Refining and partitioning Atlantic salmon marine survival and quantifying dam impacts on population demographics

Impacts from dams and poor marine survival are the primary drivers of Atlantic salmon abundance and are hindering contemporary recovery efforts (NRC 2004). Despite this, a comprehensive understanding of the impact these factors have on Atlantic salmon populations is limited and the marine phase has often been considered as 'black-box'. While dams are known to negatively impact Atlantic salmon productivity, limited monitoring effort was generally deferred to dam owners. Additionally, marine survival dynamics were once only available on a very coarse scale, interpreted from estimates of large parr abundance, pro-rated by assumed overwinter survival to estimate the emigrating smolt abundance, and compared with estimates of adult returns. To increase the recovery potential of Atlantic salmon, NEFSC efforts have focused on improving our understanding of these critical impacts while incrementally migrating our attention further out to sea to focus on the marine phase of the species.

Early efforts to understand drivers of marine survival focused on the impact of thermal habitat on growth and survival, and suggested that favorable growth conditions before the first winter at sea determined recruitment (Friedland et al. 1993; Friedland et al. 1998). Concurrent efforts initiated in 1996 focused on improving large parr estimates in freshwater and estimating smolt abundance emigrating into the Gulf of Maine via rotary screw traps (Music et al. 2010, USASAC 2014).

An **ultrasonic tracking** program was initiated in 1997 to obtain information on emigration dynamics and identify survival bottlenecks in rivers, estuaries, and nearshore habitats. Initial efforts focused on a single drainage and tracked a small group of tagged smolts with a small number of fixed receivers through riverine, estuarine and nearshore marine habitats. The tracking program has expanded to include five river-embayments and migration information from over 3,500 individuals. Unique to each system, tracking array resolution and distance has generally increased over time. In some systems, salmon are tracked for 90 km, from their release point 45 km up-river through their migration to a distance 45 km offshore (Kocik et al. 2009, Renkawitz et al. 2012). These studies have shown that migration is generally surface oriented (< 5 m), rapid (~1 $km \cdot h^{-1}$), and that survival is highly variable among systems. Annual variation is likely depended on a host of synergistic factors including migration timing (Renkawitz et al. 2012), predator suites (Hawkes et al. 2013, Goulette et al. 2014), prey fields or foraging behaviors (Renkawitz et al. 2011), and physiological factors influenced by salinity and thermal regimes (McCormick et al. 1998). NEFSC telemetry data has revealed insights into the complexities of behavior, survival, and postsmolt dynamics during the early marine migration.

A US **nearshore pelagic trawl survey** was conducted from 2001-2005 to investigate the ecology of Penobscot River Atlantic salmon postsmolts further into the Gulf of Maine (Sheehan et al. 2011). This effort was the first survey of Atlantic salmon in US territorial waters, and generated novel information on early marine-phase dynamics and ecology of US postsmolts. Several important findings catalyzed subsequent investigations. First, catch rates differed for different release groups, but these proportions were consistent with subsequent adult returns. This suggests that stocking location influenced riverine and estuarine survival, a likely result from dam-related passage impacts (Holbrook et al. 2011), but didn't influence marine survival. Second, dietary analyses demonstrated differences in the type and quantity of prey consumed by postsmolts from different rearing origins (i.e., naturally-reared versus hatchery-stocked; Renkawitz et al. 2011) and may be contributing to the differential mortality observed between these two groups (USASAC 2014). Third, the hypothesized benefits of an Atlantic salmon predator refuge based on the co-occurring species complex in nearshore embayments (Saunders et al. 2006) was considered minimal for emigrating postsmolts given the substantial size mismatch with other species and the low abundance at which those species occurred (Sheehan et al. 2011). Across the Gulf of Maine in Canadian waters, NEFSC researchers collaborated with a Department of Fisheries and Oceans' (DFO) **pelagic trawl survey** conducted in 2002-2003, which captured marked US origin postsmolts approximately 89-240 km from their river of origin, 16-43 d post-release. These marine surveys indicated that postsmolts formed loose aggregations within specific coastal corridors during the migration, suggesting mitigation against potential losses in targeted areas could be possible if appropriate management actions were determined (Lacroix et al. 2012).

The continued evolution of US telemetry efforts has led to new partnerships with a variety of entities, including the **Ocean Tracking Network (OTN)**. US postsmolts are now tracked during their migration through the Gulf of Maine (GOM) via **platforms of opportunity** (i.e., oceanographic buoys, commercial fishing gear, and ocean drifters, Goulette et al. 2014). These partnerships and platforms of opportunity provide significant infrastructure for a wide array of other researchers working on a variety of other species to capitalize on. In addition to the Atlantic salmon detections, over 18,800 detections of 12 species released by 23 organizations have been recorded since 2005. NEFSC efforts have demonstrated that these opportunistic platforms are a low-cost approach, provide benefits to a wide array of researchers and species, and foster dialogue and research sharing to strengthen interdisciplinary and stakeholder communication (Goulette et al. 2014). Further out to sea, detections of US origin postsmolts at OTN telemetry arrays cross the Scotian Shelf, Canada have revealed that postsmolts traverse approximately 600 km in 13-41 d, similar to the approximations in Lacroix et al. (2012). The data obtained from these telemetry projects has allowed for the development of **migration models** that have identified potential trajectories and refined likely ocean migration paths used by postsmolts based on oceanographic features and environmental variables (Byron et al. 2014). These pieces of information are critical to determine if implementation of management actions to improve survival to the Labrador Sea can be undertaken.

Retrospective analyses have also generated new insights into marine survival dynamics. A large-scale marking program for US Atlantic salmon was undertaken from 1962-1996, in which over 1.5 million tagged smolts (primarily Carlin tags) were released in US rivers (Miller et al. 2012a, b). Over 8500 fish were recovered on the high seas: approximately 26% were recovered in Greenland territorial waters, 23% in Canada, and 51% from US waters. Analyses of biological characteristics and environmental variables indicated that the North Atlantic Oscillation, the Atlantic Multi-decadal Oscillation, local sea surface temperatures, and sea age influenced survival relative to US returns (Miller et al. 2012a, b).

Since 2001, the NEFSC has led annual biological sampling and monitoring efforts at the **internal-use West Greenland fishery** NEFSC (ICES 2014, Sheehan et al. 2015). In addition to collecting biological characteristics and harvest related information required for international stock assessment activities, US efforts have focused on continent and country of origin determinations from the West Greenland and other mixed-stock fisheries that US stock contribute to (ICES 2014). Contemporary country of origin determination relies on genetic markers to distinguish the proportional origin of the **Atlantic salmon harvests** in Greenland (King et al. 2001, Sheehan et al. 2010), Labrador (Bradbury et al. 2015), and St. Pierre et Miquelon (ICES 2006). This novel information provides US scientists and managers vital information for international negotiations.

To improve on a broad understanding of the ocean ecology of Atlantic salmon and factors that influence survival, domestic and **international collaborations** have been undertaken. Salmon at Sea (SALSEA) was a large scale international collaborative and multi-disciplinary marine research program designed to follow cohorts of fish from natal rivers to marine feeding grounds and back to spawning grounds on both sides of the Atlantic (ICES 2012). NEFSC scientists partnered with DFO scientists to conduct pelagic ecosystem surveys in the Labrador Sea (**SALSEA North America**) during 2008 and 2009 to sample postsmolts and immature adults originating from North American rivers (Sheehan et al. 2012). While catches were low, multiple smolt cohorts were captured, indicating that postsmolts and returning adults from different rivers in North America have similar autumnal habitat requirements. Postsmolts were only caught at night suggesting they may use deeper habitats during the day as a predator avoidance strategy. Irrespective of life stage, the consumption of diverse and similar prey species and the presence of significant parasite loads suggested Atlantic salmon foraged opportunistically on the available prey base and may have had compromised health via parasitic infestation. A second aspect of SALSEA was a NEFSC coordinated sampling of immature adults salmon at West Greenland (**SALSEA Greenland**) from 2009-2011 to gain insights into the origin, age, growth, diet, trophic ecology, health (disease and parasite) at their summer feeding grounds. Total consumption and diet composition varied among years but not between North American and European stock complexes. A variety or prey were consumed (primarily capelin and *Themisto* sp.) over a broad size spectrum which was similar to historic data from 1965-1971 (Renkawitz et al. 2015). While stable isotope analyses indicated Atlantic salmon are omnivorous, they maintain a high level of dependence on the pelagic food web at sea from which they sequester most of their carbon (Dixon et al. 2012, Dixon et al. *in review*).

Early investigations into the **trophic ecology and resource quality available to** Atlantic salmon expanded as understanding of marine dynamics evolved. Across the North Atlantic, salmon populations have experienced concurrent declines in abundance despite diverse population structures and management regimes. Chaput et al. (2005) identified a **phase shift in marine productivity**, which has altered the survival, productivity, and abundance of Atlantic salmon. It has been hypothesized that poor trophic conditions, likely due to large-scale climate-driven environmental factors and warmer ocean temperatures throughout their marine habitat, are constraining the productivity and recovery of North American populations through bottom-up processes (Mills et al. 2013). The changes in marine climate have resulted in changes in the quality and composition of the zooplankton community (i.e., switch from large energy-rich to small energy-poor species). As a keystone forage species in the North Atlantic, capelin is a primary energetic link between the zooplankton and higher trophic levels. Foraging on lower quality zooplankton has resulted in significant decreased in the size and energy density (~40%) of capelin between 1968 and 2008 (Renkawitz et al. *in review*) and suggests that foraging efficiency is significantly lower than it was 40 years ago. These results suggest that altered trophic dynamics caused by changing ocean conditions negatively influenced Atlantic salmon abundance and likely many other commercially, culturally, and ecologically important species in the Northwest Atlantic.

Deleterious impacts of passage barriers including mortality of migrating juveniles and adults, loss of habitat connectivity, and lax industry regulation have been identified as critical threats to the management, conservation and restoration of Endangered US Atlantic salmon populations (NRC 2004). These are also critical issues for all native diadromous species in the New England watersheds (Lipsky et al. 2012) and work is ongoing to monitor the diadromous species community in the estuary as it relates to Atlantic salmon survival (Stevens et al. 2010). Mitigating these threats first requires a mechanistic understanding of how they impact survival.

Collaborative telemetry programs have been established to track migrating adults during the upstream spawning migration and smolts during downstream emigration to quantify the effects of passage over, though, and around in-river barriers (dams) to understand the impacts on short-term (direct) and long-term (latent) survival of Atlantic salmon (Holbrook et al. 2009, Holbrook et al. 2011, Stich et al. 2014, Sigourney et al. 2015, Stich et al. 2015a, b, c, d). These studies highlight the complex interactive effects of cumulative dam passage under changing river conditions on Atlantic salmon passage efficiency and survival, and demonstrate that direct effects, indirect effects, and latent effects of dam passage have negative consequences on Atlantic salmon survival. Continued work is required to identify the magnitude of, and mitigate against, specific dam-induced threats to Atlantic salmon at different life stages to increase survival and recover the species.

Distinguishing between dam-induced and marine mortality is important to define potential management options that assist Atlantic salmon population restoration. The **PenPass model** (Stevens et al. 2015) was developed to refine survival estimates and determine the historic impact of dams on stocked Atlantic salmon smolts in the Penobscot River Watershed, Maine. Results demonstrated that total cohort survival rate of hatchery smolts reaching the estuary ranged annually from 53.9-93.1% (1970-2012) and was significantly influenced by river discharge and spatial stocking distribution. These results further support the assertions dam impacts influence composition of spawning returns from a smolt cohort (Sheehan et al. 2011), helped further refine the precision and accuracy of stage-specific survival estimates, and will improve future restoration activity planning.

A generic watershed-scale **Dam Impact Analysis (DIA) model** was developed to incorporate biological, environmental, and hydroelectric facility parameters to predict ecological and demographic responses of diadromous fish populations to passage barriers on the Penobscot River, Maine (Nieland et al. 2014, Nieland et al. 2015). This model was used to support Atlantic salmon-specific permitting efforts through the FERC regulatory process for numerous facilities located on the Penobscot River. Model results showed that abundance, distribution, and the number and proportion of wild-origin fish in the upper reaches of the Penobscot watershed increased when dams were removed or passage efficiency was increased. Increasing indirect latent mortality parameters lowered survival, as suggested by field studies (Stich et al. 2015a). Abundance increased as marine or freshwater survival rates were increased, but the increase in abundance was larger when marine survival was increased than when freshwater survival was increased demonstrating the importance of improvements in marine survival to Atlantic salmon recovery. The model design is adaptable and is currently being modified for other river systems and other diadromous species to support future licensing actions.

Low marine survival and barriers to migration at different life stages remain the primary threats to Endangered Gulf of Maine Atlantic salmon populations. Identifying the magnitude of specific spatiotemporal survival bottlenecks during the marine phase is a critical component to determine if management actions can be undertaken to improve survival. Fish passage has a significant influence on the population demographics of other native diadromous species as well and minimizing or eliminating the negative effects of barriers is essential for the recovery diadromous species. By utilizing a multi-method approach (i.e., smolt trapping, marking, acoustic and satellite telemetry, pelagic trawls, fishery sampling, and modeling, etc.) the NEFSC has partitioned the marine phase into several discrete spatiotemporal phases resulting in improvements in the accuracy and precision of stage-specific survival estimates. These studies have increased our understanding of **Atlantic salmon and their ecosystems** significantly and identifying conditions that directly and indirectly influence salmon abundance and productivity is essential for current management and conservation efforts and the eventual recovery of the species and the diadromous species complex as a whole.

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