



Council

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The Effects of Marine Predation on US Stocks of Atlantic Salmon

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Introduction

Predation has long been recognized as a potential factor that limits the abundance of Atlantic salmon (*Salmo salar*) populations throughout their range. In freshwater environments, predation has been relatively well studied and in some cases these studies have led to a more quantitative understanding of the salmon's role in aquatic food webs (e.g., Larsson 1985, van den Ende 1993). However in marine environments, this level of understanding has not been achieved, largely because of the difficulty studying them in ocean habitat due to the varying spatial scales at which populations can be studied in the open ocean, the myriad of potential predators that salmon encounter, and the relatively small role that salmon play in marine food webs (Cairns 2001a). A recent review of the potential causes for declines in salmon abundance (Cairns 2001b) underscores the importance of considering marine predation with five of the leading 12 hypotheses being related to predation. Abundance of remnant US stocks are presently so low that the National Marine Fisheries Service and the US Fish and Wildlife Service recently determined that the Gulf of Maine Distinct Population Segment (DPS) is in danger of extinction throughout its range (65 Fed Reg 69459). These critically low abundance levels exacerbate the problems of understanding the role of predation in structuring US salmon stocks. The purposes of this paper are to summarize our understanding of predation on US stocks of Atlantic salmon since the last comprehensive summary (Anthony 1996) was written, to identify the most critical uncertainties related to salmon predation, and to describe how these could be overcome as we move forward with salmon restoration.

Several recent advances in our understanding of salmon predation have occurred since Anthony (1996) wrote the last comprehensive assessment for NASCO. These advances include both species-specific investigations as well as investigations that clarify the mechanisms for particularly high predation at various life stages, especially as smolts and post-smolts transition to life at sea. We will first consider the recent literature pertaining to species specific interactions.

Seabirds

Northern gannets (*Morus bassanus*) are the largest seabirds in the north Atlantic that can prey on post-smolts throughout their first year at sea (Cairns 2001a). Montevecchi et al. (2002) examined the diets of northern gannets on Funk Island, Newfoundland for 24 years. Atlantic salmon post-smolts comprised between 0 and 6.37% of the northern gannets' diet. Atlantic salmon consumption by northern gannets varied greatly across years but consumption was highest during the 1990s. Overall, northern gannets consumed an estimated 0.22% of North American post-smolt biomass in August from 1977 to 1989 and 2.70% of North American post-smolt biomass in August from 1990 to 2000. The highest consumption of Atlantic salmon occurred in 1993 when northern gannets consumed an estimated 43.4 tons of salmon in August alone. The higher post-smolt predation rates in the 1990s appear to be associated with colder surface water, though many other factors may have affected this shift (e.g., the collapse of ground fish stocks). Tags of salmon from US stocks (Penobscot River, Maine) were found in this

colony. The extent of predation by northern gannets specific to US stocks remains unclear though it is likely to be roughly equal to the overall proportion of the US stock in the Northwest Atlantic mixed stock complex.

Unlike northern gannets, double-crested cormorants (*Phalacrocorax auritus*) have long been recognized as important predators of smolts and post-smolts (Meister and Gramlich 1967). Breeding pairs of cormorants in Maine have increased by 87% between 1977 and 1985 to around 2,900 pairs and this population been stable since the early 1990's (Baum 1997, Anthony 1994). Blackwell et al. (1997) demonstrated that smolts were among the most frequent prey items of double-crested cormorants in the Penobscot River, Maine during the smolt emigration period. Observations by Blackwell et al. (1997) and Blackwell and Krohn (1997) suggest that cormorants prefer to forage near dams where smolts are delayed above the dam and smolts that have gone through the dam are disoriented. These mechanisms may lead to the high levels of predation observed by Moring et al. (1999). Recent studies in eastern Canada also underscore the importance of predation by cormorants on emigrating smolts. Smolts comprised 3.3% of cormorants' diet in the Maritime Provinces during the smolt run (Cairns 1998). This study was not targeted at the major salmon rivers and instead represents an overall assessment of cormorant diet throughout the study area. Thus, overall predation intensity by cormorants is still unknown (Cairns 2001a).

Vulnerability windows have recently been established for most of the major seabird predators of salmon (Cairns and Reddin 2000). Smolts and post-smolts are vulnerable to seabird predation as soon as they leave the river until they attain a critical size at which they are no longer vulnerable to a specific predator. Post-smolts out-grow northern fulmars (*Fulmarus glacialis*), black-legged kittiwakes (*Rissa tridactyla*), and common murrelets (*Uria aalge*) by early July; shearwaters (*Puffinus* spp.) by late July; and gulls (*Larus* spp.) by early September (Cairns and Reddin 2000). This review did not include great cormorants (*Phalacrocorax carbo*) or double-crested cormorants because they are inshore predators and salmon are only available as prey as they migrate through estuaries and near-shore areas. Northern gannets were also not included in this review. However, the vulnerability window to northern gannet predation is known to be considerably wider than other seabirds because of specialized feeding adaptations that allow them to feed on medium-size fish (Cairns and Reddin 2000).

Marine Mammals

Direct evidence of salmon predation by seals in the northwest Atlantic remains sparse. One harbor seal (*Phoca vitulina*), two grey seals (*Halichoerus grypus*), and two harp seals (*Phoca groenlandica*) have been documented with wild salmon remains or tags in their stomachs (Cairns 2001a). Seal predation is better known in the northeastern Atlantic, especially the U.K. where seals affect commercial fisheries (Harwood 1984, Gulland 1987). Predation on free-swimming salmon is not as well documented. Most records of seal predation occur near salmon nets (Pierce et al. 1991).

Harbor seals are of particular concern in Maine, USA where seal bites on returning wild salmon have increased during the last decade (Baum 1997). Harbor seal populations in Maine have increased sharply over the last two decades (Gilbert 2003, pers. comm.). This increase clearly coincides with more bite marks on salmon, however actual consumption of wild Maine salmon by harbor seals has never been recorded.

Harbor seals also pose an indirect threat to endangered salmon by damaging aquaculture net pens. Not only are seal attacks on the pens a significant cause of predation, they also damage nets. These attacks can lead to large escapes of domesticated salmon which may lead to disruption of wild salmon redds, competition for food and habitat, interbreeding with wild salmon, disease transmission, and benthic habitat degradation (Windsor and Hutchinson 1990, Saunders 1991, Webb et al. 1993, Youngson et al. 1993, Clifford et al. 1998). Because the aquaculture industry has become such an important industry to the communities near the DPS rivers, the US is funding an ongoing study to assess the impacts of seal predation on aquaculture sites. From this information, we hope to begin to understand the behavior of seals near pen sites and develop consistent approaches to deter seal predation at pen sites, along with modifications to cage design to decrease losses due to predators.

Another potential salmon predator is the grey seal, which ranges across the north Atlantic to the southern Gulf of Maine, inhabiting both coastal and offshore waters. Predation on salmon in the Gulf of Maine by grey seals has not been documented. However, predation by grey seals has been documented in the northwest Atlantic on two occasions (Cairns and Reddin 2000). Salmon remains have been found in the stomachs of grey seals from the Gulf of St. Lawrence, although no salmon remains were found in the stomachs of grey seals from the Scotian Shelf (Anthony 1994). All other accounts of grey seals feeding on salmon are from the northeastern Atlantic. Salmon predation by seals has been documented in many studies conducted in the U.K. though many incidences of predation are likely net-caught fish (Boyle et al. 1990).

Harp seals are abundant in the north Atlantic and usually inhabit pack ice (Lawson et al. 1998). Harp seal populations in the north Atlantic have increased during the last decade, with breeding populations in Newfoundland, the Gulf of St. Lawrence, and Greenland (Hammill and Stenson 2000). Harp seals feed selectively on capelin (*Mallotus villosus*) and arctic cod (*Boreogadus saida*) but will prey on other available fishes (Lawson et al. 1998). Hammill and Stenson (2000) estimated that Harp seals consumed 82% (3.3 million t) of all food eaten by seals in eastern Canadian waters in 1996. Thus if salmon predation is proportional to overall consumption, harp seals may be important salmon predators even though predation on wild salmon in the northwest Atlantic has only been recorded twice (Cairns and Reddin 2000). Further, the abundance of harp seals appears to be inversely correlated with salmon recruitment in the north Atlantic (Amiro 1998). This correlation, however, may not be due to a cause and effect relationship between seals and salmon (e.g. seal predation on salmon), but attributable to an environmental condition that favors harp seals but reduces salmon recruitment.

Overall, seal predation is likely to have risen substantially over the last decade concurrent with increases in overall seal abundance in the northwest Atlantic. Hammill and Stenson (2000) estimated that overall consumption of salmon by harp, hooded (*Cystophora cristata*), grey, and harbor seals steadily increased from 2,467 t in 1990 to 3,229 t in 1996. However, the vast majority (93% in 1996) of all salmon predation by seals is thought to occur in NAFO areas 4R and 4S (i.e., the western side of Newfoundland). US salmon stocks are thought to migrate through and over-winter on the eastern side of Newfoundland (Meister 1984, Baum 1997). Though this migration pattern is not known with certainty, Hammill and Stenson's (2000) results suggest that post-smolts migrating through and over-wintering on the eastern side of Newfoundland may

have considerably lower predation risks than those on the western side of Newfoundland. However these consumption estimates, and subsequent predation rates, are based on the few records of salmon predation available.

As with seabirds, vulnerability windows were recently established for the major seal predators of salmon (Cairns and Reddin 2000). Vulnerability windows for hooded, harbor, and grey seals are quite variable and depend largely on spatial co-occurrence. Vulnerability for harp seals is more straight-forward with both post-smolts and 1SW salmon being vulnerable throughout the year.

The extent of predation by other marine mammals is still poorly understood. The only indication that cetaceans may prey on salmon is from a single salmonid otolith found in a harbor porpoise (*Phocoena phocoena*) stomach (Cairns 2001b), though Thompson and Mackay (1999) suggest that odontocete cetaceans may have inflicted many of the marks attributed to seals instead. Without meaningful consumption estimates, it is currently impossible to assess the impacts of cetacean predation. However, the distribution of several odontocete cetaceans clearly overlaps the distribution of Atlantic salmon. Furthermore, Pacific salmon (*Oncorhynchus* spp.) have been reported from the stomachs of nine species of cetaceans (Fiscus 1980). Thus, cetaceans may harvest a substantial portion of Atlantic salmon biomass even if salmon are a small portion of their diet (Cairns 2001b).

Fish

Striped bass (*Morone saxatilis*) are presumed to be important predators of smolts and post-smolts as they migrate through nearshore waters. This presumption has recently gained credibility by two studies that documented the intensity (Blackwell and Juanes 1998) and the spatial variability (Beland et al. 2001) of striped bass predation on Atlantic salmon. Blackwell and Juanes (1998) documented striped bass preying on salmon smolts in the tailrace of the Essex Dam on the Merrimack River, Massachusetts, USA. Smolts represented approximately 80% of prey recovered. This was during the peak smolts emigration period (May 6 to May 28) and most smolts were hatchery origin fish either stocked as fry or smolts. In addition, Schulze (1996) demonstrated that the spatial and temporal distributions of striped bass and emigrating smolts in the Connecticut River estuary overlap substantially and further concluded that only early migrating smolts would not be subject to striped bass predation. Striped bass predation has also been documented in the Narraguagus River (Beland et al. 2001), one of the rivers containing an endangered population of Atlantic salmon in eastern Maine, USA (65 Fed Reg 69459). Though the extent of striped bass predation on endangered salmon is still unclear, the risk of population effects upon salmon is presently high given low smolt production (Beland et al. 2001) and high striped bass abundance (Field 1997).

Underlying Mechanisms

Emigrating smolts are subject to intense predation as they enter estuaries (Järvi 1990, Dieperink et al. 2002) and predation rates may approach 25% (Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1987). Thus many researchers consider smolt predation important in structuring salmon populations (Mather 1998). Smolts are especially vulnerable to predation upon entering saltwater because they encounter new habitats and predators while simultaneously being subject to osmotic stress while adapting

to the saltwater environment (Järvi 1989). Stress levels alone may elevate predation risk to emigrating smolts by reducing the amount of energy available for normal activities (Barton and Schreck 1987) such as proper anti-predator behavior (Handeland et al. 1996). Thus the mechanism responsible for the observed high predation rates may be osmotic stress (Staurnes et al. 1996). This problem is likely exacerbated in many Maine rivers where the smoltification process appears to be especially difficult given the low pH experienced by emigrating smolts (Magee et al. 2001). As more energy is required to simply maintain homeostatic balance, less energy is available for normal activities and predator avoidance behaviors appear to be compromised resulting in higher predation rates (Handeland et al. 1996). In addition, episodic acidification, such as those experienced during spring freshets (Whiting 2003), leads to disrupted osmoregulation as smolts transition to seawater (Magee et al. 2003) with mortality often occurring via predation in the wild (Kocik 2003 pers. comm.).

In addition to water quality perturbations, the decreased abundance of other anadromous stocks may also play a role in the perceived elevated predation risks as smolts and post-smolts transition to saltwater. Prior to European settlement, many anadromous species were more abundant than they are today. Many US and southern Canadian rivers historically supported large and diverse anadromous fish populations including alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), American shad (*Alosa sapidissima*), and rainbow smelt (*Osmerus mordax*) in addition to Atlantic salmon. For some stocks, declines have been as dramatic as Atlantic salmon declines. For example, US landings of American shad exceeded 22,000 mt in 1896. Today, landings rarely exceed 2,000 mt and have averaged less than 1,350 mt since 1980 (Kocik 1998). These populations likely served as an important predation buffer allowing predators to focus on more abundant and energy rich prey species (Schulze 1996, Brown et al. 2002). However, some of the same anthropogenic perturbations (e.g., dams, pollution, etc.) that lead to salmon declines have also diminished other anadromous populations (Collette and Klein-MacPhee 2002). The extent to which declines in other anadromous populations have led to higher smolt predation is yet to be assessed quantitatively.

Critical Uncertainties

Sea surface temperature (SST) is another factor that may mediate Atlantic salmon predator-prey dynamics. Accumulating evidence suggests that changes in the SST regime in the northwest Atlantic can fundamentally change predator prey dynamics. For example, Montevecchi et al. (2002) recorded a substantial increase in Atlantic salmon post-smolts in the diet of northern gannets beginning in 1990. This increase coincided with a shift from warm-water to cold-water pelagic prey (Montevecchi and Myers 1997). This shift was likely influenced by colder SSTs in the 1990s that likely inhibited highly migratory, warm-water mackerel (*Scomber scombrus*) and short-finned squid (*Illex illecebrosus*) from moving into the Newfoundland region (Templeman and Fleming 1953 cited in Montevecchi and Myers 1997). The extent to which changes in SST regime are impacting other predator-prey relationships in the northwest Atlantic is largely unknown. The observations by Montevecchi and Meyers (1997) and Montevecchi et al. (2002) were made possible by long-term data sets that span the decadal changes in SST regimes. Thus similar patterns with other species may be occurring without our knowledge because such comprehensive data sets are relatively rare.

Further uncertainty stems from the cumulative, perhaps synergistic (Järvi 1989), nature of the impacts of many anthropogenic perturbations to Atlantic salmon ecosystems. Järvi (1989) described the effects of osmotic stress and stress due to the presence of a predator as synergistic (i.e., greater than the sum of the two effects alone). Similarly, the impacts of dams, elevated predator abundance, and water quality perturbations may be leading to the very high mortality experienced by emigrating smolts in US rivers. For example, the presence of dams alone would likely have minimal impacts to emigrating smolts if the dams only delayed migration and killed a small portion of the total smolt biomass. However, when you consider the habitat preference of double-crested cormorants (Blackwell et al. 1997), the migration delay due to dams (Blackwell et al. 1998), physical striking caused by turbines (Raymond 1988), decreased predator avoidance behaviors due to acid rain (Handeland et al. 1996), and the lack of emigrating Alosids as a predation buffer for emigrating smolts (Brown et al. 2002), a different picture emerges. Many anthropogenic impacts to Atlantic salmon ecosystems appear to cause system-wide destabilizations that are perceived as predator-prey dynamics issues.

Regardless of ultimate causes, many predation issues must be addressed because stocks of Atlantic salmon have been listed as endangered in the US and Canada. There are several approaches to consider as we move forward with Atlantic salmon research and management. Further research is clearly warranted as long as the problems with quantifying marine predation, clearly outlined by Cairns (2001a), are considered. The results of further studies may be problematic for US managers as critically low abundance further exacerbates the problem of even documenting predation in the open ocean. However, Cairns' (2001a) proposed assessments of life history, ocean temperatures, and schooling behavior would clearly provide important insights into the tradeoffs between predation risk and high growth potential. Further examination of novel approaches (e.g., fatty acid signature analysis, genetic analysis of seal scat) to detection and measurement of predation may also produce useful information for identifying localized predation issues.

Several management options for US stocks are available for mitigating particularly high predation events once they are identified. First, non-lethal seal exclusion from a particular estuary could be examined. This approach has recently been shown to deter harbor seal predation on Pacific salmon in British Columbia, Canada (Yurk and Trites 2000) and these techniques may be transferable. Second, open sea releases of hatchery smolts could be used to minimize predation as smolts transition to seawater. This approach increased return rates by as much as 111% in Norway (Gunnerød et al. 1988). In addition to increasing return rates, this study showed, albeit indirectly, the importance of smolt predation in limiting subsequent adult abundance. A third approach to minimize predation losses would be an experimental liming of a river that experiences episodic low pH events. This approach might ameliorate the impacts of low pH (including low calcium and high aluminum concentrations) on the smoltification process and is rapidly gaining support in Maine as a viable strategy to increase smolt survival and subsequent adult returns on such rivers in the DPS. Finally, double-crested cormorant control may become increasingly common as the US Fish and Wildlife Service recently issued a proposed rule (68 Fed Reg 12653) that would authorize state and tribal agencies to implement double-crested cormorant management programs. The proposed rule would change US Fish and Wildlife Service policy to allow state fish and wildlife agencies, federally recognized tribes, and US Department of Agriculture Wildlife Services professionals to lethally take double-crested cormorants without a Federal permit when they are causing damage to public resources (e.g., fish, wildlife, plants, etc.). However, this proposed rule would only

apply to land and freshwater not estuarine or marine environments. Thus, lethal take of double-crested cormorants in estuaries would still require a federal permit even if they were feeding on emigrating smolts. These four management options may seem somewhat drastic but may be worth pursuing given the endangered status of some US and Canadian stocks. Each technique would clearly require an adaptive management approach, including continually evaluating the effects our actions on Atlantic salmon populations.

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