

## Research Article

## A biological risk assessment for an Atlantic salmon (*Salmo salar*) invasion in Alaskan waters

John J. Piccolo<sup>1,2\*</sup> and Ewa H. Orlikowska<sup>3,4</sup>

<sup>1</sup> University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Fisheries Center, 11120 Glacier Hwy, Juneau, Alaska, USA

<sup>2</sup> Current address: Biology Department, Karlstad University, 651 88, Karlstad, Sweden

<sup>3</sup> 4431 Taku Blvd., Juneau, Alaska, USA

<sup>4</sup> Current address: Tjusbolsgatan 3, 654 69, Karlstad, Sweden

E-mail: [john.piccolo@kau.se](mailto:john.piccolo@kau.se) (JJP), [eorlikowska@yahoo.com](mailto:eorlikowska@yahoo.com) (EHO)

\*Corresponding author

Received: 16 February 2011 / Accepted: 20 September 2011 / Published online: 6 October 2011

### Abstract

We present an event-tree biological risk assessment for a non-native Atlantic salmon (*Salmo salar*) invasion into Alaskan waters. Atlantic salmon farming is prohibited in Alaska, USA, but large numbers of them are reared in ocean net-pens in Washington (WA) USA, and British Columbia (BC), Canada. Large numbers of Atlantic salmon escape each year, and they have been recovered in both saltwater and freshwater in WA, BC, and Alaska. There is limited evidence of successful spawning and rearing in BC, but none from Alaska. No stream-reared smolts are known to have returned successfully from ocean migrations, but survey efforts for escaped adults and reared juveniles in streams have been very limited in time and space. Given recurring, large-scale escape events, propagule pressure could be great enough in any given year for a successful invasion. To date, such large numbers of adults have not been recorded ascending Alaskan streams, but again, monitoring is very limited. Atlantic salmon could most likely successfully spawn and rear in Alaskan streams, so successful ocean migration appears to be the factor most likely to limit their success. Successful invasion of BC waters, where propagule pressure is greater, followed by a subsequent invasion of a pre-adapted stock by straying to Alaskan waters, may pose the greatest risk. The lack of adequate surveys, under-reporting of escapes and recoveries, and inherent ecosystem variation, make it impossible to assign meaningful probabilities to the risk of an invasion of Alaskan waters. We conclude that the short-term risk of invasion generally appears low, but that it might increase over time. We also note that invasion is only part of the ecological risk of Atlantic salmon farming in Pacific waters. Disease, parasites, and pollution may also pose risks to local ecosystems – we do not assess these risks here.

**Key words:** Atlantic salmon, salmon farming, biological invasion, Alaska, British Columbia

### Introduction

Atlantic salmon (*Salmo salar* Linnaeus, 1758) are native to the Atlantic coasts of Europe and North America (Mills 1989). Although wild populations of Atlantic salmon have declined severely over the past several hundred years due to human impacts (Netboy 1974; Mills 1989; Fay et al. 2006), Atlantic salmon farming has become a major industry worldwide, and current production exceeds 1,500,000 metric tons per year (FAO 2011). Farmed Atlantic salmon constitute >90 percent of the farmed salmon market worldwide, and >50 percent of the total global salmon market (FAO 2011). Production occurs in the North Atlantic and the North and South Pacific Oceans. Norway, Chile, and the United Kingdom, respectively, and are currently the world's largest producers of farmed Atlantic

salmon, but large numbers are also produced off the Pacific coast of British Columbia (BC) and Washington state (WA) (BCMAL 2010; WDFW 2010).

Farmed Atlantic salmon is the top agricultural product in BC, where production is over 50,000 metric tons per year, 70% of which is exported to the United States (Thorstad et al. 2008; BC MAL 2010). Production in BC has grown steadily since the 1980s, and there are currently 131 salmon farms operating in BC waters, from Vancouver Island north to near Prince Rupert (BCMAL 2010). Production in Washington State is over 5,000 metric tons per year (WDFW 2010). In a typical production cycle juvenile salmon are raised in freshwater hatcheries, then placed in ocean net pens at age 8–16 months, followed by two years of ocean growth before harvest (FAO 2011). Fish are held in high

densities in the net pens, and fast growth is achieved by artificial feeding.

During the development of their aquaculture programs, both WA and BC went through environmental reviews to assess the potential risks of Atlantic salmon culture (Waknitz et al. 2002; Nash 2003; Waknitz et al. 2003; DFO 2010). State and provincial management agencies have had programs to monitor escape events and potential invasions (ADFG 2010, DFO 2010, WDFW 2010), but the geographic scope of this task is enormous, and recent monitoring activity has been limited. Salmon farm owners are required by law to report escape events, and fisheries management agencies in WA and BC have authority to do site inspections of salmon farms. Commercial and sport fishermen are encouraged to report catches of Atlantic salmon, and periodic stream surveys are conducted to search for feral juveniles and adults.

Although the potential for Atlantic salmon invasion in the Pacific Ocean has been considered low (Waknitz et al. 2002; DFO 2010), Bisson (2006) concluded that there is a significant long-term (>5 years) risk of a successful invasion in the Pacific Northwest (PNW) or Alaska. Each year, numbers of farmed salmon in BC and WA escape from their net pens due to weather conditions, equipment failure, or accidental releases (ADFG 2010; CAAR 2010; DFO 2010; PSMFC 2010). In addition, "leakage", i.e., deliberate or accidental releases of slow-growing fish is also a concern (Naylor et al. 2005; ADFG 2002; LOS 2010), although current BC regulations prohibit this practice (BCMAL 2010). The potential for large numbers of fish to escape has raised concerns that Atlantic salmon may successfully invade watersheds in the Pacific Northwest and Alaska (Volpe et al. 2000; ADFG 2002; Naylor et al. 2005; Bisson 2006).

The Alaska Department of Fish and Game (ADFG) considers Atlantic salmon an invasive threat, and they have been active in advocating research and management efforts to minimize the risk of invasion in Alaska. Former Alaska Governors Tony Knowles and Frank Murkowski, and former ADFG Commissioner Frank Rue, have all written official letters calling for restrictions on, or elimination of Atlantic salmon farming in BC (ADFG 2010). ADFG maintains a website with information on identifying and handling Atlantic salmon, with links to reports and other information (ADFG 2010). They

collect data on captures of Atlantic salmon from both random sampling of commercial and sport fisheries, and from voluntary reports (Table 1). They have also published a white paper that summarizes potential risks of an Atlantic salmon invasion in Alaska (ADFG 2002). Currently, however, the website does not include data later than 2004. To date there has been no biologically-based risk assessment to better understand the potential of a successful invasion of self-sustaining populations of Atlantic salmon in Alaskan waters.

Our objective is to use historical data on escapes, combined with a synthesis of the literature on Atlantic salmon life history, to assess the biological risk of an Atlantic salmon invasion in Alaskan waters. We use a life history-based event tree to assess the possibility of a successful invasion, we identify key research and management issues that remain unresolved, and we propose possible solutions to these. We wish to state at the outset that this risk assessment is for an invasion of Alaskan waters only – the risk in WA or BC may be greater due to nearer proximity of salmon farms. Also, this risk assessment does not include the potential dangers of disease, parasites, pollution, or competition with native Pacific salmon, all of which may be substantial (see CAAR 2010).

#### *Overview of Atlantic salmon life history*

Throughout their native range, Atlantic salmon are iteroparous fall spawners (Mills 1989). Adults may enter rivers or streams at nearly any month of the year, depending upon the distance and timing of upstream migration (Baum 1997; Jonsson and Jonsson 2009). In North America, adult migrations into freshwater begin in spring and peak in June, with spawning occurring in October and November; fry emerge in early spring (Baum 1997). Some adults may survive to spawn again, but generally less than 10 percent are repeat spawners (Mills 1989). Juveniles rear for one or more years in freshwater streams before smolting and migrating to sea. Duration of freshwater residence has been shown to be under both genetic and environmental regulation (Metcalf 1998). Duration of time at sea also varies, with some adults returning after one summer, and others remaining for one or more years at sea (Mills 1989). Lake-dwelling landlocked populations of Atlantic salmon are also known from North America and Europe (Behnke 2002; Klemetsen et al. 2003).

**Table 1.** The number of farmed Atlantic salmon reported to have escaped and been recovered from Washington state (WA), British Columbia (BC), and Alaska (AK), 1987-2009. There is little official data since 2006. Sources: Alaska Department of Fish and Game (ADFG), Department of Fisheries and Oceans Canada (DFO), Pacific States Marine Fisheries Commission (PSMFC) websites.

Year	Number of escaped fish reported			Number of recovered fish reported							
	Adults, marine waters		Juveniles, freshwater	Adults, marine waters		Adults, freshwater			Juveniles, freshwater		
	WA	BC	BC	WA	BC	AK	WA	BC	AK	WA*	BC
1987	no data	1	no data	no data	1	no data	no data	1	no data	no data	no data
1988	no data	no data	no data	6	106	no data	no data	no data	no data	no data	no data
1989	no data	no data	no data	52	8	no data	no data	no data	no data	no data	no data
1990	no data	no data	no data	453	2	1	7	3	no data	no data	no data
1991	no data	6,650	no data	1,028	31	7	58	8	no data	no data	no data
1992	no data	9,546	no data	166	349	2	9	48	no data	18	no data
1993	no data	9,000	no data	256	4,543	27	83	23	no data	22	no data
1994	no data	62,809	7,000	378	1,037	27	40	50	no data	57	no data
1995	no data	51,883	941	204	678	23	79	57	no data	82	no data
1996	107,000	13,137	40,000	128	673	135	39	211	no data	191	54
1997	369,000	7,472	10,464	2,271	2,664	77	152	129	no data	7	26
1998	22,639	80,975	300	46	136	155	23	90	1	32	114
1999	115,000	35,954	no data	14	190	19	11	184	no data	68	150
2000	0	31,855	no data	1	7,834	81	1	131	1	147	12
2001	0	55,414	247	2	179	35	no data	116	1	18	3
2002	0	11,257	no data	0	562	6	no data	40	no data	29	8
2003	0	30	no data	19	no data	3	no data	no data	no data	143(394)	no data
2004	24,552	43,969	no data	17	no data	1	21	no data	no data	15(29)	no data
2005	2,500	21	no data	13	no data	3	2	no data	no data	2	no data
2006	0	17	no data	10	no data	1	no data	no data	no data	8(25)	no data
2007	no data	19,223	no data	no data	no data	no data	no data	no data	no data	1	no data
2008	no data	111,769	no data	no data	no data	no data	no data	no data	no data	no data	no data
2009	no data	48,857	no data	no data	no data	no data	no data	no data	no data	no data	no data
Totals	640,691	599,838	58,953	5,054	18,993	602	525	1,091	3	840	367

\*numbers in parenthesis are juvenile Atlantic salmon observed during snorkel surveys, but not captured. The total does not include these fish.

Atlantic salmon share a broad range of thermal tolerance with all species of Pacific salmon (0 – ~25°C), and in fact they can endure slightly higher temperatures (Elliott 1994; McCullough 1999). An excellent table showing referenced thermal tolerances for each life stage can be found at the KRIS Sheepscot website (KRIS 2010). In general, temperature preferences overlap with those of Pacific salmon (McCullough 1999), and it appears unlikely that thermal limitations would prohibit an Atlantic salmon invasion in Alaska.

In summary, Atlantic salmon display the wide variety of life history types and the flexible life history strategies typical of the family Salmonidae (Klemetsen et al. 2003). These are thought to be adaptations to the constantly-changing environmental conditions in recently de-glaciated environments (Hendry and Stearns 2004).

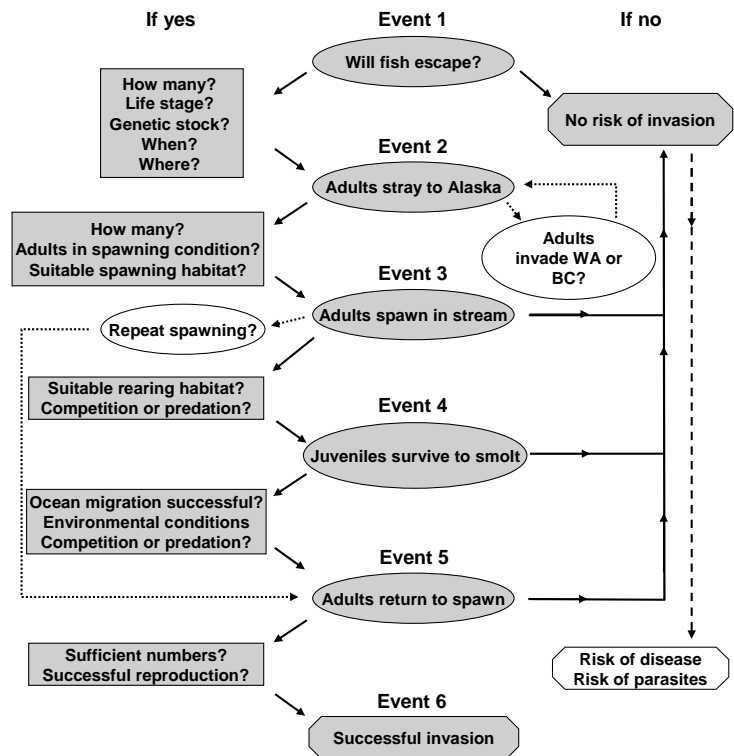
## Risk Assessment

Our risk assessment is based on an event tree that illustrates the steps that would be necessary for a successful Atlantic salmon invasion of Alaskan waters (Figure 1). We use primary literature and reports to provide a qualitative assessment of risk for each event depicted in Figure 1.

### *Event 1: Farmed Atlantic salmon escapes*

From 1990-2009 the reported numbers of adult Atlantic salmon escapes were 599,838 from BC and 640,691 from WA (Table 1). An additional 58,953 juveniles were reported to have escaped in BC, and several hundred from WA. Large escape events of adults, from net pens or from boats during transit, are often due to inclement weather. Juveniles have been reported to have escaped from hatcheries, and also during transit.

**Figure 1.** An event tree for a successful Atlantic salmon invasion in Alaska. Events 1-6, listed in bold, are represented by ovals in the center of the tree. Boxes on the left are qualifiers that allow invasion to proceed to the next event. Octagons are endpoints – either failed, or successful invasion (shaded), or the possibility of parasite/disease transmission (unshaded). The unshaded oval after Event 2 represents the possibility that escaped salmon may invade WA or BC, then follow the subsequent steps necessary to invade Alaska. The unshaded oval after Event 3 represents the possibility that adults may repeat spawn.



The number of fish escaping in WA appears to have declined since 1990, but there was one large escape in 2004, and no data are available after 2006. Large escapes have also continued in BC, with a peak escape of over 100,000 fish in 2008. The numbers of reported escapes do not include leakage, which at one time was estimated at approximately 350,000 fish per year (ADFG 2002). Leakage occurs when fish are transferred to pens with larger mesh size, after which smaller, slower-growing fish are able to escape freely through the nets. These fish are called “non-performing” by salmon farmers, and their loss is considered a normal part of business costs. Although leakage is currently prohibited by BC law (BCMAL 2010), it is still considered a threat (Naylor et al. 2005; LOS 2010).

The frequency and magnitude of escape events might be expected to decrease as industry practices improve. Due to the nature of salmon farming, however, large accidental escapes are likely to continue to occur sporadically. For example, since 2004, large escapes have occurred in both WA and BC, despite recent efforts to improve holding facilities.

Although reporting escapes is required by law, there is evidence that at least some large escapes may go unreported (Morton and Volpe 2002; LOS 2010). Morton and Volpe (2002), for example, reported 10,826 Atlantic salmon captured in BC waters during their 17-day survey in summer 2000. To date, however, both the DFO and ADFG websites still list the total number of recoveries from BC in 2000 as 7,834. From the standpoint of assessing biological risk, substantial under-reporting of escapes, combined with any escapes due to leakage, make it difficult to assign meaningful probabilities to the proportion of fish that stray to Alaska (see Event 2).

In summary, accidental escapes, combined with potential leakage, suggest that escaped Atlantic salmon will continue to be present in Pacific marine waters as long as farming continues. These fish serve as a potential parent stock for invasion. Prompt and complete reporting of dates, locations, and numbers of escaped fish is necessary in order to assess the possibility that fish may enter Alaskan waters.

*Event 2: Adults stray to Alaska: reported recoveries, migration and behavior, propagule pressure and Allee effects*

Between 1987 and 2006, 24,649 Atlantic salmon were reported to have been captured in Pacific marine waters, 602 (2.4%) of which were reported from Alaskan waters. Reported catches in Alaska peaked at 155 fish in 1998, and have declined to less than 10 per year since 2002. The 155 fish captured in 1998 represented 0.14% of the total 111,607 fish reported to have escaped in that year. The great majority of reports from Alaska have been from southern Southeast port sampling (ADFG 2010), but fish have been found as far north as the Bering Sea (Brodeur and Busby 1998). One recent adult recovered from Cook Inlet in Alaska was identified by an otolith thermal mark to have originated from a Washington farm, but the origins of most fish are unknown. Currently, WA requires thermal marking of Atlantic salmon, but BC does not. This makes it impossible assign an escape location or date to recovered BC salmon, so migration speed and distances cannot be estimated.

Migration patterns of escaped Atlantic salmon in the North Pacific Ocean have not been researched, but recoveries show that they commonly migrate to Southeast Alaska, and occasionally to the northern Gulf of Alaska (GOA) and the Bering Sea (ADFG 2002). Whether any of the migrants to Alaska return to BC or WA is unknown. Many stocks of Pacific salmon from WA and BC migrate through Southeast Alaska and into the northern GOA, where they spend one or more years (Groot and Margolis 1991; Quinn 2005). These fish are thought to migrate within the Alaska Current, which runs north along the coast from southern BC into the northern GOA. To what extent Atlantic salmon follow these migration routes is unknown, but this may influence whether they return south when mature, or seek Alaskan streams to spawn. Thermal marking of otoliths for BC salmon farms would facilitate a better understanding of migration patterns, because fish could be assigned to a location, and possibly a date, of escape. Also, research to document the migratory life histories of the wild Atlantic salmon from which WA and BC brood stocks are descended might offer clues as to their potential migration behavior in the Pacific Ocean.

Waknitz et al. (2003) suggested that poor foraging ability of escaped Atlantic salmon may

minimize the risk of negative interactions with Pacific salmon, and reduce their ocean survival. The limited research on feeding behavior of escaped Atlantic salmon indicates that they are capable of foraging on a variety of fish and invertebrate prey, although foraging success is not great (Brodeur and Busby 1998; Soto et al. 2001; Morton and Volpe 2002). Morton and Volpe (2002) reported that the diet of Atlantic salmon may overlap with Pacific salmon to some extent, and they found one incidence of predation on a Pacific salmon smolt. They also found that the percentage of fish foraging on wild prey increased over a 14-day period, suggesting that escaped fish have improved foraging success over time. Soto et al. (2001) found that in Chile, escaped Atlantic salmon tended to stay near net pens to forage on pellet food, and that they had poorer foraging success than did escaped rainbow trout or coho salmon. Whether or not escaped salmon would need to forage in order to become sexually mature and spawn has not been addressed, but Volpe et al (2000, 2001b) provide strong evidence for at least one successful spawning of farmed salmon in BC streams. No other events have thus far been documented.

*Propagule pressure and Allee effects*

The probability of a successful biological invasion increases with propagule pressure, i.e. the number of organisms introduced (Kolar and Lodge 2001). Conversely, Allee effects are predicted to decrease the probability that a small population will persist, due to invaders having difficulty finding mates (Drake 2004). Drake and Lodge (2006) provide a population biology model of invasion by an invasive species by combining the concepts of propagule pressure and Allee effects. They estimate that for a population without Allee effects, the probability of a successful invasion will approach 100% with ~40 individuals with no additional immigration (i.e. a one-time event, or low propagule pressure). With increasing immigration rates, initial populations as low as 10 individuals may be successful over time. Adding Allee effects to the model increases the initial population size required for a 100% probability of invasion to ~100 individuals at all but the highest immigration rates. Based on Drake (2004) Atlantic salmon would be expected to display an Allee effect, although there is little documentation of this in any fish population (Liermann

and Hilborn 1997). Assuming an Allee effect and no immigration (i.e. a one time straying event to a given stream), ~100 individual Atlantic salmon would need to ascend and successfully spawn in an Alaskan stream to invade it. To date, only three Atlantic salmon have been documented in freshwater streams in Alaska, each in different years (see below).

There are a number of difficulties in developing a risk assessment for Atlantic salmon in Alaskan waters based on propagule pressure. The numbers of adult fish entering Alaskan marine waters each year are extremely uncertain. The numbers of reported Atlantic salmon peaked at 155 in 1998, and have declined since then. These numbers are problematic because the potential of unreported fish is high, and the catch represents an unknown fraction of the fish at large. Many Atlantic salmon probably go unreported because of difficulty in identifying them, or lack of incentive to report them. The majority of the 600 recovered fish were sampled randomly at ports, presumably by ADFG personnel (ADFG 2010). It is unknown what percentage of port samplers are trained to identify Atlantic salmon, but the task can be so difficult that Nielsen et al. (2003) suggested that all reported fish be confirmed by genetic analysis. Furthermore, the recent recovery of Atlantic salmon with no spots on their heads has raised concerns that identifying and reporting escaped fish recovered in fisheries may become more difficult (head spots are a commonly-cited way to identify Atlantic salmon) (Morton and Volpe 2002). The numbers of fish in Alaskan waters must be considerably greater than the number of reported captures. Rough estimates are that in recent years up to 700 Atlantic salmon are caught per year, and that 3000 are present in Alaskan waters per year (ADFG 2002). The methods used to develop these estimate, however, are undocumented.

To date, only three adult Atlantic salmon have been recovered from streams in Alaska, one in each of three years, and all in different locations (Table 1). A pair of adults was reported from Ward Creek, near Ketchikan, but only one was captured. Estimates of the numbers of adult Atlantic salmon ascending streams, however, is just as uncertain as are estimates of the numbers in marine environments. Counts of adult spawning salmon are conducted on a limited number of reference streams each year by ADFG personnel. The great majority of these are done by aerial survey making identification impossible, and most are done during the late

summer/early fall. Adult Atlantic salmon, however, may enter streams during almost any month of the year (Baum 1997), and they tend to spawn later than do Pacific salmon, so they could go undetected. The only opportunity for adults to be recovered by biologists in freshwater would be during weir or foot surveys, and these are conducted on only a few streams per year. The possibility of anglers reporting sport-caught Atlantic salmon also exists, but again, identification can be difficult, and reporting incentive may be low.

Given the difficulties of estimating the numbers of Atlantic salmon in both marine and freshwater habitats in Alaska, any attempt to quantify propagule pressure would be trivial. What can be said is that propagule pressure in Alaska: 1) appears to have declined in recent years (Table 1), 2) may increase if the number of salmon farms in northern BC increases, and 3) can increase unpredictably due to a large escape event. If the rough estimate of 3,000 fish present in Alaskan waters is used (ADFG 2002), it is possible that groups of 100 or more fish traveling together that could find a spawning stream. To date there is no evidence that this has occurred in Alaska.

The lack of the ability of Atlantic salmon to successfully establish populations during early stocking efforts is commonly cited as justification that the risk of farmed salmon invasion Pacific watersheds is very low (Alverson and Ruggerone 1997; Waknitz et al. 2002; Nash 2003). Seeb et al. (2003), however, suggested that propagule pressure is much greater currently than it was in the past, when deliberate releases of Atlantic salmon were undertaken in order to establish populations in the Pacific Northwest (MacCrimmon and Gots 1979). They compared the number of juveniles intentionally released between 1951–1991 (76,000 total) with estimates of the number of adult net pen escapes between 1996–1999 (>400,000 total). They further note that net pen escapes occur across a broader geographic area, they come from multiple brood sources (i.e. greater genetic variation), and that they occur at multiple life stages. Their analysis does not include the following factors, which may also play a role in successful invasion: 1) adult farmed salmon have been acclimated to the Pacific marine environment, 2) farmed salmon are usually much closer to reproductive age than were intentionally-released fry or smolt; they are well-fed and in good condition, 3) overall

mortality of adults would be expected to be much lower than it would for juveniles released in streams, due to both duration of marine residence and size-selective mortality.

#### Invasion of WA or BC and subsequent invasion of Alaska

In Figure 1, after Event 2, we show the possible event that Atlantic salmon may become established in WA or BC, and subsequently invade Alaska from there. In this case the subsequent Events 3–6 would be the same, i.e. if adults from an established BC population stray to Alaska, Events 3–6 still need to occur for successful invasion. The likelihood of fish being successful at Events 3–6, however, may be greater in the case of invasion via an established population. Gross (1998) and Bisson (2006) both suggest that farmed Atlantic salmon may be selected to survive better under Pacific Ocean conditions over time. Because propagule pressure in WA and BC streams has historically been much greater than is presumed for Alaskan streams (Table 1), it is likely that an initial invasion would occur there, and there is evidence of natural reproduction in Tsitika River, BC (Volpe et al. 2000). There is no evidence, however, of any of these fish having smolted and returned as adults to spawn. Nor is there evidence of any further reproduction in BC waters, although survey effort has been limited.

If a self-sustaining population of Atlantic salmon were to become established in BC, individuals would be expected to have at least some adaptations related to spawning, rearing, smolting, and ocean migration. Because salmon often colonize new environments by straying from their natal streams (Milner and Bailey 1989; Quinn et al. 2001), these populations might be expected to invade Alaska over time. Straying is considered an adaptation that allows salmon to colonize new habitats in the face of changing environmental conditions (Thorpe 1994; Nickelson and Lawson 1998). Straying rates of 6% have been reported for wild Atlantic salmon (Jonsson et al. 2003).

We note here that fish from locally-adapted feral populations would be more likely to succeed at each of Events 2–6, because all of these are dependent in part upon fish surviving in novel environments. In light of this we recommend close cooperation with WA and BC fisheries agencies in monitoring Atlantic salmon recoveries throughout the Pacific Northwest.

#### *Event 3: Escaped Atlantic salmon spawning in freshwater streams*

Although farmed salmon are generally believed to have lower spawning success than do wild salmon (e.g. Jonsson and Jonsson 2006), there is clear evidence from British Columbia, the British Isles, Chile, and Norway, that farmed Atlantic salmon are capable of spawning successfully in the wild (Hansen et al. 1998, Thorstad et al. 2008; Ekinaro et al. 2010). Volpe et al (2000) concluded that escaped Atlantic salmon had successfully reproduced in Tsitika River drainage, BC. They did not document spawning behavior, but inferred reproduction from multiple age classes of juveniles. Suspected wild juvenile salmon have also been recovered from two other streams in BC, suggesting possible reproduction in these as well (Table 1). To date there are no other records of escaped Atlantic salmon spawning in Pacific coast streams, although surveys for adults are limited (see Event 2), as are those for juveniles (see Event 4).

Bisson (2006) suggested that Atlantic salmon may compete with Pacific salmon for spawning areas. This appears unlikely in Alaska, because Atlantics tend to spawn later in the year (September–October) than do pink, chum, and sockeye (July–August), the most common native salmon (Groot and Margolis 1991; Halupka et al. 2000). This, in fact may allow Atlantic salmon to superimpose redds over those of native salmon, giving them a potential advantage in percentage of eggs that hatch (Fukushima et al. 1998). Competition for spawning habitat might be most likely between Atlantic and Chinook salmon both of which typically spawn in relatively fast and deep water, and, in Alaska, possibly at the same time of year (Mills 1989; Groot and Margolis 1991). In Great Lakes tributaries Chinook have been found to impede recovery of native Atlantic salmon because of competition during spawning (Scott et al. 2003). Competition between Atlantic and coho salmon might be less likely, because coho tend to spawn in small tributaries (Groot and Margolis 1991), whereas Atlantics prefer larger streams (Mills 1989). Atlantic salmon in northern latitudes spawn at temperatures down to or below 5°C (Jonsson and Jonsson 2009), which broadly overlaps with spawning temperatures for Pacific salmon in Alaska (Groot and Margolis 1991).

Most recoveries of Atlantic salmon in marine waters of Alaska have been in Southeast Alaska

(ADFG 2010), probably because of the proximity to BC salmon farms. Southeast has thousands of anadromous salmon streams, with pink and chum salmon being by far the most abundant species, so overlap in spawning timing may not be likely. Many of these streams would have suitable spawning habitat (i.e. streamflow, substrate) for Atlantic salmon. If sufficient numbers were to ascend a stream, it seems likely that they would find suitable habitat, and limited, if any, competition for spawning there.

*Event 4: Juveniles survive freshwater phase until smolting*

A successful invasion by Atlantic salmon will require them to out-compete or coexist with native Pacific salmon during the freshwater juvenile phase, which may last one-two years. Volpe et al. (2001a) investigated the potential for competition between juvenile Atlantic salmon and native BC steelhead in laboratory stream channels. They concluded that Atlantic salmon are capable of competing successfully against native steelhead, particularly if they were prior residents. Most research suggests that size and prior residence are key factors in determining the outcome of competitive interactions among stream salmonids (see Volpe et al. 2001). Other studies have concluded that the outcome of competition between Atlantic and species of Pacific salmon is dependent upon environmental and biological conditions (Gibson 1981; Hearn and Kynard 1986), and still others have concluded that habitat segregation between Atlantic and Pacific salmonids may allow both to coexist, in some cases allowing for increased overall production (Raffenberg and Parrish 2003).

Bisson (2006) reviewed the literature on juvenile life histories of Atlantic and Pacific salmon in an effort to assess the risk of a successful Atlantic salmon invasion in the Pacific Northwest and Alaska. He concluded that feral juvenile Atlantic salmon have the potential to compete successfully with native Pacific salmonids, particularly steelhead and cutthroat trout. Because Atlantic salmon are fall spawners, their fry would emerge earlier than those of spring-spawning steelhead and trout, giving them a potential size and prior-residence advantage. The potential for competition with steelhead is of particular concern in Alaska, where the species is considered sensitive due to relatively small

spawning populations in many streams (Lohr and Bryant 1999). Effects on other Pacific salmonids would likely include competition for food resources, due to a general overlap of diet among stream salmonids.

To date, no juvenile Atlantic salmon have been found in Alaskan streams. Specific efforts to document their presence, however, have been very limited (i.e. snorkel observations in parts of three streams during one season). In addition, although sampling of juvenile Pacific salmon occurs each year in Alaska, the percentage of biologists or technicians that have been trained specifically to identify juvenile Atlantic salmon is unknown.

In general, the outcome of competition between native and non-native salmonids is difficult to predict. Fausch (1988, 1998) reviewed the literature on competition between Atlantic salmon and other stream salmonids. He found that evidence for competition was based largely on empirical observations, and that the underlying mechanisms remain poorly understood. Studies have been plagued with difficulties, such as lack of replication or poor experimental design. This makes it difficult to extrapolate the results across temporal or spatial scales, so the evidence for competition is largely restricted to the individual study sites during the specific times when the studies were conducted. The best available evidence suggests that at least in some cases, juvenile Atlantic salmon will be able to out-compete or coexist with native Pacific salmonids.

*Event 5: Stream-reared smolts return as adults to spawn*

The lack of the ability of Atlantic salmon to successfully establish populations during early stocking efforts is commonly cited as justification that the risk of farmed salmon invading Pacific watersheds is very low (Alverson and Ruggerone 1997; Waknitz et al. 2002; Nash 2003). Despite years of deliberate stocking of juvenile Atlantic salmon in streams worldwide, very few self-sustaining populations have become established outside their native range (MacCrimmon and Gots 1979; Thorstad et al. 2008). Also, although large numbers of feral juveniles have been observed in streams (Table 1), there are no documented cases of wild-reared smolts returning as adults to these streams to spawn. Stocking of anadromous salmonid



species in general has usually resulted in failure (Huey et al. 2005), with the notable exception of Chinook salmon in New Zealand (Quinn and Unwin 1993), and most recently in South America (Correa and Gross 2008). It seems likely that the difficulties in surviving and completing an ocean migration in an environment to which they are not pre-adapted is a major factor in limiting colonization by anadromous salmon (see Event 2). Introductions of landlocked Atlantic salmon to lakes outside of their native range have been successful (Behnke 2002; Thorstad et al. 2008) – presumably survival and migration in a novel lake is less problematic than it is in a novel ocean environment.

Although the survival and return of smolts as adults appears to be the event most likely to prohibit an Atlantic salmon invasion in Alaska, Gross (1998) and Bisson (2006), suggest that salmon-farm broodstock may be selected for at least some adaptation to Pacific ocean conditions over time. This could make it more likely for them to survive ocean migrations. Biological data on survival of Atlantic salmon smolts in the Pacific is not likely to be forthcoming because any smolts captured would not be released. Examination of scale patterns of captured adults might indicate whether they had been farm- or stream-reared, but we are unaware of any efforts to assess this. Also, otolith marking of all farm-reared fish would be a powerful tool to help biologists determine if captured adults were stream-reared. ADFG has a world-leading program on otolith marking and recovery (<http://www.taglab.org/>), which is considered to be low-cost and highly reliable. They could likely provide accurate estimates of the costs of marking and mark recovery.

#### *Event 6: Successful invasion: Evidence for Atlantic salmon invasions outside their native range*

There is currently no documented case of a self-sustaining feral population of Atlantic salmon in Washington, British Columbia, or Alaska. Successful spawning of adults and rearing of juveniles in Tsitika River, BC has been documented (Volpe et al. 2000). Follow-up surveys of Tsitika River in 2001, however, did not document presence of either adult or juvenile Atlantic salmon (DFO 2010). There are documented cases of escaped farm-raised

Atlantic salmon establishing self-sustaining populations in Europe, South America, and New Zealand (MacCrimmon and Gots 1979; Soto et al. 2001; Pascual et al. 2002; Naylor et al. 2005). In Europe these have been within the native range of Atlantic salmon, and presumably the fish were pre-adapted to local conditions, particularly ocean migrations. In South America and New Zealand, only landlocked (i.e. lake) populations have become established.

#### *Risk of parasites and disease*

In addition to the risk of invasion, strong concern has also been expressed that Atlantic salmon farming may introduce disease or parasites to native salmon, whether or not fish escape (Naylor et al. 2005; Bisson 2006; Krkosek et al. 2006a). There is strong evidence, for example, that sea lice from Atlantic salmon farms have negative effects on wild Pacific salmon, and this is currently a hotly debated issue in British Columbia (Brooks 2005; Morton et al. 2005; Krkosek et al. 2006a; Krkosek et al. 2006b). Conversely, it has been suggested that risk of disease spreading from farmed fish to wild fish is low (Nash 2003). There is an immense body of literature on parasites and disease in farmed fish, and this issue clearly warrants further consideration.

#### **Conclusions**

Volpe (2001) stated that all potential ecological effects of Atlantic salmon farming in BC are simply unknown. Our risk assessment of an invasion in Alaskan waters supports this assertion, in terms of assigning probabilities to any given events: lack of ecological surveys, possible under-reporting of escapes and recoveries, and the inherent variation in ecosystem responses, make it impossible to assign meaningful probabilities to the risk of invasion. We concur with Bisson (2006) that the short term (<5 yr) risk of a successful invasion of Alaska by Atlantic salmon appears to be low. To date only three adults and no juveniles have been reported from Alaskan streams. Unless there are feral populations that are currently undocumented, it is difficult to envision an invasion occurring in the short term. We also concur with Bisson (2006) that the long-term risk (>5 years) of invasion is greater, particularly in the case of a locally-adapted, feral stock

spreading along the coast after an initial invasion in WA or BC. Increased propagule pressure, in the case of increased production and/or northward expansion of farm locations, may also increase the long-term risk of a successful invasion in Alaska. Although Atlantic salmon farming remains prohibited in Alaska, provincial regulations in BC are currently under review, the outcome of which will influence potential propagule pressure in BC and Alaska (BCMAL 2010). Our event tree analysis suggests that ocean migration and survival of either escaped adults or stream-reared smolts are the factors most likely to limit an invasion. We also agree with Bisson (2006) and Naylor et al. (2005), however, that invasion only represents a portion of the biological risk of Atlantic salmon farming to native Pacific salmon, and to Pacific ecosystems. Parasites, disease, and pollution appear to pose at least as great a risk.

### Recommendations

Unless pen-culture of Atlantic salmon in WA and BC is outlawed, which is unlikely, there will continue to be a risk of invasion in Alaska for the foreseeable future. Our analysis highlights the difficulties in assigning a meaningful probability to this risk. To best manage the risk, therefore, we recommend the following:

1. Insure adequate and timely reporting of all escaped Atlantic salmon. This may require additional government oversight.

2. Improve reporting of recoveries: this will require improved training and outreach efforts to insure that biologists and sport and commercial fisherman are able to identify Atlantic salmon.

3. Close cooperation among Alaska, WA, and BC fisheries agencies in monitoring Atlantic salmon recoveries throughout the Pacific Northwest.

4. Elimination of feral populations that become established in WA or BC. This would greatly reduce the likelihood of an invasion in Alaska.

5. Development of otolith marking of all farm-raised Atlantic salmon – codes should be unique to date and fish farm location.

6. Conduct systematic sampling for Atlantic salmon in fresh- and saltwater – this might best be achieved by simply coordinating with ongoing surveys for Pacific salmon, through training survey crews to accurately identify Atlantic salmon.

### Acknowledgements

J.P. was partially funded by the Biology Department, Karlstad University, Sweden. This project was funded by the U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.

### References

- ADFG (2002) Atlantic salmon: a white paper. Alaska Department of Fish and Game website. [http://www.adfg.state.ak.us/special/as/docs/as\\_white2002.pdf](http://www.adfg.state.ak.us/special/as/docs/as_white2002.pdf) (Accessed 27 September 2010)
- ADFG (2010) Atlantic salmon are considered to be an invasive threat. Alaska Department of Fish and Game website. [http://www.adfg.state.ak.us/special/as/as\\_home.php](http://www.adfg.state.ak.us/special/as/as_home.php) (Accessed 27 September 2010)
- Alverson DL, Ruggerone GT (1997) Escaped farm salmon: environmental and ecological concerns. Prepared for the BC Environmental Assessment Office, Salmon aquaculture review. Natural Resources Consultants, Seattle
- BCMAL (2010) British Columbia Ministry of Agriculture and Lands Website. [http://www.al.gov.bc.ca/fisheries/bcsalmon\\_aqua.htm](http://www.al.gov.bc.ca/fisheries/bcsalmon_aqua.htm) (Accessed 27 September 2010)
- Baum ET (1997) Maine Atlantic Salmon: A National Treasure. Atlantic Salmon Unlimited. Hermon, ME, 224 pp
- Becker LA, Pascual MA, Basso NG (2007) Colonization of the southern Patagonia ocean by exotic chinook salmon. *Conservation Biology* 21:1347–1352, <http://dx.doi.org/10.1111/j.1523-1739.2007.00761.x>
- Behnke RJ (2002) Trout and salmon of North America. The Free Press, New York
- Bisson PA (2006) Assessment of the risk of invasion of national forest streams in the Pacific Northwest by farmed Atlantic salmon. USDA Pacific Northwest Research Station General Technical Report PNW-GTR-697, Portland, 28 pp
- Brodeur RD, Busby MS (1998) Occurrence of an Atlantic salmon *Salmo salar* in the Bering Sea. *Alaska Fisheries Research Bulletin* 5:64–66
- Brooks K (2005) The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. *Reviews in Fisheries Science* 13: 177–204, <http://dx.doi.org/10.1080/10641260500207109>
- CAAR (2010) Escapes and alien species. Coastal Alliance for Aquaculture Reform website. <http://www.farmedanddan.gov.org> (Accessed 4 October 2010)
- Correa C, Gross MR (2008) Chinook salmon invade southern South America. *Biological Invasions* 10: 615–639, <http://dx.doi.org/10.1007/s10530-007-9157-2>
- DFO (2010) Department of Fisheries and Oceans, Canada. Atlantic salmon watch program (ASWP). <http://www.pac.dfo-mpo.gc.ca/science/aquaculture/aswp/index-eng.htm> (Accessed 27 September 2010)
- Drake JM (2004) Allee effects and the risk of biological invasion. *Risk Analysis* 24: 795–802, <http://dx.doi.org/10.1111/j.0272-4332.2004.00479.x>
- Drake JM, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. *Biological Invasions* 8: 365–375, <http://dx.doi.org/10.1007/s10530-004-8122-6>
- Elliott JM (1994) Quantitative Ecology and the Brown Trout. Oxford University Press, Oxford
- Ekinaro J, Niemelä E, Vähä J-P, Primmer CR, Brørs S, Hassinen E (2010) Distribution and biological characteristics of escaped farmed salmon in a major subarctic wild salmon river: implications for monitoring. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 130–142, <http://dx.doi.org/10.1139/F09-173>

- FOCS (2010) Friends of Clayoquot Sound website. <http://www.focs.ca/news/050201.asp> (Accessed 27 September 2010)
- FAO (2011) *Salmo salar* (Linnaeus, 1758). FAO Species Fact Sheets, <http://www.fao.org/fishery/species/2929/en> (Accessed 16 September 2011)
- Fausch KD (1988) Tests of competition between native and introduced salmonids in streams: What have we learned? *Canadian Journal of Fisheries and Aquatic Sciences* 45: 2238–2246, <http://dx.doi.org/10.1139/f88-260>
- Fausch KD (1998) Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): On testing effects and evaluating the evidence across scales. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Suppl. 1):218–231
- Fay C, Bartron M, Craig S, Hecht A, Pruden J, Saunders R, Sheehan T, Trial J (2006) Status review for anadromous Atlantic salmon (*Salmo salar*) in the United States. Report to the National Marine Fisheries Service and U.S. Fish and Wildlife Service, 294 pp. <http://www.nmfs.noaa.gov/pr/species/statusreviews.htm> (Accessed 7 October 2010)
- Fukushima M, Quinn TJ, Smoker WW (1998) Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 618–625, <http://dx.doi.org/10.1139/f97-260>
- Gibson RJ (1981) Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*) at the juvenile fluvial stage. Canadian Technical Report of Fisheries and Aquatic Sciences 1029, 121 pp
- Groot C, Margolis L (1991) Pacific salmon life histories. UBC press, Vancouver, 564 pp
- Gross MR (1998) One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Canadian Journal of Fisheries and Aquatic Sciences* 55:131–144, <http://dx.doi.org/10.1139/d98-024>
- Halupka KC, Bryant MD, Willson MF, Everest FH (2000) Biological characteristics and population status of anadromous salmon in southeast Alaska. U S Forest Service General Technical Report PNW-GTR-468, pp 1–255
- Hansen LP; Windsor ML, Youngson AF (1998) Interactions between Salmon Culture and Wild Stocks of Atlantic salmon: The Scientific and Management Issues. Introduction. *ICES Journal of Marine Science* 54: 963–964, <http://dx.doi.org/10.1006/jmsc.1997.9998>
- Hearn WE, Kynard BE (1986) Habitat utilization and behavioral interaction of juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*S. gairdneri*) in tributaries of the White River of Vermont. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1988–1998, <http://dx.doi.org/10.1139/f86-244>
- Hendry AP, Stearns SC (2004) Evolution Illuminated: Salmon and their relatives. Oxford University Press, Oxford, 520 pp
- Huey R B, Gilchrist GW, Hendry AP (2005) Using invasive species to study evolution: case studies with *Drosophila* and Salmon. In: Sax DF. et al. (eds), Species Invasions: Insights into Ecology, Evolution and Biogeography, Sinauer Associates, Sunderland, pp 139–164
- Jonsson B, Jonsson N, Hansen LP (2003). Atlantic salmon straying from the River Imsa. *Journal of Fish Biology* 62: 641–657, <http://dx.doi.org/10.1046/j.1095-8649.2003.00053.x>
- Jonsson B, Jonsson N (2006) Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *ICES Journal of Marine Science* 63: 1162–1181, <http://dx.doi.org/10.1016/j.icesjms.2006.03.004>
- 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 relevance to water temperature and flow. *Journal of Fish Biology* 75: 2381–2447, <http://dx.doi.org/10.1111/j.1095-8649.2009.02380.x>
- KRIS (2010) Water temperature and Gulf of Maine Atlantic salmon. KRIS Sheepscot website, [http://www.krisweb.com/kris/sheepscot/krisdb/html/krisweb/stream/temperature\\_sheepscot.htm](http://www.krisweb.com/kris/sheepscot/krisdb/html/krisweb/stream/temperature_sheepscot.htm)
- Klemetsen AP, Amundsen A, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, 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, <http://dx.doi.org/10.1034/j.1600-0633.2003.00010.x>
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199–204, [http://dx.doi.org/10.1016/S0169-5347\(01\)02101-2](http://dx.doi.org/10.1016/S0169-5347(01)02101-2)
- Krkosek MM, Lewis M, Morton A, Frazer N, Volpe J (2006a) Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences of the United States of America-Biology* 103: 15506–15510
- Krkosek MM, Lewis M, Volpe J, Morton A (2006b) Fish farms and sea lice infestations of wild juvenile salmon in the Broughton Archipelago—a rebuttal to Brooks (2005). *Reviews in Fisheries Science* 14: 1–11
- LOC (2010) Escaped Atlantic salmon. Living Oceans Society website. [http://www.livingoceans.org/programs/fishfarms/environment/escaped\\_salmon.aspx](http://www.livingoceans.org/programs/fishfarms/environment/escaped_salmon.aspx) (Accessed 4 October 2010)
- Liermann M, Hillborn R (1997) Depensation in fish stock: a hierarchical Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1976–1984, <http://dx.doi.org/10.1139/cjfas-54-9-1976>
- Lohr SC, Bryant MD (1999) Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. USDA Pacific Northwest Research Station General Technical Report PNW-GTR-407. Juneau, 29 pp
- MacCrimmon HR, Gots BL (1979) World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada* 36:422–457, <http://dx.doi.org/10.1139/f79-062>
- McCullough D (1999) A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. U.S. Environmental Protection Agency. EPA 910-R-99-010, 279 pp
- Metcalf NB (1998) The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 55 (Suppl. 1): 93–103, <http://dx.doi.org/10.1139/d98-005>
- Mills DH (1989) Ecology and management of Atlantic salmon. Chapman and Hall, London, 372 pp
- Milner AM, Bailey RG (1989) Salmonid colonization of new streams in Glacier Bay National Park, Alaska. *Aquaculture Research* 20: 179–192, <http://dx.doi.org/10.1111/j.1365-2109.1989.tb00343.x>
- Morton A, Routledge RD, Williams R (2005) Temporal patterns of sea louse infestation on wild Pacific salmon in relation to the fallowing of Atlantic salmon farms. *North American Journal of Fisheries Management* 25: 811–821, <http://dx.doi.org/10.1577/M04-149.1>
- Morton A, Volpe J (2002) A description of escaped farmed Atlantic salmon *Salmo salar* captures and their characteristics in one Pacific salmon fishery area in British Columbia, Canada, in 2000. *Alaska Fisheries Research Bulletin* 9: 102–110
- Nash CE (2003) Interactions of Atlantic salmon in the Pacific Northwest. VI. A synopsis of the risk and uncertainty. *Fisheries Research* 62: 339–347, [http://dx.doi.org/10.1016/S0165-7836\(03\)00068-7](http://dx.doi.org/10.1016/S0165-7836(03)00068-7)
- Naylor R, Hindar K, Fleming IA, Goldberg R, Williams S, Volpe J, Whoriskey F, Eagle J, Kelso D, Mangel M (2005) Fugitive Salmon: Assessing the risks of escaped fish from net-pen aquaculture. *Bioscience* 55: 427–437, [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0427:FSATRO\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0427:FSATRO]2.0.CO;2)

- Netboy A (1974) *The Salmon: Their Fight for Survival*. Houghton Mifflin, Boston, 613 pp
- Nickelson TE, Lawson PW (1998) Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: Application of a habitat-based life cycle model. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2383–2392, <http://dx.doi.org/10.1139/f98-123>
- Nielsen JL, Williams I, Sage GK, Zimmerman CE (2003) The importance of genetic verification for determination of Atlantic salmon in North Pacific waters. *Journal of Fish Biology* 62: 871–878, <http://dx.doi.org/10.1046/j.1095-8649.2003.00072.x>
- PSMFC (2010) Aquatic nuisance project fact sheet. Species: Atlantic Salmon (*Salmo salar*). Pacific States Marine Fisheries Commission website. <http://www.aquaticnuisance.org/fact-sheets/atlantic-salmon> (Accessed 27 September 2010)
- Pascual M, Macchi P, Urbanski J, Marcos F, Rossi CR, Novara M, Dell'Arciprete P (2002) Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. *Biological Invasions* 4: 101–113, <http://dx.doi.org/10.1023/A:1020513525528>
- Quinn TP (2005) *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington, Seattle, 320 pp
- Quinn TP, Kinnison MT, Unwin MJ (2001) Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112:493–513, <http://dx.doi.org/10.1023/A:1013348024063>
- Quinn TP, Unwin MJ (1993) Variation in life history patterns among New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1414–1421, <http://dx.doi.org/10.1139/f93-162>
- Raffenberg MJ, Parrish DL (2003) Interactions of Atlantic salmon (*Salmo salar*) and trout (*Salvelinus fontinalis* and *Oncorhynchus mykiss*) in Vermont tributaries of the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 279–285, <http://dx.doi.org/10.1139/f03-021>
- Scott RJ, Noakes DLG, Beamish FWH, Carl LM (2003) Chinook salmon impede Atlantic salmon conservation in Lake Ontario. *Ecology of Freshwater Fish* 12: 66–73, <http://dx.doi.org/10.1034/j.1600-0633.2003.00002.x>
- Seeb J, Smith C, Moore D, Pirkowski R, Seeb L (2003) Atlantic salmon in the Pacific Ocean: Potential consequences and risks. [http://www.psmfc.org/ans\\_presentations/SeebJ.pdf](http://www.psmfc.org/ans_presentations/SeebJ.pdf) (Accessed 5 October 2010)
- Soto D, Jara F, Moreno C (2001) Escaped salmon in the inner seas, southern Chile: Facing ecological and social conflicts. *Ecological Applications* 11: 1750–1762, [http://dx.doi.org/10.1890/1051-0761\(2001\)011\[1750:ESITIS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2001)011[1750:ESITIS]2.0.CO;2)
- Thorpe JE (1994) Significance of straying in salmonids and implications for ranching. *Aquaculture and Fisheries Management* 25: 183–190
- Thorstad EB, Fleming IA, McGinnity P, Soto D, Wennevik V, Whoriskey F (2008) Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. Report from the Technical Working Group on Escapes in the Salmon Aquaculture Dialogue. <http://www.worldwildlife.org/what/globalmarkets/aquaculture/dialogues-salmon.html> (Accessed 11 October 2010)
- Volpe JP (2001) *Super un-natural: Atlantic salmon in BC waters*. David Suzuki Foundation, Vancouver, 36 pp
- Volpe JP, Anholt BR, Glickman BW (2001a) Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 197–207, <http://dx.doi.org/10.1139/f00-209>
- Volpe JP, Glickman BW, Anholt BR (2001b) Reproduction of aquaculture Atlantic salmon in a controlled stream channel on Vancouver Island, British Columbia. *Transactions of the American Fisheries Society* 130: 489–494, [http://dx.doi.org/10.1577/1548-8659\(2001\)130<0489:ROAASI>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(2001)130<0489:ROAASI>2.0.CO;2)
- Volpe JP, Taylor EB, Rimmer DW, Glickman BW (2000) Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. *Conservation Biology* 14: 899–903, <http://dx.doi.org/10.1046/j.1523-1739.2000.99194.x>
- WDFW (2010) Aquatic invasive species. Washington Department of Fisheries and Wildlife website. [http://wdfw.wa.gov/ais/species.php?Name=salmo\\_salar](http://wdfw.wa.gov/ais/species.php?Name=salmo_salar) (Accessed 4 October 2010)
- Waknitz FW, Iwamoto RN, Strom MS (2003) Interactions of Atlantic salmon in the Pacific Northwest. IV. Impacts on the local ecosystems. *Fisheries Research* 62: 307–328, [http://dx.doi.org/10.1016/S0165-7836\(03\)00066-3](http://dx.doi.org/10.1016/S0165-7836(03)00066-3)
- Waknitz FW, Tynan TJ, Nash CE, Iwamoto RN, Rutter LG (2002) Review of potential impacts of Atlantic salmon culture on Puget Sound chinook salmon and Hood Canal summer-run chum salmon evolutionarily significant units. U.S. Department of Commerce. NOAA Technical Memo. NMFS–NWFSC–53, 83 pp