore *et al.*, 1995; Finstad *et al.*, 2005; Davidsen *et al.*, 2009; Kocik *et al.*, 2009).

Following the shoreline may also be a way of finding the direction from rivers through bays and fjords to ocean areas. A tendency for post-smolts to migrate along the shoreline is found in some studies (Lacroix *et al.*, 2004). In other studies, post-smolts were found in the middle of embayments as well as closer to the shore (Thorstad *et al.*, 2007; Davidsen *et al.*, 2009; Kocik *et al.*, 2009).

It has also been suggested that post-smolts use ambient infrasound patterns to gain information about altered water depths and distant land formations (Sand & Karlsen, 2000) and that such information about fjord and bay topography is used for orientation purposes. Wind-induced surface currents may also influence the horizontal distribution of post-smolts (Davidsen *et al.*, 2009). Oceanic migration of *S. salar* can be fast and directional, and they appear to be able to maintain overall and general movement directions without the need for learning (Hansen *et al.*, 1993; Hansen & Quinn, 1998). Hence, it is likely that post-smolts also have some sensory mechanisms enabling them to recognize compass directions.

In conclusion, post-smolt migrations can neither be described as exclusively passive and current-guided nor as random trial-and-error processes. Post-smolts are swimming actively and must have some kind of sensory mechanisms that generate

information regarding directions. There is likely a complex combination of senses and cues that are used to gain information about directions and travel routes.

Post-smolt feeding

In order to maximize survival, timing of sea entry is critical for the young first-time migrating *S. salar*. There is a positive relationship between coastal sea temperature in spring and early summer and the availability of important post-smolt prey like fish larvae (Vikebo *et al.*, 2005). Sea temperatures $>8^{\circ}\text{C}$ also result in better growth opportunities when prey are in surplus, further increasing the individual fish's survival chances (Hvidsten *et al.*, 1998; Handeland *et al.*, 2008; Rikardsen & Dempson, 2011). Thus, it is important that the post-smolts adjust their sea entry to migrate at the most profitable period to quickly obtain sufficient food in order to grow out of the risk-size window of being eaten by larger predators and to ensure a healthy body condition important for subsequent survival, migration and growth opportunities during the whole sea residency (Levings, 1994; Salminen *et al.*, 1994; Hvidsten *et al.*, 2009).

Salmo salar are opportunistic feeders, which in total may result in a remarkable mass increase up to 1000 fold or more before they return to fresh water (Rikardsen & Dempson, 2011). Post-smolts, pre-adults and adults have been reported to feed on >40 different fish species or species groups from at least 19 families and consume invertebrates from >10 major taxonomic groups. The variety of prey taken and their respective size range increases from the estuary, throughout the fjords, along the coast and into the open ocean (Rikardsen & Dempson, 2011). During sea entry, the young *S. salar* rapidly shift diet completely from mainly feeding on insects in fresh water, to feeding extensively on marine fish larvae and crustacean prey, resulting in a fast spurt in growth (Dutil & Coutu, 1988; Rikardsen *et al.*, 2004b). There is a general tendency for post-smolts to increase their feeding intensity, particularly on fish larvae, when migrating away from the estuary and in the direction of the open ocean (Levings *et al.*, 1994; Andreassen *et al.*, 2001; Rikardsen *et al.*, 2004b; Knudsen *et al.*, 2005).

There are often large spatial and temporal differences in marine feeding, which may result in considerable geographical and annual variation in *S. salar* abundance (Rikardsen *et al.*, 2004b; Haugland *et al.*, 2006). For example, northern Norwegian post-smolts generally feed more extensively on fish larva than their southern companions during their fjord migration, but feeding intensity and diet choice also vary substantially on annual basis both within fjords (Rikardsen *et al.*, 2004b) and in the different open ocean areas (Haugland *et al.*, 2006). Independent of habitat, geographical area, year and season, fishes such as sand eels *Ammodytes* spp., herring *Clupea harengus* L. 1758, capelin *Mallotus villosus* (Müller 1776) and Gadidae, or planktonic amphipods, are frequently the most important components of their diet across all life-stages and hence commonly provide the dietary life-support needed by *S. salar* to grow and survive (Rikardsen & Dempson, 2011). Although *S. salar* feed on a wide variety of prey, it is common to find only one to three marine prey species in their stomach at any time (Hansen & Pethon, 1985; Rikardsen *et al.*, 2004b). This suggests that not only does the available prey vary considerably depending on the area in question, time of day and season but also that individuals may specialize somewhat in their consumption of a certain prey organism (Andreassen *et al.*, 2001; Jacobsen & Hansen, 2001).

Throughout the sea residency, prey size is positively related to fish size (Rikardsen & Dempson, 2011). During sea entry, the post-smolts can usually feed on fish larvae up to c. 30% of their own body length. If a smolt enters the sea too early or too late, they might miss the abundance of suitable prey or the prey may be too big or too small in size for consumption. Consequently, post-smolts may suffer from reduced growth and survival. In contrast, if they enter the sea at a time when the suitable prey availability is most abundant, they may be rewarded with a higher immediate growth rate and a corresponding potential for higher overall survival. Thus, the timing of the smolt migration in relation to the size range and abundance of suitable prey (especially fish larvae) in near-shore areas may therefore be important for maximizing immediate growth efficiency and may give rise to a match–mismatch situation within seasons and between years (Rikardsen & Dempson, 2011).

In sum, as growth cannot be compromised, successful early marine feeding is a key factor for the survival of young *S. salar* at sea. With the general pattern of decline in many *S. salar* stocks, future feeding studies should focus on direct linkages between prey abundance and the prey *S. salar* consume, along with how this varies over large spatial and temporal scales in relation to survival and productivity of *S. salar* stocks in the context of a changing climate. Studies with multidisciplinary approaches that incorporate both biological and physical environmental factors (Friedland *et al.*, 2009) would be important in this regard to understand how changes in the ocean affect *S. salar* abundance over time.

NATURAL MORTALITY DURING SMOLT AND INITIAL POST-SMOLT MIGRATION

Salmo salar smolt and post-smolt migration is a transition from one life-history stage to another, and the transition introduces new dangers and potentially high mortalities (Thorstad *et al.*, 2011a). It may be difficult to separate between anthropogenic-induced and natural mortality. Most studies on smolt mortality are in response to human intervention such as hydropower development and man-made reservoirs. In the following discussion, natural smolt mortality is defined as mortality occurring without apparent links or associations with anthropogenic stress.

There are few studies of natural mortality rates during downstream migration in catchments. A summary of the few existing studies shows mortalities of 0.3–7.0% (median 2.3) km⁻¹ during the downriver migration (Table II and Fig. 1). Large annual variation in within-river mortality may occur (Thorstad *et al.*, 2011b, 2012). Predation by birds, mammals and fishes may constitute the largest natural mortality factor in the rivers, and the frequent downstream migration during night-time found early in the season may be an adaption to avoid predation (Ibbotson *et al.*, 2006). It has been demonstrated that pike *Esox lucius* L. 1758, chain pickerel *Esox niger* LeSueur 1818, brown trout *Salmo trutta* L. 1758, burbot *Lota lota* (L. 1758), pikeperch *Sander lucioperca* (L. 1758), gulls *Larus* spp., grebe *Podiceps grisegena*, goosander *Mergus merganser*, red-breasted merganser *Mergus serrator*, double-crested cormorant *Phalacrocorax auritus*, grey heron *Ardea cinerea*, American mink *Neovison vison* and European otter *Lutra lutra* prey on smolts in rivers (Ruggles, 1980; Larsson, 1985; Reitan *et al.*, 1987; Feltham & MacLean, 1996; Jepsen *et al.*, 1998; Mather, 1998; Aarestrup *et al.*, 1999; Koed *et al.*, 2002, 2006).

TABLE II. Mortality of *Salmo salar* smolts and post-smolts during migration stages in different habitats. Study site, the distance over which the mortality was recorded, mortality over the stage, mortality km^{-1} within the stage (the value from the mortality column divided by the value in the distance column, unless data were given in the publication), fish body length, fish origin and the source reference are given. All studies come from sites where mortality rates are not expected to be affected by anthropogenic factors such as turbine passage, for example

Site	Country	Distance (km)	Mortality (%)	Mortality km^{-1} (%)	Mean body lengths (mm)	Fish origin	Habitat	Reference
York River	Canada	16	19	1.2	152 L_F	Wild	River	Martin <i>et al.</i> (2009)
River Skjern	Denmark	21	11	0.5	167–195 L_T	Wild	River	Dieperink <i>et al.</i> (2002)
River Skjern	Denmark	20.5	8–22	0.3–0.7	174 L_F	Wild	River	Koed <i>et al.</i> (2006)
River Alta	Norway	11	28	1.0–2.5	146–147 L_F	Wild	River	Davidsen <i>et al.</i> (2009)
River Eira	Norway	9	64	7	239 L_F	Hatchery	River	Thorstad <i>et al.</i> (2012)
Romsdal Fjord	Norway	9	15	1.7	280 L_T	Hatchery	River	Thorstad <i>et al.</i> (2011b)
River Conwy	U.K.	4.7	3	0.6	154 L_F	Wild	River	Moore <i>et al.</i> (1995)
River Test	U.K.	2	10	5	164 L_F	Wild	River	Moore <i>et al.</i> (1998)
Bay of Fundy	Canada	<2 to >25	0–55	—	160–215 L_F^c	Wild and hatchery	Estuary	Lacroix (2008) ^b
York River	Canada	9	5	0.6	152 L_F	Wild	Estuary	Martin <i>et al.</i> (2009)
River Skjern	Denmark	13	42	3.2	167–195 L_T	Wild	Estuary	Dieperink <i>et al.</i> (2002)
River Skjern	Denmark	Not given	38–42	—	174 L_F	Wild	Estuary	Koed <i>et al.</i> (2006)
River Ellidaar	Iceland	3	56	19	166 L	Wild	Estuary	Gudjonsson <i>et al.</i> (2005)
River Ellidaar	Iceland	3	18	6	211 L	Hatchery	Estuary	Gudjonsson <i>et al.</i> (2005)
River Orkla	Norway	1	20	20	163–172 L_F	Wild and hatchery	Estuary	Hvidsten & Lund (1988)
River Surna	Norway	0.7	25	36	Not given	Wild and hatchery	Estuary	Hvidsten & Møkkelgjerd (1987)
River Testebo	Sweden	3.5	43–47	12–13	207–223 L_T	Hatchery	Estuary	Serrano <i>et al.</i> (2009)
Narraguagus Bay	U.S.A.	6.3	26–38	4.1–6.0	171 L_F	Wild	Estuary	Kocik <i>et al.</i> (2009)
Narraguagus Bay	U.S.A.	14	53–64	3.8–4.6	171 L_F	Wild	Estuary + marine (bay)	Kocik <i>et al.</i> (2009)
Bay d'Espoir Fjord	Canada	50	54 and 85 ^a	1.1–1.7	176 L_F	Wild	Marine (fjord)	Dempson <i>et al.</i> (2011)

TABLE II. Continued

Site	Country	Distance (km)	Mortality (%)	Mortality km ⁻¹ (%)	Mean body lengths (mm)	Fish origin	Habitat	Reference
Bay of Fundy	Canada	20	16	0.8	235 L_F	Hatchery	Marine (bay)	Lacroix <i>et al.</i> (2005)
Bay of Fundy	Canada	5–10	8	0.8–1.6	173 L_F	Semiwild	Marine (bay)	Lacroix <i>et al.</i> (2005)
Bay of Fundy	Canada	c. 100–230 ^b	3–70	—	160–215 L_F^c	Wild and hatchery	Marine (bay)	Lacroix (2008)
Passamaquoddy Bay	Canada	23–35	18	0.5–0.8	187–235 L_F	Wild	Marine (bay)	Lacroix <i>et al.</i> (2004)
Passamaquoddy Bay	Canada	23–35	12 and 29 ^a	0.3–0.5 and 0.8–1.3	232 L_F	Hatchery	Marine (bay)	Lacroix <i>et al.</i> (2004)
Alta Fjord	Norway	17	25	0.5–3.0	146–147 L_F	Wild	Marine (fjord)	Davidson <i>et al.</i> (2009)
Hardanger fjord	Norway	35	19	0.5	192–304 L_T	Hatchery	Marine (fjord)	Plantalech Manel-la <i>et al.</i> (2011)
Romsdal Fjord	Norway	37	68	1.8	239 L_F	Hatchery	Marine (fjord)	Thorstad <i>et al.</i> (2012)
Romsdal Fjord	Norway	37	65	1.8	152 L_T	Wild	Marine (fjord)	Thorstad <i>et al.</i> (2007)
Romsdal Fjord	Norway	37	65	1.8	198 L_T	Hatchery	Marine (fjord)	Thorstad <i>et al.</i> (2007)
Romsdal Fjord	Norway	37	71	1.9	280 L_F	Hatchery	Marine (fjord)	Thorstad <i>et al.</i> (2011b)
Bay of Gävle	Sweden	5	11–17	2.2–3.4	207–223 L_T	Hatchery	Marine (bay)	Serrano <i>et al.</i> (2009)

L_F , total length; L_F , fork length; L_T , length measurement unknown.

^aRecording of two different stocks.

^bRecording of post-smolts from 13 different rivers.

^cEstimated from figure.

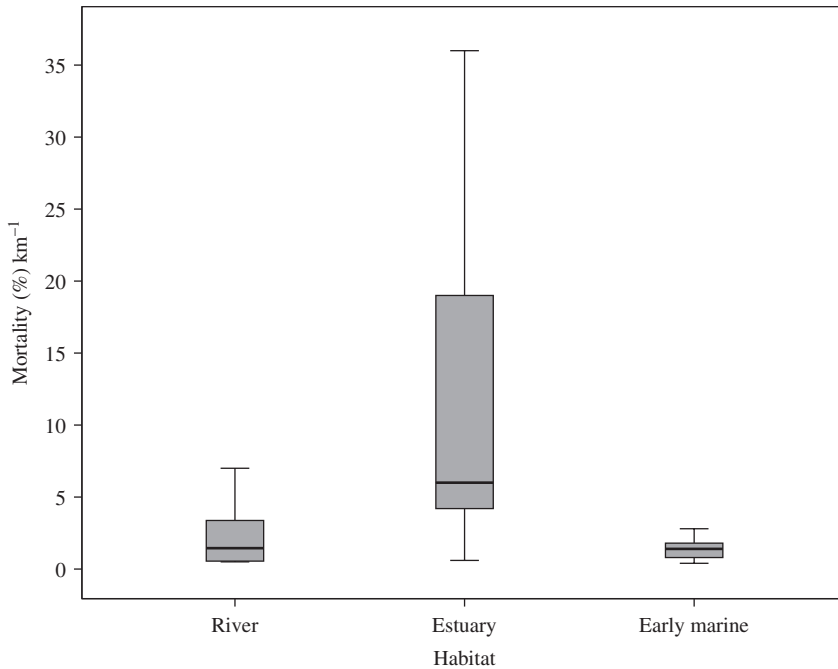


FIG. 1. Mortality of *Salmo salar* smolts and post-smolts km^{-1} in river, estuary and early marine habitats based on the studies referred to in Table II, shown as box plots. The boxes indicate values from the 25th to the 75th percentile, and the dark line in the middle of the boxes indicates the median value. The whiskers extend to 1.5 times the height of the box, or if no case has a value in that range, to the minimum and maximum values. The early marine habitats extend from the river mouth to 5 to ≥ 230 km from the river mouths.

There is little information, however, on predation rates of wild smolts in natural river stretches or lakes. Smolts may also die from injuries caused by physical impacts in the rivers. For instance, Sættem (1990) found a mortality of 37% for *S. trutta* and *S. salar* (9–24 cm body length, *L*) when passing a 30 m high natural waterfall, with 75% of the mortality occurring immediately after the impact. In this case, the waterfall was impassable for upstream migrating adults, and fish were released upstream. Even though this study demonstrated that natural waterfalls may cause injury and mortality of downstream migrating smolts, waterfalls passable for upstream migrating adults in most cases probably do not impart large mortality.

The highest natural smolt mortality occurs in estuaries and marine areas close to the river mouths (Mather, 1998; Lacroix, 2008; Serrano *et al.*, 2009; Thorstad *et al.*, 2012). A summary of different studies shows mortalities of 0.6–36% (median 6.0) km^{-1} in estuaries, which is generally larger than in rivers and the early marine phase (Table II and Fig. 1). In estuaries, predation may again be a major mortality factor. In the estuary of a Norwegian river, Atlantic cod *Gadus morhua* L. 1758 predation was estimated to be 20% (Hvidsten & Lund, 1988), and in a small area in the estuary of another river to be 25% (Hvidsten & Møkkelgjerd, 1987). Several studies indicate that the pattern of night migration activity is stronger in the estuary than in the river or early marine phase (Lacroix *et al.*, 2004; Davidsen *et al.*, 2009),

which may also indicate a strong selection pressure to avoid visual predators in the estuary. Jepsen *et al.* (2006) observed that the highest predation rate in an estuary was in an area where the depth increased from 1 to >25 m and that a large number of predatory fishes aggregated in this area. *Gadus morhua* and saithe *Pollachius virens* (L. 1758) captured in this area had an average of 3.3 smolts in their stomach (Jepsen *et al.*, 2006). The length and characteristics of estuaries differ widely among rivers and different geographic areas, which may explain the large variation in mortalities recorded across studies (Table II and Fig. 1). Lacroix (2008), working in the Bay of Fundy region, noted that the estuarine mortality was lowest in steep-gradient rivers with short estuaries, possibly because of absence of available habitats for potential predators. The reason for the high predation rate in many estuaries may be that a large number of post-smolts have to pass a restricted area during a relatively short period, potentially encountering large numbers of predators from several environments (marine, freshwater, land and air). *Gadus morhua* seem to gather near the river mouths during the smolt run and may adjust their behaviour and habitat use to exploit the smolt resource (Hvidsten & Møkkelgjerd, 1987; Hedger *et al.*, 2011).

Marine mortalities in fjords and bays varied between 0.3 and 3.4% (median 1.4%) km^{-1} in the studies conducted to date (Table II and Fig. 1). Frequently, the exact causes of mortality are not identified. Thorstad *et al.* (2011b, 2012) used depth-sensing transmitters to identify post-smolts eaten by fish predators such as *G. morhua* and *P. virens*, as these predators usually reside at greater depths than post-smolts. In the study by Thorstad *et al.* (2012), total post-smolt mortality was 37% during the first 2 km after leaving the river, and mortality of at least 25% of the tagged fish could be identified as predation from marine fishes. The marine mortality over the next 35 km was 50%, demonstrating a larger mortality rate km^{-1} close to the river mouth (19% km^{-1}) than farther out (1.4% km^{-1}). As the sonic tags continued to emit a signal from the stomachs of the predator, swim depth data were imperative for evaluating whether a tagged smolt was alive or within a predator; otherwise mortality would have been underestimated (26 instead of 37% during the first 2 km). In the same study, transmitters from consumed post-smolts remained within fish predators for up to 47 days (average 29 days). Some predators' movements were similar to those expected by post-smolts except for the depth at which they were occurring, clearly showing that the use of acoustic transmitters without depth-sensing transmitters can underestimate predation and mortality rates (Thorstad *et al.*, 2012). On the other hand, results from telemetry studies can also overestimate mortality rates, as capture, handling and tagging effects may increase mortalities compared to untagged fish (Jepsen *et al.*, 2002). Tag expulsion and tag failure can also contribute to overestimation of mortality rates.

Few studies have been able to show which characteristics or behaviour of a smolt or post-smolt may affect mortality risks. A number of studies, somewhat surprisingly, have not found any effect of body size or fish origin (hatchery *v.* wild) on predation or mortality rates (Hvidsten & Lund, 1988; Thorstad *et al.*, 2007; Lacroix, 2008; Serrano *et al.*, 2009). A size-selective effect on mortality, however, cannot be entirely ruled out as many of the studies have tagged the largest smolts in the population following size constraints when trying to fit acoustic transmitters into an individual's body cavity. Furthermore, the number of fish included in each study has often been relatively low. It may be that the fastest migrating fish, *i.e.* those passing high-risk areas in the shortest time, will have the highest survival. In support of this, Thorstad *et al.* (2007) found that the slowest migrating post-smolts had the largest mortality and concluded

that the risk of being preyed upon may increase with time spent in the fjord system. The alternative explanation, that fish with the lowest speeds were the weakest fish and therefore were more likely to become prey, could also account for this result.

METHODS OF STUDYING SMOLT MIGRATION PATTERNS AND SURVIVAL

No single method is available that adequately addresses tagging *S. salar* to answer the scientific questions on migration patterns and survival. Historically, information about the movements of *S. salar* came from fisheries. An example of this is that significant catches of *S. salar* off the coast of Greenland, coupled to the fact that Greenland itself had only one small *S. salar* producing river, indicated that individuals from many rivers migrated to the sea off Greenland (Dunbar & Thomson, 1979).

The presence of fisheries meant that sampling of fish at sea was occurring. This provided a tool for fisheries biologists, who concluded that if smolts could be tagged with an individual-specific, visible mark, and get fishers to return the information on when and where the marked fish were captured, then a much better documentation and understanding of the movements of fish at sea could be achieved. By the mid-1960s, extensive tagging programmes were underway in both Europe and North America using external, individually numbered tags (most frequently using the Carlin tag) whose recovery in fisheries and subsequent fusion with catch data were used to document migration patterns and infer effects of fisheries upon *S. salar* mortality (Carlin, 1969; Piggins, 1971; Ritter, 1989). Confidence in predictions about mortality rates was always tempered by low recapture rates of tagged fish, and frequent lack of knowledge about variability in the effort of fishers and their tag reporting rates. The information gained on migration patterns was broad-scale and limited only to sampling from places where fisheries were carried out. Commercial fishers also concentrated their efforts on the large maturing fish, and not on the small smolts and post-smolts, which left a gap in the understanding of smolt and post-smolt movements. Finally, the external tags were time consuming to place, and hence expensive, and could wound the fish, causing decreased survival.

To decrease costs and tag wounds, and increase the number of fish tagged, new methods of mass tagging were developed. The most prevalent is the use of small (1 mm long) coded wire tags (CWT), which are injected into the head of fish. Each CWT has an individual identification code engraved into the metal. The CWTs are also magnetized such that they can be detected in whole fish using a specially designed magnet detector. These tags are widely used in some countries (ICES, 2011), but have the disadvantage that they are not externally visible. To recover CWTs, each fish caught must be scanned with a specialized detector before the tags are dissected out. Thus, the use of CWTs generally requires a large-scale and comprehensive monitoring programme.

Within river systems, valuable information has been gained on the movements of *S. salar* through the use of traps and video camera systems (Davidsen *et al.*, 2005), frequently in association with the placement of external tags or by batch marking groups of fish with fin clips or the injection of dyes or other marks. These methods, however, are confined to fresh water, tend to sample a small portion of a river's smolt

production, are sensitive to environmental conditions and are difficult to execute in large river systems.

More recently, scientists have profitably been employing newly developed radio and sonic telemetry techniques to document movements and survival. The costs of tagging individual fish are two to three orders of magnitude more expensive than other methodologies, but the fact that data can be obtained without recapturing the fish is an advantage. In fresh water, radio telemetry is probably the most effective methodology to use. Radio signals carry over great distances, making locating the fish relatively easy. Radio frequencies, however, are blocked by dissolved salts, which mean that investigators lose contact with radio-tagged fish if they move into brackish or salt water. In contrast to radio telemetry, acoustic (sonic) telemetry works in both fresh water and the sea. Acoustic signals do not carry over the large distances that radio signals do, requiring that arrays composed of many acoustic receivers be placed across putative migration routes to ensure detection of fish. This is logistically challenging and expensive, especially in the vast spaces of the oceans. Finally, the small sizes of smolts and post-smolts impose a limit on the size of telemetry (both radio and acoustic) tag that they can carry. This in turn limits the battery size of the tag and hence its life. At this time, the batteries on tags suitable for smolts and post-smolts typically last only for a few months. Passive integrated transponder (PIT) tag systems with longer lasting and cheaper tags can be used to monitor fish behaviour in small river systems (Svendsen *et al.*, 2007).

ANTHROPOGENIC EFFECTS ON SMOLT AND POST-SMOLT MIGRATION BEHAVIOUR AND SURVIVAL

Areas along the migration routes of *S. salar* smolts and post-smolts in rivers, through estuaries and near coastal areas are often affected or modified by human activities. Consequently, habitats are suffering from degradation by many factors that may affect smolt and post-smolt behaviour and survival, including river regulation, water diversion, habitat fragmentation, pollution, harbours, fish farming, drainage and filling. The known effects on smolts and post-smolts from different stressors are synthesized here.

HYDROPOWER REGULATION

Power stations, dams, weirs and other river regulations may lead to major passage problems, and may cause altered water discharges, water temperatures and water quality. Thus, hydropower regulation may affect the timing of migration and smolt behaviour and survival. The effects of a specific river regulation will vary among rivers because of variation in environmental cues triggering smolt migration. To be able to predict the effect of a regulation scheme, it is necessary to know how factors like water temperature and discharge influence smolt migration in the river in question.

Smolts may suffer high mortalities when passing over spillways at dams or if they pass through power station turbines (Ruggles, 1980; Doherty & McCarthy, 1997; Hvidsten & Johnsen, 1997; Larinier & Travade, 2002). The mortality rate at a power station depends on: (1) predation in the reservoir or river stretch above the

power station dam, (2) the proportion of smolts passing through the turbines, (3) the immediate and delayed mortality of smolts passing through the turbines and (4) the mortality of smolts using alternative passages around power stations. Injured fish with large scale loss may have a reduced osmoregulatory ability (Zydlewski *et al.*, 2010), with a subsequent increased mortality in the ocean. Some power stations may also produce supersaturated water below the power station, which may lead to gas bubble disease and mortality (Weitkamp & Katz, 1980). The proportion of smolts passing through the turbines is often related to the proportion of water diverted through the turbines (Ruggles, 1980; Hvidsten & Johnsen, 1997; Serrano *et al.*, 2009).

Increased predation in reservoirs

Reservoirs and slack water above dams may create favourable habitats for predatory fish species that normally do not occur in faster flowing river stretches and may also delay downstream migration and thereby further increase predation (Jepsen *et al.*, 1998, 2000; Aarestrup *et al.*, 1999; Serrano *et al.*, 2009). Both Jepsen *et al.* (1998) and Aarestrup *et al.* (1999) recorded 90% mortality through a reservoir, largely due to predation by *E. lucius* (56% of the mortality) and avian predators (31% of the mortality) such as *P. grisegena* and *A. cinerea*. Koed *et al.* (2002) also found a high predation rate for smolts released immediately downstream of a power station (70%) and suggested that these predators were attracted to this area in a response to the smolt-run.

Mortality due to injuries in turbines

Causes of mortality for smolts passing through turbines may be mechanical damage such as grinding or collisions with moving parts of the turbine, pressure-induced damage, shearing action damage due to passage through areas of extreme turbulence and cavitation damage (Ruggles, 1980; Montén, 1985). The mortality risk increases with increasing fish length (Montén, 1985; Ferguson *et al.*, 2008; Larinier, 2008) and depends on turbine type and operational procedures. Pelton turbines are usually used at high heads, and smolts are unlikely to survive in this turbine type. Kaplan and Francis turbines are often used on *S. salar* rivers. The mortality through Kaplan and Francis turbines can vary considerably among power stations, usually with higher and more variable mortalities reported for Francis than Kaplan turbines [up to 100% mortality for Francis turbines and up to 46% for Kaplan turbines (Larinier, 2008; Ruggles, 1980)]. Francis turbines are often regarded as more harmful for fish than Kaplan turbines because of the larger number of blades. Other characteristics of the power station may be more important determinants of the mortality rates than turbine type. Characteristics of turbines associated with elevated mortalities are high heads, high rotation speeds of the turbines and small turbines (Ferguson *et al.*, 2008; Larinier, 2008). Hence, mortalities in small-scale power stations may be large due to the small size and fast rotation of the turbine (Larinier, 2008). Efforts have been made to construct more fish-friendly turbines, but much work remains to be done before such solutions are available (Čada, 2001). Mortality in turbines can be avoided by increasing the proportion of smolts using alternative bypasses or by closing the power station during the smolt run. River-specific models based on time series of water discharge and temperature can be developed to be able to predict the timing of the smolt migration in different years. By closing or reducing power production for 1–3 weeks during the predicted main run, smolt survival may increase significantly.

Alternative passages past the power station

Alternative passages past the power station may be through spillways over dams, purpose-built bypasses, old river beds or other alternatives. Fish may be directed into alternative passages by using behavioural or physical barriers. If the approach velocity in the water intake area is too high [$>25\text{--}30\text{ cm s}^{-1}$, depending on smolt size (Larinier & Travade, 2002)], the smolts will be unable to avoid entrainment in the flow towards the turbine. Hence, it may be more challenging to bypass turbines in large rivers with fast flowing water than in smaller rivers. Bypass channels should be constructed such that the smolts avoid all classes of injuries. For instance, the velocity in a bypass at the point where it delivers a fish to the water surface downstream of a dam should not be too high, to avoid fatal injury (Ruggles, 1980; Larinier & Travade, 2002). Also, rough concrete walls and rocks in a passageway may result in abrasions and injuries.

Behavioural and physical barriers

Behavioural barriers are facilities that induce fish to swim in a given direction by taking advantage of their natural response to various stimuli. Such barriers include bubbles, sound, light and electrical screens. Even though some behavioural barriers have shown promising results in the laboratory, there are few examples of functional full-scale installations reported in the published literature. Physical barriers and other measures seem more promising (Larinier & Travade, 2002). Different types of physical barriers like louvres, travelling screens and surface guide walls have been used to guide fish away from turbines and towards bypasses (Larinier & Travade, 2002). Hvidsten & Johnsen (1997) found that a surface screen positioned in front of the water intake prevented smolts from entering a power station, which otherwise would cause a 73% mortality. Physical barriers may also be bars or screens with appropriate spacing or mesh dimensions positioned in front of the water intake [2 cm according to Ruggles (1980) and 2.5 cm according to Larinier (2008)]. The efficiency of different barriers will vary among power stations (Haro *et al.*, 1998; Coutant & Whitney, 2000) and at present, there are no standard solutions that can be used at all power stations.

OTHER RIVER REGULATIONS AND MAN-MADE INSTALLATIONS IN RIVERS

Rivers are regulated not only for hydropower. Other uses and man-made installations cause flow regulation, including irrigation systems, channel modification to facilitate boat traffic (*e.g.* locks) and building of infrastructure along the rivers. All may pose challenges similar to hydropower regulation, as they result in lost channel connectivity, altered environmental conditions and water abstraction. Estuarine barges may also impede the seaward passage of migrating smolts (Moore *et al.*, 1996). The movements of *S. salar* smolts in relation to a barrage constructed across the River Tawe, south Wales, (U.K. ($51^{\circ} 37' \text{ N}$; $03^{\circ} 55' \text{ W}$)) indicated that the structure impeded the continuous migration of fish from fresh water into the coastal environment (Moore *et al.*, 1996). On reaching the barrage, smolts ceased downstream migration and resided for periods of up to 72 h before passing the construction. The barrage modified the tidal cycle upstream of the construction and so the ebb-tide cues important in the rapid movement of smolts through estuaries had been reduced.

Smolts residing for long periods above the barrage were considered to be vulnerable to increased avian predation and poor water quality (Moore *et al.*, 1996). There are few published studies of smolt migration related to other river regulations and man-made installations than those related to hydropower development and estuarine barrages.

EFFECTS OF CONTAMINANTS AND POLLUTION

A wide range of freshwater contaminants derived from intensive agriculture and industry, including acid precipitation, can have a significant effect on a number of behavioural and physiological processes involved in controlling smoltification and migration (Magee *et al.*, 2001; Moore *et al.*, 2003, 2007, 2008; Waring & Moore, 2004; Kroglund *et al.*, 2007). Increasingly, it is evident that the conditions experienced in fresh water may modify the parr–smolt transformation, run-timing and the survival of smolts once they enter the marine environment. Exposure to agricultural pesticides in fresh water may inhibit migratory behaviour so that fish either do not migrate or there is a significant delay to the emigration (Moore *et al.*, 2007). Smolts that are delayed may miss the optimum window of opportunity, which has been shown to reduce survival and return rates as adults (Rikardsen & Dempson, 2011). Exposure to contaminant concentrations currently occurring in the environment can modify the olfactory sensitivity of smolts during the period when imprinting to the home river is considered to occur (Lower & Moore, 2007). Sublethal exposure to contaminants during smolting may therefore have implications for the return of specific *S. salar* stocks to their spawning rivers. Many contaminants and acid precipitation and its associated metal binding can severely damage fish gills, compromising smolt osmoregulatory capacity (Kroglund *et al.*, 2007). Once the smolts enter coastal waters, the movement and orientation of the fish can be modified by prior exposure to contaminants within the freshwater environment (Moore *et al.*, 2008).

FISH FARMING

Fish farming may affect smolt behaviour and survival by increasing the occurrence of, or introducing new infectious diseases caused by viruses, bacteria, fungi and parasites. There is generally little knowledge and monitoring of such effects of fish farming on wild populations (Bakke & Harris, 1998), with the exception of the marine parasite salmon louse *Lepeophtheirus salmonis*. These are naturally occurring in the distribution range of *S. salar*, but the number of hosts has increased considerably in many areas with sea-cage *S. salar* farming. At present, *L. salmonis* of farm origin are believed to represent a significant threat in some locations and for some wild populations (Revie *et al.*, 2009; Finstad *et al.*, 2011). Newly migrated post-smolts are particularly vulnerable for *L. salmonis* infestations (Revie *et al.*, 2009; Finstad *et al.*, 2011). The copepod infests the migrating post-smolts and feed on their mucus, skin and blood (Johnson & Albright, 1991; Finstad *et al.*, 2000; Heuch *et al.*, 2005). A post-smolt carrying >11 *L. salmonis*, or 0.75 g^{-1} body mass, will probably not survive (Finstad *et al.*, 2000; Heuch *et al.*, 2005). The increased metabolic demand exerted by the parasite may cause slower host growth, making the wild fish more likely to be captured by predators, or conversely causing them to take greater risks to feed, with the same end result (Revie *et al.*, 2009; Finstad

et al., 2011). Reduced host condition can also affect swimming ability, with several negative ecological consequences ranging from reduced competitive ability to slower migration. Skin damage caused by *L. salmonis* can increase the physiological cost of osmotic regulation or provide sites for secondary bacterial or fungal infection (Revie *et al.*, 2009; Finstad *et al.*, 2011).

Experimental *L. salmonis* infection of hatchery smolts released directly into the marine environment did not affect their survival or migration speeds in an 80 km long fjord (Sivertsgård *et al.*, 2007). This was explained by the migration period being too short for *L. salmonis* to develop into the more pathogenic pre-adult and adult stages. Accordingly, treatment with pharmaceutical prophylaxis against *L. salmonis* did not affect survival and migration of post-smolts in the same fjord (Sivertsgård *et al.*, 2007). The extent to which a post-smolt will be infected is dependent on the migration route after the smolts have left the inshore areas. If post-smolts stay close to the coast for a longer period, it is more likely that they will be infested with high number of *L. salmonis*. It is worth noting that higher *L. salmonis* levels will immediately compromise the physiological capacity of the smolt, *e.g.* increased stress levels (Finstad *et al.*, 2000, 2011), which may disturb migratory behaviour during their initial migratory phase in the fjord systems.

An overlying brackish water layer from the spring freshet is typically found in coastal areas, and *L. salmonis* tend to avoid water with salinities *c.* <20 (Heuch, 1995; Bricknell *et al.*, 2006). In general, post-smolts swim in the upper 1–3 m of the water column, even though this is not necessarily a result of a preference for low salinities (Plantalech Manel-la *et al.*, 2009). Thus, the brackish water layer could be a refuge from *L. salmonis* infestation for migrating post-smolts. This is of importance for management in areas where large rivers are regulated for hydropower purposes. The water discharge, and hence the freshwater input to coastal areas, may be highly reduced during the post-smolt migration because reservoirs that have been emptied during winter are being replenished.

The majority of the smolts leave the rivers during spring when the ocean temperature is relatively low and when the number of *L. salmonis* in coastal waters is low, as the *L. salmonis* population growth is temperature dependent (Boxaspen & Naess, 2000). Until now, this mismatch situation is commonly believed to be the situation for *S. salar* in its northern distribution area, while in the southern part, with occasionally warmer seawater temperatures during the post-smolt migration through fjords, there may, in some years, be a match situation with the start of the *L. salmonis* bloom (Bjørn *et al.*, 2007). With a possible future increasing sea temperature, such a match situation may be more common over the whole *S. salar* distribution area, and post-smolts over larger geographic areas may be negatively affected by *L. salmonis*.

Another possible effect of fish farming in coastal areas may be that post-smolts are attracted to and delayed by the fish farms. The presence of *S. salar* farms both in the estuary and along the migration route of fish from one of the rivers in the Passamaquoddy Bay, Canada, however, did not delay migration. The highest losses of post-smolts occurred in areas near *S. salar* farms where potential predators were believed to be abundant (Lacroix *et al.*, 2004). In Norway, large numbers of marine fishes are attracted to *S. salar* farms where they feed on waste pellets. *Pollachius virens* and *G. morhua* are among those species most commonly associated with farms (Dempster *et al.*, 2009). Both these species prey on out-migrating post-smolts (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006). Salmonids, however, were not found

in stomach content analyses of >300 *P. virens* and 200 *G. morhua* caught during the summer months (June to August) at nine *S. salar* farms along the Norwegian coast (Dempster *et al.*, 2009). Whether or not attraction of marine predators to coastal fish farms represents an increased predation pressure on wild salmonids is thus unknown, but it may be reasonable to expect increased predation when fish farms are located close to river mouths. On the other hand, it may actually be possible that fish farms reduce smolt predation pressure, as potential smolt predators aggregated at farms in parts appear to switch from a fish diet to pellets from farms.

At present, fish farming within the geographic range in which wild *S. salar* occur is nearly exclusively the farming of *S. salar*. Alternate species, including *G. morhua*, are now being farmed (Jensen *et al.*, 2010). It is expected that there will be escapes from such farms. If this occurs, it has been suggested that escaped farmed *G. morhua* might increase predation on wild *S. salar* smolts (Brooking *et al.*, 2006).

Fish farms may be found not only in the sea but also along smolt migration routes in rivers. Water may be withdrawn from the river to flow through the fish farm, before entering the river again downstream of the fish farm. Migrating smolts may enter the fish farms and may be preyed upon by the farmed fish. In a Danish stream, employment of a weir to create sufficient slope through such fish ponds caused a wild smolt loss of 53%, and a 9 days delay in the downstream migration for the survivors (Aarestrup & Koed, 2003). Losses might have been due to fish penetrating grids erected at fish farm inlets, predation and delays, which may lead to desmoltification. It was concluded that the low survival may seriously threaten the long-term viability of wild salmonid populations (Aarestrup & Koed, 2003). Similar to results at hydropower stations, an increased proportion of total river discharge allocated to fish passage increased the smolt survival past the weir at fish farms (Aarestrup & Koed, 2003; Svendsen *et al.*, 2010).

PARASITES AND DISEASES AFFECTED BY ANTHROPOGENIC INFLUENCE OTHER THAN FISH FARMING

As for almost all wild animals, *S. salar* are throughout their life cycle assailed by a range of pathogens that at different degrees utilize the host's energy reserves; some cause fatal diseases, whereas others only a slightly but nevertheless deleterious energetic cost on the host (Bakke & Harris, 1998; Harris *et al.*, 2011). Although parasites may affect any life stage of *S. salar*, the most crucial phases are in the juvenile and parr stages and in the subsequent smolt and post-smolt phases. Unfortunately, almost nothing is known about the latter stage and especially the later ocean phase. Research into the fate of parasitized smolts and post-smolts is urgently needed (Harris *et al.*, 2011).

Anthropogenically introduced parasites where the local *S. salar* stocks have not developed any, or only a low, immunological defence mechanism against the foreign parasite may be fatal for the *S. salar* stock. One such example is the introduction of the *Gyrodactylus salaris* into Norwegian watercourses from the early 1970s (Johnsen & Jensen, 1991). So far, the parasite has been found in nearly 50 rivers, and is regarded as one of the biggest threats to Norwegian *S. salar* populations as it may cause up to 99% mortality of *S. salar* in the river (Anon, 2011). *Gyrodactylus salaris* was introduced to Norwegian hatcheries with imported *S. salar* and spread through anthropogenic stocking. Further spreading is assumed to have happened from primary

infected rivers to nearby watercourses (secondary infected rivers), where the most obvious infection route is anadromous fishes carrying the parasite while migrating between nearby watercourses (Johnsen & Jensen, 1991; Paisley *et al.*, 1999; Jansen *et al.*, 2007).

Gyrodactylus salaris is a monogenean flatworm that feeds on the skin mucus of the fish. It is shown to have limited salinity tolerance, but can survive on its host in brackish water for several days (Soleng *et al.*, 1998). Although some post-smolts have been found to migrate to nearby rivers, the vast majority of the post-smolts migrate directly to the open ocean (Thorstad *et al.*, 2004; Davidsen *et al.*, 2009). It is not known if heavily infected post-smolts may have an anomalous behaviour, for example, due to potential osmoregulatory problems related to high *G. salaris* infections. If so, there is reason to believe that such post-smolts can carry the parasite to nearby watercourses by utilizing brackish surface layers and subsequently return to fresh water to restore their salinity balance, for instance in a similar way as observed for *S. trutta* heavily infected with *L. salmonis* (Birkeland, 1996).

Gyrodactylus salaris has been successfully exterminated in nearly half of the infected Norwegian catchments by eradicating all the hosts (*i.e.* *S. salar*) by use of chemicals (rotenone). The parasite cannot live in the river without available hosts, so the parasite will be exterminated if all the hosts are removed for a time period. In several rivers, the treatment failed and the parasite again bloomed after a few years. One such area is the Skibotn region in northern Norway, where the River Skibotn (69° 23' N; 20° 14' E) was rotenone treated in 1995, and the parasite again observed in the river in 1997, and subsequently for the first time in the neighbouring River Signaldal in 2000 (Jansen *et al.*, 2007). Kristoffersen *et al.* (2005) suggested a controversial theory that it may have been the failure of the treatment of River Skibotn that had contributed to the spreading of the parasite to River Signaldal. When the parasite was almost wiped out in 1995, several *S. salar* parr were allowed to grow up uninfected. In 1998 and 1999, when the infection again exploded, several fish could have been heavily infected just upon smolt migration. This may have resulted in several heavily infected post-smolts with possible osmoregulatory problems and anomalous behaviour, resulting in a behaviour pattern where they carried the parasite 30 km through brackish surface layers until the uninfected River Signaldal. This is an example where a parasite or disease may affect the behaviour of the fish and lead to unforeseen introductions of foreign parasites with catastrophic consequences and complex and large management challenges.

OTHER ANTHROPOGENIC FACTORS IN COASTAL AREAS

Besides effects of fishing, there is little information about how anthropogenic factors in coastal areas could be or are affecting *S. salar* survival and movements at sea. As human development activity on the oceans increase (Bulleri & Chapman, 2010), scientists and managers are thus poorly positioned to deal with the challenges that it may pose. In many coastal areas, post-smolts need to pass anthropogenic interventions such as fish farms, harbours, piers, bridges and industrial developments during their migration, and little is known how such installations may affect water currents, and migratory routes and behaviour.

Energy sector developments are one class of ocean activity that is anticipated to grow in the near future. Offshore wind farms are sending the power generated to

the shore through sub-sea cables, which are generating electromagnetic fields. In both North America and Europe, sub-sea cables are now being planned to transfer power from major hydroelectric sites to populated areas. No work has been done to investigate how *S. salar* will respond to such fields. If they are a barrier to migration, it could have negative effects on *S. salar*. Tidal-power turbines are also being developed. Their transmission lines will generate electromagnetic fields. In addition, the spinning turbines could have direct physical impacts upon migrating *S. salar* if they are placed along a migration route.

A growing portion of the ocean is also now being lit up at night. This stems from the construction of port facilities with piers or tethering systems that extend far offshore, which is required by the increasing size of ocean-going vessels. It is known that these facilities in some circumstances are projected to extend into *S. salar* coastal migration routes. Other plans for ocean development include sub-sea mining, but again it is not known how this will affect migrating *S. salar*.

ALTERED PREDATION LEVELS AS AN EFFECT OF HUMAN INTERVENTIONS

Anthropogenic activities may lead to changes in habitats, the occurrence of predators or the presence of different prey species, which potentially could increase or reduce natural predation rates. Human interventions may even alter the occurrence of predators to such an extent that entire *S. salar* populations may be at risk (Jepsen *et al.*, 1998; Koed *et al.*, 2002). For instance, the creation of reservoirs and slow-flowing river sections may create favourable habitats for predators and extraordinarily high smolt mortality rates. Introduction of new and frequently exotic predator species may further increase the predation risk in such habitats, as is the case with introduced *S. lucioperca* in a regulated river in Denmark (Koed *et al.*, 2002). Human activities causing altered smolt migration speed through areas with particularly high predator density may also contribute to increased predation risks. Jutila *et al.* (2009) suggested that the smolts spent a longer time in the estuary of the River Simojoki, Finland, in cold than in warm springs. *Esox lucius* density in the estuary was high, and the longer residence time in the cold years may have reduced the overall sea survival owing to high predation. The occurrence of alternative prey may significantly influence the predation rate of smolts (Svenning *et al.*, 2005), and anthropogenic factors affecting the occurrence of such prey species may indirectly affect the smolt predation rates. Fisheries and aquaculture may alter distribution, abundance and diversity of predators in the coastal and ocean environment, and these changes could potentially affect smolt survival. Although, human impacts may affect smolt predation rates in unpredictable ways, few studies have demonstrated altered predation on *S. salar* populations related to anthropogenic effects (Mather, 1998; Harris *et al.*, 2008). Predator–prey interactions are complex, and understanding the context or combination of conditions that determine when this process affects the prey community is important.

CLIMATE CHANGE

Water discharge and temperature may affect both the smolting process and the timing of the downstream migration. Any alteration in such environmental factors by climate change may thus affect the smolting and migration. If climate change

results in a sub-optimal timing of the migration and alterations in age at smoltification, this may affect smolt survival. In the River Bush, Northern Ireland, U.K. (55° 13' N; 06° 32' W) an earlier onset of the smolt migration period during the three past decades has been associated with increasing river temperatures in the spring (Kennedy & Crozier, 2010). During the same time period, there was a significant decline in the marine survival. The thermal difference between fresh and salt water during the smolt migration period increased during the study period. It was suggested that climatic variability had resulted in an increased contrast between environmental variables in marine and fresh water, and thereby a temporal mismatch with the local marine spring bloom, and a consequent reduction in feeding opportunities and survival prospects for young post-smolts (Kennedy & Crozier, 2010). The abundance of *L. salmonis* in coastal areas has been shown to increase with increasing temperatures throughout the summer (Bjørn *et al.*, 2010). Climatic change is predicted to lead to elevated ocean temperatures, which may increase the abundance of *L. salmonis* as a result of reduced life cycle periods and increased number of *L. salmonis* generations per year (Johnson & Albright, 1991; Boxaspen & Naess, 2000). Hence, negative effects of *L. salmonis* might become more severe over larger geographical areas as a result of climate changes. There are several recent reviews on the potential effects of climate change on *S. salar* (Friedland, 1998; Friedland *et al.*, 2003; Jonsson & Jonsson, 2009; Todd *et al.*, 2011), and the topic is, therefore, not further discussed here.

PERFORMANCE OF HATCHERY-REARED SMOLTS COMPARED WITH WILD SMOLTS AND POST-SMOLTS

The release of artificially produced *S. salar* smolts from hatcheries is a common management practice over large parts of the distribution area to enhance wild populations, for example to compensate for destroyed spawning areas or to re-establish lost populations (Einum & Fleming, 2001; Finstad & Jonsson, 2001). Hatchery-reared *S. salar* have a lower total survival than wild post-smolts during the ocean stay, both in the Atlantic Ocean and Baltic Sea (survival rate *c.* half of that of wild *S. salar*, Jonsson *et al.*, 1991; Kallio-Nyberg *et al.*, 2004). Even when these smolts are from the same strains as the wild smolts, they differ from wild smolts in physical condition and physiological status, and they have been protected from many of the selective factors encountered in the wild (McCormick *et al.*, 1998). Such differences may affect migration timing and patterns of the hatchery-reared smolts as well as their preparedness to survive in the wild. It has been speculated that the fast growth under an accelerated development regime in the hatchery, and in particular the large body size and high fat content obtained in a hatchery, may affect life-history characteristics and reduce the willingness of an individual to migrate to sea, especially if it is released near freshwater lakes where they may reside (Thorstad *et al.*, 2012). Hatchery fish also show more poorly developed antipredator behaviour than wild fish, perhaps due to the lack of exposure to predators under hatchery conditions and relaxed selection on antipredator traits in hatchery populations (Einum & Fleming, 2001).

Little is known about the performance of hatchery-reared compared with wild smolts during the riverine migration. It is believed that hatchery-reared smolts suffer

a larger mortality if they pass through turbines because of their larger body size, as the mortality through turbines increases with fish length (Hvidsten & Johnsen, 1997).

Surprisingly, several studies did not find a difference in survival, migration rates and behavioural patterns between wild and hatchery-reared *S. salar* during the early marine post-smolt stage (Thorstad *et al.*, 2004, 2007; Gudjonsson *et al.*, 2005; Hyvärinen *et al.*, 2006; Økland *et al.*, 2006; Lacroix, 2008). The hatchery-reared post-smolts, however, may have a faster swimming speed due to their larger body size (Thorstad *et al.*, 2007). Hence, the larger size may compensate for other possible inferiorities of hatchery-reared *S. salar*, as they may swim faster through dangerous areas, may have a faster escape response, and because large size also means that predators have to be larger to consume them (due to gape limitations of predators). Kallio-Nyberg *et al.* (2004) found a significant positive relationship between smolt size and survival among reared, but not among wild *S. salar*, and concluded that the larger smolt size of the reared groups to some extent compensated for their lower ability to live in the wild. Another contributing factor to the successful performance of hatchery-reared *S. salar* in tagging studies may be that they seem less affected by negative tagging effects than wild *S. salar* (Peake *et al.*, 1997). In conclusion, several long-term studies have shown the inferiority of hatchery-reared *S. salar* in the wild and a low overall sea survival, but based on the studies referred to earlier this difference seems to occur at a later stage than the migration through coastal areas near the home river.

DISCUSSION AND CONCLUSION

Mortality during the smolt and early post-smolt migration may be significant. This phase is thus clearly a critical stage and a bottle neck in the *S. salar* life cycle, both because of the physiological transformations and migrations through unknown habitats. The migration route of smolts and post-smolts through rivers, estuaries and near coastal areas is in most areas significantly affected by pollution, power production, fish farming or other anthropogenic activities that may increase mortality by being directly lethal or by delaying or inhibiting migration.

Natural mortality rates in various studies (*i.e.* studies where anthropogenic factors were not assumed to explain the observed mortality) ranged from 0.3–7.0% (median 2.3%) km⁻¹ during the downriver migration, 0.6–36% (median 6.0%) km⁻¹ in estuaries and 0.3–3.4% (median 1.4%) km⁻¹ in marine areas (in studies up to 37 km from the river mouth; Table II and Fig. 1). During this migration, estuaries and river mouths are the most dangerous habitats, comprising the sections with the highest mortalities (Table II and Fig. 1). Variation in mortality among studies clearly demonstrates variation among sites, years and groups of fish. Many studies, however, are based on small sample sizes, a limited number of years of observation, and hatchery-reared fish, which may all contribute to the observed variability. The mortality rates varied more among studies in estuaries than in rivers and marine areas (Table II and Fig. 1), which probably reflects that there is a huge variation in their characteristics among estuaries. The main natural cause of mortality during the smolt and initial post-smolt migration seems to be predation by different birds, mammals, freshwater and marine fishes. Although predation may be the direct cause of mortality, there may also be other indirect contributors to the ultimate mortality due

to predation. For instance, the monitoring of diseases and fish quality is often poor in wild populations. Further, the natural causes of mortality are often difficult to detect.

The total mortality during the early marine migration (during the first 5 km to >230 km from the river mouths) varied between 8 and 71% in different studies ($0.3\text{--}3.4\%$ km⁻¹). These mortality estimates must be regarded as maximum mortalities as these studies are based on fish tagged with acoustic transmitters and include possible mortality due to capture, handling and tagging. When comparing these results with studies showing a total mortality during the entire marine migration of up to 90–99% (Ritter, 1989; Cunjak & Therrien, 1998; Crozier & Kennedy, 1999; Antonsson & Gudjonsson, 2002; Hvidsten *et al.*, 2004), it is clear that there must also be a high mortality during later stages of the marine migration. Considering the short duration of the initial post-smolt migration (from a few days up to 4 weeks) compared with the total period in the ocean (often from 10 months to 3 years or more), the mortality rate is by far the largest during the first few kilometres after entering the marine environment.

Smolts swim actively and fast during the smolt and initial post-smolt migration. In areas with strong currents, a smolt's own movements may be overridden by current-induced transport. Smolts seem to be seawater tolerant prior to outward migration, and usually do not stay long in the transition zone between fresh and salt water. A fast smolt and post-smolt migration through areas of high predation pressure might be an adaptation to reduce the mortality risk. Considering the high cost of migration, there should be a strong evolutionary pressure to favour behavioural strategies that reduce the mortality risk. The night-time migration shown in many studies, and which is especially pronounced through estuaries, may be such an adaptation. The same might also be true for the synchronous migration towards the sea. The hypothesis that individual behavioural strategies may influence the mortality risk and have fitness implications, is mainly based on circumstantial and indirect evidence as few studies demonstrate a direct link between different behavioural strategies and mortality risk. One reason is that such studies often include small sample sizes, with subsequent large variation in results. The exception is several studies demonstrating the differences in sea survival among smolts entering the sea at different timings and during different sea temperatures, emphasizing the importance of entering the sea during optimal conditions. There is a strikingly large individual variation in migration speeds and patterns, which may indicate that individuals in stochastic estuarine and marine environments experience highly variable selection regimes, resulting in different responses to environmental factors on both temporal and spatial scales (Davidsen *et al.*, 2009). Behavioural traits closely related to fitness and subject to strong genotype-by-environment interactions will tend to have lower heritabilities, and higher genetic and non-genetic variability than characters under weak selection (Garcia de Leaniz *et al.*, 2007).

Salmo salar populations differ both ecologically and genetically among rivers, and precise homing to the natal river may generate and maintain local adaptations through natural selection (Taylor, 1991; Verspoor *et al.*, 2005; Garcia de Leaniz *et al.*, 2007). There is indirect evidence for local adaptation in *S. salar* for a number of traits, but few studies have documented inherited differences in behaviour among natural populations (Garcia de Leaniz *et al.*, 2007). Some studies designed as common garden experiments (*i.e.* with different populations reared under similar hatchery conditions

attempting to dissociate heritable from environmentally induced phenotypic variation) have documented differences in smolt and post-smolt migration patterns when fish have been released in natural environments (Aarestrup *et al.*, 1999; McGinnity *et al.*, 2007; Plantalech Manel-la *et al.*, 2011). This indicates that inherited variations in behavioural traits during the smolt and initial post-smolt migration have the potential to result in local adaptations, either due to directional selection on the traits themselves or on other, correlated traits (Garcia de Leaniz *et al.*, 2007). Plantalech Manel-la *et al.* (2011) demonstrated a faster progression and higher survival through marine areas of post-smolts originating from a stock with a long migration distance through fjords before entering the open ocean, than of post-smolts originating from a stock with a shorter fjord migration. They suggested that the distance a *S. salar* population must travel to reach the open coastline may influence its early marine migratory behaviour and performance. The selective pressures of fjord predation and arrival time at feeding areas in the ocean may be stronger for populations with a long fjord migration, creating more efficient migrants over time (Plantalech Manel-la *et al.*, 2011). Hence, local adaptations probably exist in *S. salar* also for some smolt and post-smolt behavioural traits.

While the smolt and initial post-smolt stages involve a large natural mortality, a large additional mortality from anthropogenic activity also occurs in many areas. The effects of hydropower development is the most thoroughly studied human stressor that influences survival and behaviour during this migration stage, which probably reflects the fact that this has been one of the most widespread and severe human interventions influencing smolt and post-smolt migrations. Smolt mortality caused by river regulation may reach 90–100% in some populations, and such mortality at the worst may result in the extermination of wild populations and hinder efforts to re-establish populations. Even single power stations causing small losses may contribute to threatening entire populations when a series of power stations are located along the same river. For smolts that must pass 10 consecutive power stations, even with a high mean survival rate of, for instance, 90% at each power station, the cumulative mortality rate past all power stations will be 65%.

Water pollution also significantly affects smolt and post-smolt behaviour and survival, but the effects have in the past usually been studied in laboratories or with fish kept in cages. Only recently, studies on effects of pollution have been performed on free-swimming fish in nature. One of the reasons may be that there is growing awareness that smolts subjected to some types of pollution in fresh water only manifest a negative effect when they enter salt water. One reason for such delayed effects may be that the mortality occurs due to osmoregulatory problems, which only become acute after they have entered salt water. Another reason may simply be that it takes some time after exposure for the negative effects to manifest themselves and that the smolt in the meantime has left the river and entered the sea. Pollution in the brackish and marine environment may further affect the post-smolts.

Factors other than pollution may show similar delayed effects, where the stressor acts in one habitat but the effect does not emerge before the fish has entered a different habitat. This may be the case for *L. salmonis* that may infest post-smolts in coastal waters, but that may not cause mortality before *L. salmonis* have developed into adult stages and the *S. salar* have reached the open ocean. Another example may be altered freshwater input to near coastal areas caused by river regulation that affects

the stratification of fresh and salt water, which again may affect post-smolt behaviour and survival in the early marine phase. Consequences of such cross-over effects are difficult to detect, because of the large distances separating cause and effect. For migrating species, such as *S. salar*, it is important that the different habitats and their interactions are seen in connection with each other.

Several negative factors may act in concert, making it difficult to identify the different elements and isolate the significance and effect of each of them. Unexpected consequences may also arise from such interactive or synergistic effects. Few studies have focused on consequences of interactive effects, but one study on the interactive effects of acidification and *L. salmonis* infestation on post-smolt survival showed that post-smolts were increasingly susceptible to *L. salmonis* infestations after exposure to even moderate acidification (Finstad *et al.*, 2007). This study demonstrated that factors acting in concert may have much more dramatic consequences for *S. salar* populations than predicted from examining each of the factors independently.

This synthesis of the smolt and initial post-smolt phases of *S. salar* clearly shows that this is a life stage with a high mortality, both naturally and induced by human interventions. The question is then, which consequences may such mortality have at the population level? Salmonid populations are generally believed to be regulated by density-dependent mortality during the early stages after the fry emerge from the spawning gravels and parr stage. After the early regulatory phase, mortality is controlled mainly by density-independent factors (Milner *et al.*, 2003). Survival in the smolt and post-smolt stages is usually regarded as density-independent, which means there should be a positive correlation between number of smolts leaving the river, and the number of returning spawners of a cohort (*i.e.* the more smolts, the more returning spawners; Jonsson *et al.*, 1998). Hence, factors affecting mortality during the smolt and post-smolt stages will not contribute to regulate abundance, but to determine abundance of a population (Milner *et al.*, 2003). The consequences of mortality factors acting at the smolt and initial post-smolt stages will depend on the status of the *S. salar* population in question and whether the population has reached its carrying capacity of (especially female) spawners. If the number of spawners is above the population's carrying capacity, despite a large mortality at the smolt and post-smolt stages, this mortality may not limit the production of this population. If mortality at the smolt and post-smolt stages reduces the number of spawners to below the carrying capacity, this mortality will directly limit the production of the population. Furthermore, for species exploited by humans, like *S. salar*, the stock surplus (number of spawners above carrying capacity) might be harvested through both commercial and recreational fisheries.

With a situation where many *S. salar* populations throughout the distribution range have declined and may be below their carrying capacity, mortality at the smolt and post-smolt stages may considerably contribute to limit *S. salar* production, and the consequences of human-induced mortality at this stage may be severe. With strong population-limiting mechanisms operating during the smolt and post-smolt phases, development of management actions and strategies to increase survival and fitness at this life stage is crucial to re-establish or maintain wild *S. salar* populations. The most pressing areas may be to re-establish connectivity of migration routes and reduce mortality due to river regulation, reduce *L. salmonis* induced mortality and other potentially negative effects by fish farming, and to reduce effects of water pollution and improve water quality.

REQUIREMENTS AND DIRECTIONS OF FUTURE RESEARCH

Scientists and managers have in the past relied much on laboratory experiments or data from fish traps for understanding the smolt and post-smolt phases. With the development of new techniques such as video and telemetry, much novel information is gained on the behaviour and survival during these phases in the last 10–15 years. Until recently, much focus has been on descriptive studies of the smolt and post-smolt behaviour and survival, which is a crucial baseline knowledge for the spatial and temporal management of *S. salar*. More studies have covered the estuary and early marine phases than the river phase, so descriptive studies of especially the within-river smolt migration are still needed. To understand better the general mechanisms affecting behaviour and survival, empirical studies based on hypothesis testing and with larger sample sizes and multiple years of observation are needed in the future. It will also be important to incorporate the information in the comprehensive existing time series from external mark and recapture studies into ecological models where relevant environmental and anthropogenic co-variables are included. Many studies have used hatchery-reared fish for extending the understanding of smolt and post-smolt migration. As hatchery-reared fish for many reasons might be different from wild fish, it will be important to carry out more in-depth studies with respect to differences between hatchery-reared and wild fish. Furthermore, a large number of studies have now increased the understanding of the post-smolt migration during the first 20–30 km after leaving the river mouth, but studies on the marine phase after the smolts have left the near river areas are basically lacking. Such studies are required in order to understand, *e.g.* effects of *L. salmonis*.

Human activities during smolt and post-smolt migration have the potential to reduce or even eliminate wild populations and to hamper the re-establishment of wild *S. salar* populations. It is therefore imperative to understand the negative effects of human interventions and how to implement efficient mitigation measures. For the riverine smolt migration, the environmental factors that influence movements have largely river-specific effects. Hence, to provide mitigation measures for human disturbances such as hydropower installations, river-specific models will have to be developed. Many smolts in certain rivers are killed owing to water abstractions, power stations and artificial barriers. There is an important need for novel research on ways to assist the smolts to avoid these hazards during their migrations, and to determine how this can be done in a cost-efficient manner. It may, for instance, be possible to optimize hydropower production and still preserve smolt production. Further, smolts are also vulnerable to contaminants, but the understanding of how different contaminants may affect the migration and survival of wild populations is still sparse. Cross-over effects such as contaminants and *L. salmonis* that act in one habitat but the effect is not fully seen before the fish enters a new habitat are particularly challenging to study and understand. The same is true for the cumulative or synergistic effects of several factors, *e.g.* climate change and *L. salmonis*. Larger investigations combining controlled experiments in the laboratory and studies of wild fish in nature are needed to improve the understanding of such effects in the future.

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References

- Aarestrup, K. & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish* **12**, 169–176.
- Aarestrup, K., Jepsen, N., Rasmussen, G. & Økland, F. (1999). Movements of two strains of radio tagged Atlantic salmon, *Salmo salar* L., smolts through a reservoir. *Fisheries Management and Ecology* **6**, 97–107.
- 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.
- Allan, I. R. H. & Ritter, J. A. (1977). Salmonid terminology. *Journal du Conseil international pour l'Exploration de la Mer* **37**, 293–299.
- Andreassen, P. M. R., Martinussen, M. B., Hvidsten, N. A. & Stefansson, S. O. (2001). Feeding and prey-selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology* **58**, 1667–1679.
- Anon (2011). The status of Norwegian salmon stocks in 2010. *Report from the Norwegian Scientific Advisory Committee for Atlantic Salmon Management* **3**, 1–285 (in Norwegian).
- Antonsson, T. & Gudjonsson, S. (2002). Variability in timing and characteristics of Atlantic salmon smolt in Icelandic rivers. *Transactions of the American Fisheries Society* **131**, 643–655.
- Bakke, T. A. & Harris, P. D. (1998). Diseases and parasites in wild Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 247–266.
- Bakshanskiy, E. L., Nesterov, V. D. & Neklyudov, M. N. (1980). The behaviour of young Atlantic salmon, *Salmo salar*, during downstream migration. *Journal of Ichthyology* **20**, 93–100.
- Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon lice (*Lepeophtheirus salmonis* Krøyer): migration, growth and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2808–2813.
- Bjørn, P. A., Finstad, B., Kristoffersen, R., McKinley, R. S. & Rikardsen, A. H. (2007). Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Krøyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords. *ICES Journal of Marine Science* **64**, 386–393.
- Bjørn, P. A., Finstad, B., Nilsen, R., Uglem, I., Asplin, L., Skaala, Ø. & Hvidsten, N. A. (2010). Nasjonal lakselusovervåkning 2009 på ville bestander av laks, sjøørret og sjørøye langs Norskekysten samt i forbindelse med evaluering av nasjonale laksevassdrag og laksefjorder. *NINA Rapport* **547**, 1–50 (in Norwegian).
- Bjornn, T. C. (1971). Trout and salmon movements in two Idaho streams as related to temperature, stream flow, cover and population density. *Transactions of the American Fisheries Society* **100**, 423–438.
- Boeuf, G. (1994). Salmonid smolting: a pre-adaptation to oceanic environment. In *Fish Eco-physiology* (Rankin, G. C. & Jenson, G. B., eds), pp. 105–135. London: Chapman & Hall.
- Booth, R. K. (1998). Swimming performance of anadromous Atlantic salmon, *Salmo salar* L., during their spawning migration in the Exploits River, Newfoundland, Canada. PhD Thesis: University of Waterloo, ON, Canada.
- Bourgeois, C. E. & O'Connell, M. F. (1988). Observations on the seaward migration of Atlantic salmon (*Salmo salar* L.) smolts through a large lake as determined by radiotelemetry and Carlin tagging studies. *Canadian Journal of Zoology* **66**, 685–691.
- Boxaspen, K. & Naess, T. (2000). Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. *Contributions to Zoology* **69**, 51–55.
- Bricknell, I. R., Dalesman, S. J., O'Shea, B., Pert, C. C. & Luntz, A. J. M. (2006). Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Diseases of Aquatic Organisms* **71**, 201–212.

- Brooking, P., Doucette, G., Tinker, S. & Whoriskey, F. G. (2006). Sonic tracking of wild cod, *Gadus morhua*, in an inshore region of the Bay of Fundy: a contribution to understanding the impact of cod farming for wild cod and endangered salmon populations. *ICES Journal of Marine Science* **63**, 1364–1371.
- Buck, R. J. G. & Youngson, A. F. (1982). The downstream migration of precociously mature Atlantic salmon, *Salmo salar* L., parr in autumn; its relation to the spawning migration of mature adult fish. *Journal of Fish Biology* **20**, 279–288.
- Bulleri, F. & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* **47**, 26–35.
- Čada, G. F. (2001). The development of advanced hydroelectric turbines to improve fish passage survival. *Fisheries* **26**, 14–23.
- Carlin, B. (1969). *Migration of Salmon*. Montreal, QB: Atlantic Salmon Association Special Publication.
- Carlsen, K. T., Berg, O. K., Finstad, B. & Heggberget, T. G. (2004). Diel periodicity and environmental influence on the smolt migration of Arctic charr, *Salvelinus alpinus*, Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Norway. *Environmental Biology of Fishes* **70**, 403–413.
- Coutant, C. C. & Whitney, R. R. (2000). Fish behaviour in relation to passage through hydropower turbines: a review. *Transactions of the American Fisheries Society* **129**, 351–380.
- Crozier, W. W. & Kennedy, J. A. (1999). Relationships between marine growth and marine survival of one sea winter Atlantic salmon, *Salmo salar* L., from the River Bush, Northern Ireland. *Fisheries Management and Ecology* **6**, 89–96.
- Cunjak, R. A. & Chadwick, E. M. P. (1989). Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1466–1471.
- Cunjak, R. A. & Therrien, J. (1998). Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Fisheries Management and Ecology* **5**, 209–223.
- Davidsen, J. G., Svenning, M. A., Orell, P., Yoccoz, N., Dempson, J. B., Niemelä, 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.
- Davidsen, J. G., Plantalech Manel-la, N., Økland, F., Diserud, O. H., Thorstad, E. B., Finstad, B., Sivertsgård, R., McKinley, R. S. & Rikardsen, A. H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology* **73**, 1065–1074.
- Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., Skarðhamar, J. & Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *Journal of Fish Biology* **75**, 1700–1718.
- Dempson, J. B., Robertson, M. J., Pennell, C. J., Furey, G., Bloom, M., Shears, M., Ollerhead, L. M. N., Clarke, K. D., Hinks, R. & Robertson, G. J. (2011). Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. *Journal of Fish Biology* **78**, 1976–1992.
- Dempster, T., Uglem, I., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R. & Bjørn, P. A. (2009). Coastal salmon farms attract large and persistent aggregations of wild fish: an ecosystem effect. *Marine Ecology Progress Series* **385**, 1–14.
- 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.
- Doherty, D. & McCarthy, K. (1997). The population dynamics, foraging activities and diet of great cormorants (*Phalacrocorax carbo carbo* L.) in the vicinity of an Irish hydro-electricity generating station. *Supplemento alle Ricerche di Biologia della Selvaggina* **XXVI**, 133–143.
- Døving, K. B., Westerberg, 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.

- Dunbar, M. J. & Thomson, D. H. (1979). *West Greenland salmon and climactic change. Meddelelser om Grønland* 202, No. 4. Copenhagen: Nyt Nordisk Forlag Arnold Busk.
- Dutil, J. D. & Coutu, J. M. (1988). Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the Northern Gulf of St Lawrence. *Fishery Bulletin* **86**, 197–212.
- Einum, S. & Fleming, I. A. (2001). Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research* **75**, 56–70.
- Evans, D. H. & Claiborne, J. B. (2006). *The Physiology of Fishes*. Boca Raton, FL: CRC Press Taylor and Francis Group.
- Fängstam, H. (1993). Individual downstream swimming speed during the natural smolting period among young Baltic salmon (*Salmo salar*). *Canadian Journal of Zoology* **71**, 1782–1786.
- Feltham, M. J. & MacLean, J. C. (1996). Carlin tag recoveries as an indicator of predation on salmon smolts by goosanders and red-breasted mergansers. *Journal of Fish Biology* **48**, 270–282.
- Ferguson, J. W., Ploskey, G. R., Leonardsson, K., Zabel, R. W. & Lundqvist, H. (2008). Combining turbine blade-strike and life cycle models to assess mitigation strategies for fish passing dams. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1568–1585.
- Finstad, B. & Jonsson, N. (2001). Factors influencing the yield of smolt releases in Norway. *Nordic Journal of Freshwater Research* **75**, 37–55.
- Finstad, B., Bjørn, P. A., Grimnes, A. & Hvidsten, N. A. (2000). Laboratory and field investigations of salmon lice (*Lepeophtheirus salmonis* Krøyer) infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. *Aquaculture Research* **31**, 795–803.
- Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A. & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology* **66**, 86–96.
- Finstad, B., Kroglund, F., Strand, R., Stefansson, S. O., Bjørn, P. A., Rosseland, B. O., Nilsen, T. O. & Salbu, B. (2007). Salmon lice or suboptimal water quality - reasons for reduced postsmolt survival? *Aquaculture* **273**, 374–383.
- Finstad, B., Bjørn, P. A., Todd, C. D., Whoriskey, F., Gargan, P. G., Forde, G. & Revie, C. W. (2011). The effect of sea lice on Atlantic salmon and other salmonid species. In *Atlantic Salmon Ecology* (Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J., eds), pp. 253–276. Oxford: Wiley-Blackwell.
- Friedland, K. D. (1998). Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 119–130.
- Friedland, K. D., Hansen, L. P., Dunkley, D. A. & MacLean, J. C. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science* **57**, 419–429.
- Friedland, K. D., Reddin, D. G., McMenemy, J. R. & Drinkwater, K. F. (2003). Multidecadal trends in North American Atlantic salmon (*Salmo salar*) stocks and climate trends relevant to juvenile survival. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 563–583.
- Friedland, K. D., MacLean, J. C., Hansen, L. P., Peyronnet, A. J., Karlsson, L., Reddin, D. G., Maoiléidigh, Ó. & McCarthy, J. L. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* **66**, 289–204.
- 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* **82**, 173–211.
- Garnås, E. & Hvidsten, N. A. (1985). The food of Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta* L. smolts during migration in the Orkla river, Norway. *Fauna Norvegica Series A* **6**, 24–28.
- Gudjonsson, S., Jonsson, I. R. & Antonsson, T. (2005). Migration of Atlantic salmon, *Salmo salar*, smolt through the estuary area of River Ellidaar in Iceland. *Environmental Biology of Fishes* **74**, 291–296.
- Handeland, S., Imsland, A. K. & Stefansson, S. O. (2008). The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolt. *Aquaculture* **283**, 36–42.

- Hansen, L. P. (1993). Movement and migration of salmon at sea. In *Salmon in the Sea and New Enhancement Strategies* (Mills, D., ed.), pp. 26–39. Oxford: Fishing News Books Ltd.
- Hansen, L. P. & Jonsson, B. (1985). Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa. *Aquaculture* **45**, 237–248.
- Hansen, L. P. & Jonsson, B. (1994). Homing of Atlantic salmon: effects of juvenile learning on transplanted post-spawners. *Animal Behaviour* **47**, 220–222.
- Hansen, L. P. & Pethon, P. (1985). The food of Atlantic salmon, *Salmo salar* L., caught by long-line in northern Norwegian waters. *Journal of Fish Biology* **26**, 553–562.
- Hansen, L. P. & Quinn, T. P. (1998). The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 104–118.
- Hansen, L. P., Jonsson, B. & Døving, K. B. (1984). Migration of wild and hatchery reared smolts of Atlantic salmon, *Salmo salar* L., through lakes. *Journal of Fish Biology* **25**, 617–623.
- Hansen, L. P., Jonsson, N. & Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal Behaviour* **45**, 927–941.
- Harden Jones, F. R. (1968). *Fish Migration*. London: Edward Arnold Ltd.
- Haro, A., Odeh, M., Noreika, J. & Castro-Santos, T. (1998). Effect of water acceleration on downstream migratory behaviour and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. *Transactions of the American Fisheries Society* **127**, 118–127.
- Harris, C. M., Calladine, J. R., Wernham, C. V. & Park, K. J. (2008). Impacts of piscivorous birds on salmonid populations and game fisheries in Scotland: a review. *Wildlife Biology* **14**, 395–411.
- Harris, P. D., Bachmann, L. & Bakke, T. A. (2011). The parasites and pathogens of the Atlantic salmon: lessons from *Gyrodactylus salaris*. In *Atlantic Salmon Ecology* (Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J. eds), pp. 221–252. Oxford: Wiley-Blackwell.
- Hasler, A. D. (1966). *Underwater Guideposts; Homing of Salmon*. Madison, WI: University of Wisconsin Press.
- Haugland, M., Holst, J. C., Holm, M. & Hansen, L. P. (2006). Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science* **63**, 1488–1500.
- Hedger, R. D., Martin, F., Hatin, D., Caron, F., Whoriskey, F. & Dodson, J. (2008). Active migration of wild Atlantic salmon *Salmo salar* through a coastal embayment. *Marine Ecology Progress Series* **355**, 235–246.
- Hedger, R. D., Uglem, I., Thorstad, E. B., Finstad, B., Chittenden, C. M., Arechavala-Lopez, P., Jensen, A., Nilsen, R. & Økland, F. (2011). Behavioural strategies of Atlantic cod, a marine fish predator, during Atlantic salmon post-smolt migration. *ICES Journal of Marine Science* **68**, 2152–2162.
- 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.
- Heuch, P. A. (1995). Experimental evidence for aggregation of salmon louse copepodids (*Lepeophtheirus salmonis*) in steep salinity gradients. *Journal of the Marine Biological Association of the United Kingdom* **75**, 927–939.
- Heuch, P. A., Bjørn, P. A., Finstad, B., Holst, J. C., Asplin, L. & Nilsen, F. (2005). A review of the Norwegian national action plan against salmon lice on salmonids: the effect on wild salmonids. *Aquaculture* **246**, 79–92.
- Hoar, W. S. (1988). The physiology of smolting salmonids. In *Fish Physiology, Vol. XIB* (Hoar, W. S. & Randall, D. J., eds), pp. 275–343. New York, NY: Academic Press.
- Høgåsen, H. R. (1998). Physiological changes associated with the diadromous migration of salmonids. *Canadian Special Publication of Fisheries and Aquatic Sciences* **127**, 1078–1081.
- Holm, M., Holst, J. C., Hansen, L. P., Jacobsen, J. A., O'Maoiléidigh, N. & Moore, A. (2003). Migration and distribution of Atlantic salmon post-smolts in the North Sea and

- North-East Atlantic. In *Salmon at the Edge* (Mills, D., ed.), pp. 7–23. Oxford: Blackwell Science.
- Huntingford, F. A., Thorpe, J. E., Garcia de Leaniz, C. & Hay, D. W. (1992). Patterns of growth and smolting in autumn migrants from a Scottish population of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **41** (Suppl. B), 43–51.
- Hutchison, M. J. & Iwata, M. (1998). Effect of thyroxine on the decrease of aggressive behaviour of four salmonids during the parr-smolt transformation. *Aquaculture* **168**, 169–175.
- 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. A. (1988). Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla. *Journal of Fish Biology* **33**, 121–126.
- Hvidsten, N. A. & Møkkelgjerd, P. I. (1987). Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna. *Journal of Fish Biology* **30**, 273–280.
- Hvidsten, N. A., Jensen, A. J., Vivås, H., Bakke, Ø. & Heggberget, T. G. (1995). Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic Journal of Freshwater Research* **70**, 38–48.
- Hvidsten, N. A., Heggberget, T. G. & Jensen, A. J. (1998). Sea water temperature at Atlantic salmon smolt entrance. *Nordic Journal of Freshwater Research* **74**, 79–86.
- Hvidsten, N. A., Johnsen, B. O., Jensen, A. J., Fiske, P., Ugedal, O., Thorstad, E. B., Jensås, J. G., Bakke, Ø. & Forseth, T. (2004). Orkla - et nasjonalt referanseassdragsdrag for studier av bestandsregulerende faktorer hos laks. *NINA Fagrapport* **079**, 1–96 (in Norwegian).
- Hvidsten, N. A., Jensen, A. J., Rikardsen, A. H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. & Johnsen, B. O. (2009). Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. *Journal of Fish Biology* **74**, 1532–1548.
- Hyvärinen, P., Suuronen, P. & Laaksonen, T. (2006). Short-term movements of wild and reared Atlantic salmon smolts in a brackish water estuary—preliminary study. *Fisheries Management and Ecology* **13**, 399–401.
- Ibbotson, A. T., Beaumont, W. R. C., Pinder, A., Welton, S. & Ladle, M. (2006). Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecology of Freshwater Fish* **15**, 544–551.
- Iwata, M. (1995). Downstream migratory behaviour of salmonids and its relationship with cortisol and thyroid hormones: a review. *Aquaculture* **135**, 131–139.
- Jacobsen, J. A. & Hansen, L. P. (2001). Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science* **58**, 916–933.
- Jansen, P. A., Matthews, L. & Toft, N. (2007). Geographic risk factors for inter-river dispersal of *Gyrodactylus salaris* in fjord systems in Norway. *Diseases of Aquatic Organisms* **74**, 139–149.
- Jensen, Ø., Dempster, T., Thorstad, E. B., Uglem, I. & Fredheim, A. (2010). Escapes of fish from Norwegian sea-cage aquaculture: causes, consequences, prevention. *Aquaculture Environment Interactions* **1**, 71–83.
- Jepsen, N., Aarestrup, K., Økland, F. & Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia* **372**, 347–353.
- Jepsen, N., Pedersen, S. & Thorstad, E. (2000). Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research and Management* **16**, 189–198.
- Jepsen, N., Thorstad, E. B., Baras, E. & Koed, A. (2002). Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia* **483**, 239–248.
- Jepsen, N., Holthe, E. & Økland, F. (2006). Observations of predation on salmon and trout smolts in a river mouth. *Fisheries Management and Ecology* **13**, 341–343.
- Johnsen, B. O. & Jensen, A. J. (1991). The *Gyrodactylus* story in Norway. *Aquaculture* **98**, 289–302.

- Johnson, S. C. & Albright, L. J. (1991). Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda, caligidae) under laboratory conditions. *Journal of the Marine Biological Association of the United Kingdom* **71**, 425–436.
- Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* **75**, 2381–2447.
- Jonsson, B. & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 593–595.
- 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, N., Jonsson, B. & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **67**, 751–762.
- Jonsson, B., Jonsson, N. & Hansen, L. P. (2003). Atlantic salmon straying from the River Imsa. *Journal of Fish Biology* **62**, 641–657.
- Jutila, E. & Jokikokko, E. (2008). Seasonal differences in smolt traits and post-smolt survival of wild Atlantic salmon, *Salmo salar*, migrating from a northern boreal river. *Fisheries Management and Ecology* **15**, 1–9.
- Jutila, E., Jokikokko, E. & Julkunen, M. (2005). The smolt run and postsmolt survival of Atlantic salmon, *Salmo salar* L., in relation to early summer water temperatures in the northern Baltic sea. *Ecology of Freshwater Fish* **14**, 69–78.
- Jutila, E., Jokikokko, E. & Ikonen, E. (2009). Post-smolt migration of Atlantic salmon, *Salmo salar* L., from the Simojoki river to the Baltic Sea. *Journal of Applied Ichthyology* **25**, 190–194.
- 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 Simojoki River in the Baltic Sea. *Journal of Fish Biology* **65**, 122–134.
- Kennedy, R. J. & Crozier, W. W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology* **76**, 1786–1805.
- 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. *Ecology of Freshwater Fish* **12**, 1–59.
- Knudsen, R., Rikardsen, A. H., Dempson, J. B., Bjørn, P. A., Finstad, B., Holm, M. & Amundsen, P.-A. (2005). Trophically transmitted parasites in wild Atlantic salmon post-smolts from Norwegian fjords. *Journal of Fish Biology* **66**, 758–772.
- Kocik, J. F., Hawkes, J. P., Sheehan, T. F., Music, P. A. & Beland, K. F. (2009). Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. *American Fisheries Society Symposium* **69**, 293–310.
- Koed, A., Jepsen, N., Aarestrup, K. & Nielsen, C. (2002). Initial mortality of radio-tagged Atlantic salmon (*Salmo salar* L.) smolts following release downstream of a hydropower station. *Hydrobiologia* **483**, 31–37.
- Koed, A., Baktoft, H. & Bak, B. D. (2006). Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River Research and Applications* **22**, 69–78.
- Kristoffersen, R., Rikardsen, A. H., Winger, A. C., Adolfsen, P. & Knudsen, R. (2005). Arctic charr as a long-term host of *Gyrodactylus salaris* in River Skibotn, Northern Norway. *NINA Rapport* **36**, 1–27 (in Norwegian with English summary).
- Kroglund, F., Finstad, B., Stefansson, S. O., Nilsen, T. O., Kristensen, T., Rosseland, B. O., Teien, H. C. & Salbu, B. (2007). Exposure to moderate acid water and aluminium reduces Atlantic salmon post-smolt survival. *Aquaculture* **273**, 360–373.
- LaBar, G. W., McCleave, J. D. & Fried, S. M. (1978). Seaward migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts in the Penobscot River estuary, Maine: open

- water movements. *Journal du Conseil international pour l'Exploration de la Mer* **38**, 257–269.
- Lacroix, G. L. (2008). Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2063–2079.
- Lacroix, G. L. & McCurdy, P. (1996). Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology* **49**, 1086–1101.
- Lacroix, G. L., McCurdy, P. & Knox, D. (2004). Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society* **133**, 1455–1471.
- Lacroix, G. L., Knox, D. & Stokesbury, M. J. W. (2005). Survival and behaviour of post-smolt Atlantic salmon in coastal habitat with extreme tides. *Journal of Fish Biology* **66**, 485–498.
- Larinier, M. (2008). Fish passage experience at small-scale hydro-electric power plants in France. *Hydrobiologia* **609**, 97–108.
- Larinier, M. & Travade, F. (2002). Downstream migration: problems and facilities. *Bulletin Français de la Pêche et de la Pisciculture* **364** (Suppl. 2002-1), 181–207.
- Larsson, P.-O. (1985). Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. *Journal of Fish Biology* **26**, 391–397.
- Levings, C. D. (1994). Feeding behaviour of juvenile salmon and significance of habitat during estuary and early sea phase. *Nordic Journal of Freshwater Research* **69**, 7–16.
- Levings, C. D., Hvidsten, N. A. & Johnsen, B. O. (1994). Feeding of Atlantic salmon (*Salmo salar* L.) postsmolts in a fjord in central Norway. *Canadian Journal of Zoology* **72**, 834–839.
- Lower, N. & Moore, A. (2007). The effect of a brominated flame retardant on smoltification and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts. *Marine and Freshwater Behaviour and Physiology* **40**, 267–284.
- Lucas, M. & Baras, E. (2001). *Migration of Freshwater Fishes*. Oxford, Blackwell Science.
- Magee, J. A., Haines, T. A., Kocik, J. F., Beland, K. F. & McCormick, S. D. (2001). Effects of acidity and aluminium on the physiology and migratory behaviour of Atlantic salmon smolts in Maine, USA. *Water Air and Soil Pollution* **130**, 881–886.
- Martin, F., Hedger, R. D., Dodson, J. J., Fernandes, L., Hatin, D., Caron, F. & Whoriskey, F. G. (2009). Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. *Ecology of Freshwater Fish* **18**, 406–417.
- Mason, J. C. (1976). Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management* **40**, 775–788.
- 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** (Suppl. 1), 232–246.
- McCleave, J. D. (1978). Rhythmic aspects of estuarine migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts. *Journal of Fish Biology* **12**, 559–570.
- McCormick, S. D. & Saunders, R. L. (1987). Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth and metabolism. *American Fisheries Society Symposium* **1**, 211–229.
- McCormick, S. D., Hansen, L. P., Quinn, T. P., Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 77–92.
- McGinnity, P., de Eyto, E., Cross, T. F., Coughlan, J., Whelan, K. & Ferguson, A. (2007). Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture* **273**, 257–268.
- 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 B* **236**, 7–19.
- Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research* **62**, 111–125.
- Montén, E. (1985). *Fisk och turbiner. Om fiskars möjligheter att oskadda passera genom kraftverksturbiner*. Stockholm: Vattenfall.

- Moore, A., Freake, S. M. & Thomas, I. M. (1990). Magnetic particles in the lateral line of the Atlantic salmon (*Salmo salar* L.). *Philosophical Transactions of the Royal Society B* **329**, 11–15.
- Moore, A., Potter, E. C. E. & Buckley, A. A. (1992). Estuarine behaviour of migrating Atlantic salmon smolts. In *Wildlife Telemetry* (Priede, I. M. & Swift, S. M., eds), pp. 390–399. Chichester: Ellis Horwood.
- Moore, A., Potter, E. C. E., Milner, N. J. & Bamber, S. (1995). The migratory behaviour of wild Atlantic salmon (*Salmo salar*) smolts in the estuary of the River Conway, North Wales. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1923–1935.
- Moore, A., Stonehewer, R., Kell, L. T., Challiss, M. J., Ives, M., Russell, I. C., Riley, W. D. & Mee, D. M. (1996). The movements of emigrating salmonid smolts in relation to the Tawe barrage, Swansea. In *Barrages: Engineering Design and Environmental Impacts* (Burt, N. & Watts, J., eds), pp. 409–417. Chichester: John Wiley and Sons Ltd.
- Moore, A., Ives, S., Mead, T. A. & Talks, L. (1998). The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. *Hydrobiologia* **372**, 295–304.
- 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., ed.), pp. 49–64. Oxford: Fishing News Books.
- Moore, A., Scott, A. P., Lower, N., Katsiadaki, I. & Greenwood, L. (2003). The effects of 4-nonylphenol and atrazine on Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* **222**, 253–263.
- Moore, A., Lower, N., Mayer, I. & Greenwood, L. (2007). The impact of a pesticide on migratory activity and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* **273**, 350–359.
- Moore, A., Cotter, D., Rogan, G., Quayle, V., Lower, N. & Privitera, L. (2008). The impact of a pesticide on the physiology and behaviour of hatchery reared salmon smolts during the transition from the freshwater to marine environment. *Fisheries Management and Ecology* **15**, 385–392.
- 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.
- Olsen, K. H., Petersson, E., Ragnarsson, B., Lundqvist, H. & Järvi, T. (2004). Downstream migration in Atlantic salmon (*Salmo salar*) smolt sibling groups. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 328–331.
- Orell, P., Erkinaro, J., Svenning, M. A., Davidsen, J. G. & Niemelä, E. (2007). Synchrony in the downstream migration of smolts and upstream migration of adult Atlantic salmon in the subarctic River Utsjoki. *Journal of Fish Biology* **71**, 1735–1750.
- Paisley, L. G., Karlsen, E., Jarp, J. & Mo, T. A. (1999). A Monte Carlo simulation model for assessing the risk of introduction of *Gyrodactylus salaris* to the Tana river, Norway. *Diseases of Aquatic Organisms* **37**, 145–152.
- Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D. & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 281–287.
- Peake, S., McKinley, R. S., Scruton, D. A. & Moccia, R. (1997). Influence of transmitter attachment procedures on swimming performance of wild and hatchery-reared Atlantic salmon smolts. *Transactions of the American Fisheries Society* **126**, 707–714.
- Piggins, D. J. (1971). Smolt rearing, tagging and recapture techniques in a natural river system. In *Atlantic Salmon Workshop 1971* (Carter, W. M., ed.), pp. 63–82. St Andrews, NB: New Brunswick International Atlantic Salmon Foundation.
- Pinder, A. C., Riley, W. D., Ibbotson, A. T. & Beaumont, W. R. C. (2007). Evidence for an autumn downstream migration and the subsequent estuarine residence of 0+ juvenile Atlantic salmon, *Salmo salar* L., in England. *Journal of Fish Biology* **71**, 260–264.
- Plantalech Manel-la, N., Thorstad, E. B., Davidsen, J. G., Økland, F., Sivertsgård, R., McKinley, R. S. & Finstad, B. (2009). Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration. *Fisheries Management and Ecology* **16**, 147–154.

- 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 Atlantic salmon? *Journal of Fish Biology* **78**, 624–634.
- 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**, 415–428.
- 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 Series A* **8**, 35–38.
- Revie, C., Dill, L., Finstad, B. & Todd, C. D. (2009). Sea Lice Working Group Report. *NINA Special Report* **39**, 1–17.
- Riddell, B. E. & Leggett, W. C. (1981). Evidence of an adaptive basis for geographic variation of body morphology, and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 308–320.
- Rikardsen, A. H. & Dempson, J. B. (2011). Dietary life-support: the marine feeding of Atlantic salmon. In *Atlantic Salmon Ecology* (Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J., eds), pp. 115–144. Oxford: Wiley-Blackwell.
- Rikardsen, A. H., Thorpe, J. E. & Dempson, B. (2004a). Modelling the life-history variation of Arctic charr. *Ecology of Freshwater Fish* **13**, 305–311.
- Rikardsen, A. H., Haugland, M., Bjørn, P. A., Finstad, B., Knudsen, R., Dempson, J. B., Holst, J. C., Hvidsten, N. A. & Holm, M. (2004b). Geographical differences in early marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of Fish Biology* **64**, 1655–1679.
- Riley, W. D. (2007). Seasonal downstream movements of juvenile Atlantic salmon, *Salmo salar* L., with evidence of solitary migration of smolts. *Aquaculture* **273**, 194–199.
- Riley, W. D., Eagle, M. O. & Ives, S. J. (2002). The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. *Fisheries Management and Ecology* **9**, 87–94.
- Riley, W. D., Ibbotson, A. T., Lower, N., Cook, A. C., Moore, A., Mizuno, S., Pinder, A. C., Beaumont, W. R. C. & Privitera, L. (2008). Physiological seawater adaptation in juvenile Atlantic salmon (*Salmo salar*) autumn migrants. *Freshwater Biology* **53**, 747–755.
- Riley, W. D., Ibbotson, A. T. & Beaumont, W. R. C. (2009). Adult returns from Atlantic salmon, *Salmo salar* L., parr autumn migrants. *Fisheries Management and Ecology* **16**, 75–76.
- Ritter, J. A. (1989). Marine migration and natural mortality of North American Atlantic salmon (*Salmo salar* L.). *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2041**, 1–136.
- Ruggles, C. P. (1980). A review of the downstream migration of Atlantic salmon. *Canadian Technical Report on Fisheries and Aquatic Sciences* **952**, 1–39.
- Sættem, L. M. (1990). Skadefrekvens hos laksefisk etter nedvandring i foss. *Fylkesmannen i Sogn og Fjordane Miljøvernvedlegget Rapport nr. 3-1990*.
- Sakamoto, T., Hirano, T., Madsen, S. S., Nishioka, R. S. & Bern, H. A. (1995). Insulin-like growth factor I gene expression during the parr–smolt transformation of coho salmon. *Zoological Science* **12**, 249–252.
- Salminen, M., Kuikka, S. & Erkamo, E. (1994). Divergence in feeding migration of Baltic salmon (*Salmo salar* L.); the significance of smolt size. *Nordic Journal of Freshwater Research* **69**, 32–42.
- Sand, O. & Karlsen, H. E. (2000). Detection of infrasound and linear acceleration in fishes. *Philosophical Transactions of the Royal Society B* **355**, 1295–1298.
- Serrano, I., Rivinoja, P., Karlsson, L. & Larsson, S. (2009). Riverine and early marine survival of stocked salmon smolts, *Salmo salar* L., descending the Testebo River, Sweden. *Fisheries Management and Ecology* **16**, 386–394.
- Shelton, R. G. J., Turrell, W. R., Macdonald, A., McLaren, I. S. & Nicoll, N. T. (1997). Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe–Shetland Channel in June 1996. *Fisheries Research* **31**, 159–162.
- Sigholt, T. & Finstad, B. (1990). Effect of low temperature on seawater tolerance in Atlantic salmon (*Salmo salar*) smolts. *Aquaculture* **84**, 167–172.

- Sivertsgård, R., Thorstad, E. B., Økland, F., Finstad, B., Bjørn, P. A., Jepsen, N., Nordal, T. & McKinley, R. S. (2007). Effects of salmon lice infection and salmon lice protection on fjord migrating Atlantic salmon and brown trout post-smolts. *Hydrobiologia* **582**, 35–42.
- Soleng, A., Bakke, T. A. & Hansen, L. P. (1998). Potential for dispersal of *Gyrodactylus salaris* (Plathyhelminthes, Monogenea) by sea running stages of the Atlantic salmon (*Salmo salar*): field and laboratory studies. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 507–514.
- Spicer, A. V., Moring, J. R. & Trial, J. G. (1995). Downstream migratory behaviour of hatchery-reared, radio-tagged Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, Maine, USA. *Fisheries Research* **23**, 255–266.
- Stabell, O. B. (1984). Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biological Reviews* **59**, 333–388.
- Stasko, A. B., Sutterlin, A. M., Rommell, S. A. Jr. & Elson, P. F. (1973). Migration–orientation of Atlantic salmon (*Salmo salar* L.). Proceedings of the international symposium on the Atlantic salmon: management, biology and survival of the species. *International Atlantic Salmon Foundation, New York Special Publication Series* **4**, 119–137.
- Stewart, D. C., Middlemas, S. J. & Youngson, A. F. (2006). Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish* **15**, 552–558.
- Strand, J. E. T., Davidsen, J. G., Jørgensen, E. H. & Rikardsen, A. H. (2011). Seaward migrating Atlantic salmon smolts with low levels of gill Na⁺, K⁺ -ATPase activity; is sea entry delayed? *Environmental Biology of Fishes* **90**, 317–321.
- Svendsen, J. C., Eskesen, A. O., Aarestrup, K., Koed, A. & Jordan, A. D. (2007). Evidence for non-random spatial positioning of migrating smolts (Salmonidae) in a small lowland stream. *Freshwater Biology* **52**, 1147–1158.
- Svendsen, J. C., Aarestrup, K., Deacon, M. G. & Christensen, R. H. B. (2010). Effects of a surface oriented travelling screen and water abstraction practices on downstream migrating salmonidae smolts in a lowland stream. *River Research and Applications* **26**, 353–361.
- Svenning, M.-A., Borgstrøm, R., Dehli, T. O., Moen, G., Barrett, R. T., Pedersen, T. & Vader, W. (2005). The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*). *Fisheries Research* **76**, 466–474.
- Taylor, E. B. (1991). A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**, 185–207.
- Thorpe, J. E., Ross, L. G., Struthers, G. & Watts, W. (1981). Tracking Atlantic salmon smolts, *Salmo salar* L., through Loch Voil, Scotland. *Journal of Fish Biology* **19**, 519–537.
- Thorpe, J. E., Mangel, M., Metcalfe, N. B. & Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* **12**, 581–599.
- Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P. A. & McKinley, R. S. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes* **71**, 305–311.
- 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., Whoriskey, F. G., Rikardsen, A. H. & Aarestrup, K. (2011a). Aquatic nomads: the life and migrations of the Atlantic salmon. In *Atlantic Salmon Ecology* (Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J. eds), pp. 1–32. Oxford: Wiley-Blackwell.
- Thorstad, E. B., Uglem, I., Arechavala-Lopez, P., Økland, F. & Finstad, B. (2011b). Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal Environment Research* **16**, 115–120.
- Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F. & Bjørn, P.-A. (2012). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology* (in press).

- Todd, C. D., Friedland, K. D., MacLean, J. C., Hazon, N. & Jensen, A. J. (2011). Getting into hot water? Atlantic salmon responses to climate change in freshwater and marine environments. In *Atlantic Salmon Ecology* (Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J. eds), pp. 409–444. Oxford: Wiley-Blackwell.
- Verspoor, E., Beardmore, J. A., Consuegra, S., García de Leániz, C., Hindar, K., Jordan, W. C., Koljonen, M.-L., Mahkrov, A. A., Paaver, T., Sánchez, J. A., Skaala, Ø., Titov, S. & Cross, T. F. (2005). Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. *Journal of Fish Biology* **67** (Suppl. A), 3–54.
- Veselov, A. J., Sysoyeva, M. I. & Potutkin, A. G. (1998). The pattern of Atlantic salmon smolt migration in the Varzuga river (white sea basin). *Nordic Journal of Freshwater Research* **74**, 65–78.
- Vikebo, F., Sundby, S., Adlandsvik, B. & Fiksen, O. (2005). The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science* **62**, 1375–1386.
- Waring, C. P. & Moore, A. (2004). The effect of atrazine on Atlantic salmon smolts in freshwater and after saltwater transfer. *Aquatic Toxicology* **66**, 93–104.
- Weitkamp, D. E. & Katz, M. A. (1980). A review of dissolved gas supersaturation literature. *Transactions of the American Fisheries Society* **109**, 659–702.
- WWF (2001). *The Status of Wild Atlantic Salmon: a River by River Assessment*. Washington, DC: World Wildlife Fund.
- 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.
- Zydlewski, G. B., Haro, A., McCormick, S. D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behaviour of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 68–78.
- Zydlewski, J., Zydlewski, G. & Danner, G. R. (2010). Descaling injury impairs the osmoregulatory ability of Atlantic salmon smolts entering seawater. *Transactions of the American Fisheries Society* **139**, 129–136.

Electronic Reference

- ICES (2011). Report of the Working Group on North Atlantic Salmon (WGNAS). *ICES 2011/ACOM 09*. Available at http://www.ices.dk/reports/ACOM/2011/WGNAS/wgnas_2011_final.pdf