PERSPECTIVE / PERSPECTIVE

Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers

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Abstract: Knowledge of the prevalence of escaped farmed fishes in the wild is an essential first step to assessing the risk resulting from interactions between farmed and wild fishes. This is especially important in eastern North America, where Atlantic salmon (*Salmo salar*) aquaculture occurs near wild Atlantic salmon rivers and where many wild salmon populations are severely depressed. Here, we review the literature on the incidence of escaped farmed salmon in eastern North American rivers, for which there has been no comprehensive compilation to date. Escaped farmed salmon have been found in 54 of 62 (87%) rivers investigated within a 300 km radius of the aquaculture industry since 1984, including 11 rivers that contain endangered salmon populations. Averaged among all investigations, the proportional representation of farmed salmon among adults entering the rivers from the sea was 9.2% (range 0% to 100%). Where data were sufficient to examine temporal trends, farmed salmon proportions varied considerably over time, suggesting that escape events are episodic in nature. We conclude that escaped farmed salmon are sufficiently prevalent in eastern North American rivers to pose a potentially serious risk to the persistence of wild salmon populations, especially in those rivers that are adjacent to existing aquaculture sites.

Résumé: Une évaluation de la prévalence des poissons échappés de pisciculture en nature est un premier pas essentiel dans la détermination des risques reliés aux interactions entre les poissons d'élevage et les poissons sauvages. La situation est particulièrement sérieuse dans l'est de l'Amérique du Nord où des cultures de saumons atlantiques (Salmo salar) se retrouvent près de rivières à saumons atlantiques sauvages et où plusieurs des populations de saumons sauvages sont considérablement réduites. Nous faisons ici une revue de la littérature sur l'incidence de poissons échappés de culture dans les rivières de l'est de l'Amérique du Nord, dont il n'existe pas à ce jour de compilation exhaustive. On a trouvé des saumons échappés de culture dans 54 des 62 (87 %) rivières étudiées dans un rayon de 300 km de l'industrie piscicole depuis 1984, dont 11 rivières contenant des populations de saumons en voie de disparition. Dans l'ensemble des inventaires, la proportion moyenne de saumons de pisciculture parmi les saumons qui pénètrent dans les rivières à partir de la mer est de 9,2 % (étendue: 0 % à 100 %). Dans les cas où les données sont assez nombreuses pour permettre d'étudier les tendances temporelles, les proportions de saumons de pisciculture varient considérablement dans le temps, ce qui laisse croire que les incidents de fuites sont de nature épisodique. Nous concluons que la prévalence de saumons échappés de pisciculture est suffisamment grande dans les rivières de l'est de l'Amérique du Nord qu'elle représente une menace pour la persistance des populations de saumons sauvages, particulièrement dans les rivières qui sont à proximité de sites actuels d'aquaculture.

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Introduction

Worldwide declines in wild fish stocks combined with a

growing human population have resulted in increased demands for aquaculture production. Over 25% of the world's fish consumption is now of aquaculture origin, and aquacul-

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ture has been increasing at an average annual rate of 8.8% since 1970, higher than the growth rate of both capture fisheries and terrestrial animal agriculture (Naylor et al. 2000; UN Food and Agriculture Organization (FAO) 2006). The aquaculture of farmed Atlantic salmon (*Salmo salar*) is no exception to this trend. In the North Atlantic alone, farmed salmon production amounted to 817 100 tonnes (t) in 2006, a 171-fold increase in production since 1980 (International Council for the Exploration of the Sea (ICES) 2007). By comparison, the total North Atlantic nominal catch of wild salmon in 2006 was only 0.24% of its aquaculture counterpart (ICES 2007). Farmed salmon now considerably outnumber their wild conspecifics within the native range of the species (Gross 1998; Hansen et al. 1999; Hansen and Windsor 2006).

Despite preventative measures, farmed salmon escape into the wild from sea cages and juvenile hatcheries in most, if not all, regions where they are farmed; they have also been found in areas where farming does not occur. Escaped farmed salmon have been reported in, among other places, Iceland (Gudjonsson 1991), Norway (Gausen and Moen 1991; Lund et al. 1991; Fiske et al. 2006), Scotland (Youngson et al. 1997; Walker et al. 2006), Northern Ireland (Crozier 2000), the Republic of Ireland (Walker et al. 2006), England and Wales (Milner and Evans 2003; Walker et al. 2006), the Faroe Islands (Hansen and Jacobsen 2003), Greenland (Hansen et al. 1997), Chile (Soto et al. 2001), Turkey (Innal and Erk'akan 2006), Australia (The Australian 2007), the United States (Baum 1998; Lage and Kornfield 2006), and Canada (Carr et al. 1997; Volpe et al. 2000). Damage to sea cages (from storms, vandalism, or predators) has been identified as the principal cause of several major escape events, including 600 000 adult farmed salmon that escaped from one farm in a single event near the Faroe Islands in 2002 (see McGinnity et al. 2003). Many escapes go unreported. The "leaking" of juveniles from freshwater hatcheries comprises a source of underreported farmed salmon escapes (Carr and Whoriskey 2006). One recent estimate suggests that two million farmed salmon escape every year into the North Atlantic Ocean (Schiermeier 2003).

Although escaped farmed salmon are thought to incur initially high mortalities in the wild (Whoriskey et al. 2006), both adult and juvenile farmed escapees can still enter rivers in large numbers (Lacroix and Stokesbury 2004; Fiske et al. 2006). Here, they may interbreed with wild salmon, despite somewhat poorer reproductive success relative to wild salmon (Fleming et al. 1996, 2000; Weir et al. 2004). This has raised concerns about the potential detrimental effects that interactions between farmed and wild salmon can have on wild populations. For instance, artificial selection, random genetic drift, and the use of non-native stocks result in farmed salmon escapees that are genetically distinct from their wild counterparts (Mjølnerød et al. 1997; Roberge et al. 2006; Hutchings and Fraser 2008). Based on the prediction that wild salmon populations are locally adapted to their particular environments (Garcia de Leaniz et al. 2007), farmed-wild interbreeding could lead to a reduction in fitness in farmed-wild hybrids (Hutchings 1991; McGinnity et al. 2003; Fraser et al. 2008). In addition, farmed salmon may transmit disease (McVicar 1997), competitively displace wild salmon (Fleming et al. 2000), superimpose spawning nests over those of wild salmon (Lura and Sægrov 1991; Webb et al. 1993), and increase the uncertainties associated with stock assessments of wild salmon (Hansen et al. 1999).

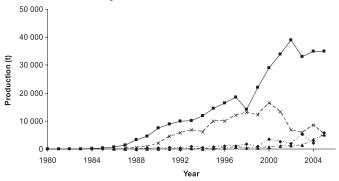
A critical first step to assessing the risk that escaped farmed salmon might pose to wild salmon populations is to quantify the frequency with which farmed salmon enter wild salmon rivers and the frequency with which such escapes recur. Farmed salmon escapees have been relatively well documented in parts of Europe (Lund et al. 1991; Hansen et al. 1999; Fiske et al. 2006). However, a similar compilation of their occurrence has not been undertaken for rivers in eastern North America (NA). This is despite the fact that much of the salmon aquaculture industry in eastern NA is concentrated in the same geographic location as the most endangered wild Atlantic salmon populations on the continent (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2006; US Atlantic Salmon Assessment Committee (US ASAC) 2006).

Most salmon farming in eastern NA occurs in the Canadian provinces of Newfoundland and Labrador (NL), New Brunswick (NB), and Nova Scotia (NS) and in the US state of Maine (ME), with ME and NB accounting for >80% of the total production (Fig. 1). Freshwater aquaculture hatcheries are often situated along rivers that contain genetically distinct and phenotypically unique wild salmon populations (King et al. 2001; Fraser et al. 2007a, 2007b), and sea cages are in close proximity to the estuaries of those rivers. Since the inception of the North American salmon farming industry in 1980, the production of farmed salmon has dramatically increased in all farming areas (Fig. 1). In 2005, eastern NA produced 51000 t of finfish (the vast majority being salmon) worth more than CAN\$305 million (Statistics Canada 2006; S. Horn Olsen, Aquaculture Policy Coordinator, Maine Department of Marine Resources, 21 State House Station, Augusta, ME 04333-0021, personal communication) and comprising 4% of global Atlantic salmon production.

Notwithstanding the absence of a comprehensive database, there is reason to believe that farmed salmon escape events may pose a threat to wild salmon populations. For example, more than 300000 farmed salmon adults are estimated to have escaped over a 6-year period (2000-2005) in ME and NB (F.G. Whoriskey, unpublished data). Despite these escapes, most published data in the primary scientific literature have been collected from a single salmon river, NB's Magaguadavic River, where the proportion of farmed salmon in two years exceeded 90% (Carr et al. 1997). This river is located in one of the world's most intensive salmon farming regions and has been systematically monitored for escapes for this reason. The extent to which this river's data can be applied to other eastern NA rivers for risk assessment is unknown. In addition, although organizations and government agencies in both Canada and the US have been collecting information on the presence of farmed salmon in several major rivers for many years, much of this information is scattered and uncollated.

In an attempt to build a comprehensive database on the escapes of farmed salmon in eastern NA, we collated all available information from both primary and secondary sources on the presence of farmed salmon in ME, NB, NL, and NS rivers from 1980 (the year in which salmon farming

Fig. 1. Annual production of farmed Atlantic salmon (*Salmo salar*) for eastern North America: Nova Scotia (♠), New Brunswick (■), Newfoundland (♠), Maine (×). Adapted from data from Newfoundland and Labrador Department of Fisheries and Aquaculture (2006) and Maine Department of Marine Resources (2006).



commenced in NA) through 2006. We had four major objectives: (i) to review and summarize available information on farmed salmon escapes from sea cages and aquaculture hatcheries in eastern NA; (ii) to determine the number of rivers in eastern NA in which the presence or absence of farmed salmon has been investigated, including rivers harbouring endangered wild salmon populations as defined under the US Endangered Species Act (ESA) and Canada's Species At Risk Act (SARA); (iii) to quantify, where possible, the proportion of escaped farmed salmon relative to wild salmon in rivers where farmed salmon have been detected; and (iv) to broadly assess whether the proportional representation of farmed salmon in wild salmon rivers varies over time.

Materials and methods

Literature search procedure

To quantify the incidence of farmed salmon in eastern NA rivers, we undertook a literature search for primary, peer-reviewed journal articles, using Web of Science and the Google Scholar search engines. Major contributing authors of these papers, as well as their reference sections, were also searched to identify additional publications of interest.

We also undertook an extensive literature search for primary or secondary reports on the occurrence of farmed salmon in eastern NA as produced by organizations such as the Atlantic Salmon Federation (ASF) (www.asf.ca), Committee on the Status of Endangered Wildlife in Canada (CO-SEWIC) 2006 (www.cosewic.gc.ca), Fisheries and Oceans Canada (DFO) (www.dfo-mpo.gc.ca), International Council for the Exploration of the Sea (ICES), including the Working Group on North Atlantic Salmon (www.ices.dk), Atlantic Salmon Commission (ASC) (www.maine.gov/asc), National Marine Fisheries Service, including the Northeast Fisheries Science Center and the US Atlantic Salmon Assessment Committee (USASAC) (www.nmfs.noaa.gov), North Atlantic Salmon Conservation Organization (NASCO) (www.nasco.int), US Fish and Wildlife Service (www.fws.

gov), and the World Wildlife Fund (WWF) (www. worldwildlife.org). For Canadian provinces, this included a review of any DFO stock assessment papers, research papers, working papers, and meeting minutes that pertained to farmed Atlantic salmon, as listed on the Canadian Science Advisory Secretariat Web site (www.dfo-mpo.gc.ca/csas). Salmon stock assessment reports were available for most years between 1984 and 2006 for either specific rivers or regions within eastern Canada. For Maine, the ASC's official reports to the ME legislature were acquired for the 2001-2004 period. Members of the ASC were contacted and tables, figures, and stock assessments created by the USASAC were provided for the years 1998–2005. Additional publications that may have been missed by directly searching all of the above-mentioned Web sites were subsequently located by searching Google and Google Scholar, using specific rivers or researchers as the search terms.

In total, 116 references were used to compile Table 1 and Supplementary Tables S2–S4 (this list of references is available from the NRC Depository of Unpublished Data²). Depending on the nature of the source (primary or secondary literature) and the level of detail reported in the study, individuals identified as the primary researchers for studies on particular river systems were in some instances contacted and additional information was requested. Sometimes unpublished information pertaining to additional rivers was also provided. The sources of these data are cited here as "personal communications".

Data compilation and definitions

Information pertaining to farmed and wild salmon for the years in which the presence of farmed salmon had been investigated were compiled from the above sources. Relevant data pertaining to farmed salmon in each eastern NA river were collated in tabular form. These data included information on (i) known escape events, (ii) numbers of farmed salmon caught, (iii) numbers of wild salmon caught (hatchery-released fish are included in the wild counts), (iv) size or age class of the farmed salmon, (vi) occurrence of European genes in the farmed salmon, (vi) methods used to capture or observe the wild and farmed salmon, (vii) means used to determine whether the salmon were farmed or wild, (viii) evidence of hybridization between farmed and wild salmon, and (ix) reasons for why data may not have been acquired for a particular year in a particular river.

There were many instances in which secondary sources were used. In some cases, the origin of the data used by the secondary source had not been identified or cited. In these circumstances, we contacted the authors of the secondary source and the necessary information was often obtained. In at least 17 instances, the secondary sources cited data from unpublished personal correspondence with a field biologist (e.g., data for the Bear and Tusket rivers (NS) in O'Neil et al. (2005)). In such cases, the biologists were contacted to confirm the data; if there was no response (8 of 17 researchers) and based on the high accuracy of the other similar instances that we verified with the biologists, the information

² Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3868. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 1. Incidence of farmed Atlantic salmon (Salmo salar) adults in eastern North American rivers.

			Total no. of wild salmon	Total no. of farmed salmon	Total no. of salmon	Farmed salmon adults	Count	
River	P or S ^a	Year	adults	adults	adults	(%)	method ^b	ID^c
Annapolis	NS	1990–1996		1				
		1995		?				
		1996	13	1	14	7	A,S	
		1999		?				
		2000		15				
Baddeck	NS	1994	231	1	232	0.4	M&R	
		1995	338	23	361	6	M&R	EX
		1995	146	8	154	5	SC	FE
		1996	214	0	214	0	SC	EX
		1997	137	1	138	0.7	SC	EX
		1998	190	5	195	3	M&R	
		1999	N/A	N/A	N/A	N/A	1110011	
		2001	N/A	N/A	N/A	N/A		
Bear	NS	Early 1990s	IVA	Many	11//1	14/74	A	
Bras d'Or Lakes	NS	1994		-			Α	
		1994 1990–1996		Detected				
Gaspereau	NS		22	5	24	4		
		1992	23	1	24	4		
		1993	8	3	11	27		
		1994	35	0	35	0		
		1995	35	1	36	3		EX
		1996		?	178	<3 ?	FW	
		1997		?		<3 ?	FW	
		1998	27	1	28	4	FW	
		2000	~49	1	~50	2	FW	
		2004		0		0		
		???		Detected				
Grand	NS	2003		0		0		
Harrington	NS	2003		Suspected				
ndian Brook	NS	2000		1				
LaHave	NS	1989	3 176	1	3 177	0.03		
zariave	110	1990–1994	3 170	0	3 177	0.03		
		1995	499	0	499	0		
		1996	422	0	422	0		
					314	0		
		1997	314	0			EXX	
	NG	1998	1 880	0	1 880	0	FW	
Liscomb	NS	1994–1998	984	0	984	0		
Margaree	NS	1987–1996	>2 000	0	>2 000	0		
/lersey	NS	2000	5	1	6	17	A	
/leteghan	NS	2000		1				
Middle	NS	1994		?	475		M&R	
		1995	183	0	183	0	SC	EX
		1996	358	1	359	0.3	SC	EX
		1997	258	0	258	0	SC	EX
		1998	213	9	222	4	M&R	
Victaux	NS	1996	38	1	39	3	D	EX,SA
		1999	5	0	5	0	FW	
		2000	5	12	17	71	FW	
North	NS	1995	154	14	168	8		
		1995	178	3	181	2	SC	
		1996	322	0	322	0	SC	FE
		1997	335	0	335	0	SC	EX
		1998	433	55	488	11	SC,M&R	LA
		1998	N/A	N/A	400 N/A	N/A	5C,IVIOLK	
		2000	N/A	N/A	N/A	N/A		
. 1	NIC	2003	N/A	N/A	N/A	N/A		
arrsboro	NS	???		Released				
ackville	NS	1996–1998	515	0	515	0		
almon (Digby)	NS	1999		2				
		2000		0		0		
Skye	NS	1996		?	71		A,S	
Stewiacke					21			

Table 1 (continued).

River	P or S^a	Year	Total no. of wild salmon adults	Total no. of farmed salmon adults	Total no. of salmon adults	Farmed salmon adults (%)	Count method ^b	${ m ID}^c$
		1996	8	0	8	0	EF	EX
		1997	o .	0	Ü	0	Li	E/X
St. Ann's Bay	NS	1998		?				
St. Mary's	NS	1992–1993, 1997–1998	796	0	796	0		
Tusket	NS	1998	>158	2	>160	~1	FW	
Whycocomagh Bay	NS	1994	116	2	118	2	HT	
		1995	34	147	181	81	HT	
		1996	10	40	50	80	HT	
		1997	N/A	N/A	N/A	N/A		
Belle Isle Bay	NB	1990		Several	280		HT	
Big Salmon	NB	Late 1980s		1				
		2000	11	0	11	0		
		2001	44	0	44	0	SH,SC	
		2002	33	0	33	0	SH,SC	
		2004		0		0		
Black River	NB	2003		Detected				G
Bocabec	NB	1999	0	2	2	100	CF	
Chamcook Stream	NB	17–23 Nov. 2005		5				
Dennis Stream	NB	2001		Detected				
Magaguadavic	NB	1983	889	51	940	5	FW	
		1984	783	0	783	0	FW	
		1985	635	0	635	0	FW	
		1988	689	0	689	0	FW	
		1983-1988		0		0		
		1990-1996		2 301			FW	
		1992	294	147	441	33	FW	FE,FL,SA
		1993	237	154	391	39	FW	FE,FL,SA
		1994	131	1 198	1 329	90	FW	FE,FL,SA
		1995	79	712	791	90	FW	FE,FL,SA
		1996	69	240	309	78	FW	FE,FL,SA
		1997	59	119	178	67		FE,SA
		1997	32	8	40	20	FW	SA
		1998	31	227	258	88	FW	EX,SA
		1999	24	90	114	79	FW	EX,SA
		1999, 2000	30	35	65		FW	EX,SA,G
		2000	14	30	44	68	FW	FE,SA
		2001	17	132	149	89	FW	FE,SA
		2002	7	35	42	83	FW	FE,SA
		2003	6	23	29	79	FW	FE,SA
		2004	2	17	19	89	FW	FE,SA
		Up to 13 Oct. 2005	9	38	47	81	FW	
		15 Nov. 2005 17–23 Nov.		6 30				
		2005						
		2005	9	69	78	88	FW	FE,SA
		2006	26	6	32	19	FW	
Miramichi	NB	1980s – 1998		0	1000s	0		
Mitchell Brook	NB	17–23 Nov. 2005		6				
Nashwaak	NB	1997	736	0	736	0	CF	
		1998	1 565	0	1 565	0	CF,M&R	FE
		1999	940	0	940	0	CF,M&R	FE
		2000	700	0	700	0	CF,M&R	
		2001	516	0	516	0	CF	
		2002	422	0	422	0	CF	FE,SA
		2005	521	1	522	0.2	CF	SA

Table 1 (continued).

D'	D	V	Total no. of wild salmon	Total no. of farmed salmon	Total no. of salmon	Farmed salmon adults	Count	ID.C
River	P or S ^a	Year	adults	adults	adults	(%)	method ^b	ID^c
		1991	13 886	80	13 966	0.57	FW	
		1992	13 788	50	13 838	0.36	FW	
		1993	7 752	6	7 758 5 909	0.08	FW	EE
		1994 1995	5 881 7 328	28 106	5 909 7 434	0.47 1.4	FW FW	FE
		1995	10 031	13	10 044	0.13	FW	
		1997	5 226	0	5 226	0.13	FW	FE
		1998	5 876	4	5 880	0.07	FW	IL
		1999	4 983	20	5 003	0.4	FW	FE,BF
		2000	3 568	6	3 574	0.17	FW	1 2,51
		2001	2 859	14	2 873	0.49	FW	
		2002	2 702	13	2 715	0.47	FW	
		2003	2 021	3	2 024	0.15	FW	
		2004	2 167	1	2 168	0.05	FW	
		2005	1 490	0	1 490	0	FW	
		2006	1 662				FW	
St. Croix	NB	1990-1996		231				
		1992	N/A	N/A	N/A	N/A		
		1994	84	97	181	54	FW	
		1995	47	13	60	22	FW	
		1996	132	20	152	13	FW	
		1997	43	27	70	39	FW	
		1998	42	25	67	37	FW	EX
		1999	13	23	36	64	FW	EX
		2000	20	30	50	60	FW	
		2001	21	56	77	73	FW	
		2002	20	6	26	23	FW	
		2003	15	9	24	38	FW	
		2004 17–23 Nov. 2005	10	4 3	14	29	FW	
		2005	6	33	39	85	FW	FE,SA
		2006	4	7	11	64		,
Upper Salmon	NB	2003		Spawning adults				G
Waweig	NB	1980s		1				
Conne	NL	1990–1996		3				
		1993		1				SA
		1994	92	2	94	2.1		SA
		1995	120	0	120	0		SA
		1996	97	0	97	0		SA
		1997	422	8	430	1.9		EX
		1997	233	2	235	0.9		SA SA
		1997 1998	476 189	4	480	0.8	CE	SA
		1998	109	2	191	1	CF A	SA
		1998	173	1	174	0.6	CF	BF,SA
		2000	216	5	221	2.3	CI	SA SA
		2001	189	0	189	0	CF,A	EX,SA,
		2002	279	0	279	0	C1 ,71	SA
		2003	181	0	181	0		SA
		2004	264	0	264	0		SA
		2005	203	0	203	0		SA
		2006		0		0	CF	EX
Little	NL	1994	84	0	84	0	CF	
		1995	135	0	135	0	CF	
		1996	801	0	801	0	CF	
		1997	478	0	478	0	CF	
		1998	311	2	313	0.6	CF	
		1999	351	5	356	1.4	CF	
		2000	616	0	616	0	CF	

Table 1 (continued).

River	P or S^a	Year	Total no. of wild salmon adults	Total no. of farmed salmon adults	Total no. of salmon adults	Farmed salmon adults (%)	Count $method^b$	ID^c
River	1 01 5	2001	161	0	161	0	CF	ID .
		2002	528	0	528	0	CF	
		2002	335	0	335	0	CF	
		2003	687	0	687	0	CF	
Androscoggin	ME	2004	4	0	4	0	Cr	
Boyden Stream	ME	???	4	Detected	4	U		
Cobscook Bay	ME	2004		273				
Cobscott Bay	ME	???		Detected				
Dennys	ME	1990–1996		67				
Deliliys	WIL	1993	40-50	20	60-70	29-33		EX,SA
		1994	5	42	47	89	W	EX,SA EX,SA
		1994	5	42	9	44	W	EX,SA EX,SA
		1995	10	21	31	68	W	EX,SA EX,SA
		1990	0	2	2	100	vv	EX,SA EX,SA
		1997	1	1	2	50	W	EX,SA EX,SA
		1998	N/A	N/A	N/A	N/A	vv	EA,3A
		2000	2	28	30	93	W	
		2000	25	65	90	93 72	W W	
		2001	23	4	6	67	W W	
			9					C A
		2003		2	11	18	W	SA
		2004	1	0	1	0	W	SA
		2005	0	8	8	100	W,GN,A,EF	
D . M 11) (F)	2006	5	4	9	44	W	
East Machias	ME	1990	69	14	83	17	A	
		1995–1999		Detected			A	
		1998	0	0	0		A	
		1999	0	0	0		A	
		2000	N/A	N/A	N/A	N/A		
		2001	N/A	N/A	N/A	N/A		
		2002	N/A	N/A	N/A	N/A		
		2003	N/A	N/A	N/A	N/A		
		2004	N/A	N/A	N/A	N/A		_
		???		Detected				G
Hobart Stream	ME	???		Detected				
Machias	ME	1998	5	0	5	0	A	
		1999	0	0	0		A	
		2000	N/A	N/A	N/A	N/A		
		2001	N/A	N/A	N/A	N/A		
		2002	N/A	N/A	N/A	N/A		
		2003	N/A	N/A	N/A	N/A		
		2004	N/A	N/A	N/A	N/A		
Narraguagus	ME	1994	51	1	52	2	FW	
		1995–1996		9				
		1995	56	0	56	0	FW	
		1996	28	8	36	22	FW	
		1997	37	0	37	0	FW	
		1998	22	0	22	0	FW	
		1999	32	3	35	9	FW	
		2000	23	0	23	0	FW	
		2001	32	0	32	0	FW	
		2002	8	0	8	0	FW	
		2003	21	0	21	0	FW	
		2004	11	0	11	0	FW	
		2005	6	0	6	0	FW	
		2006	5	0	5	0	FW	
Pennamaquan	ME	???		Detected				
Penobscot	ME	1990		1				
		1994-2001				< 0.01		
		1994		0				G
		1995		0				G
		1996		0				G

Table 1 (concluded).

River	P or S^a	Year	Total no. of wild salmon adults	Total no. of farmed salmon adults	Total no. of salmon adults	Farmed salmon adults (%)	Count method ^b	${ m ID}^c$
		1997	~1 077	0	~1 077	0		
		1998	1 210	0	1 210	0	FW	
		1998		0				G
		1999	968	0	968	0	FW	
		1999		0				G
		2000	535	0	535	0		
		2000		5				G
		2001	785	1	786	0.1	FW	
		2001		9				G
		2002	776	4	780	0.5	FW	
		2002		0				G
		2003	1 114	0	1 114	0	FW	
		2003		0				G
		2004	1 323	0	1 323	0	FW	
		2005	985	0	985	0	FW	
		2006	1 046	1	1 047	0.1		
Pleasant	ME	1997	N/A	N/A	N/A	N/A		
		1998	0	0	0		A	
		1999	0	0	0		A	
		2000	3	0	3	0	W	
		2001	11	0	11	0	W	
		2002	0	0	0		W	
		2003	2	0	2	0	W	
		2004	1	0	1	0	W	
		2005-present	N/A	N/A	N/A	N/A		
		???		Detected		2		G
Togus Stream	ME	???		Detected				G
Union	ME	1994-1998		N/A		N/A		
		1999	1	10	11	91	FW	SA
		2000	2	3	5	60	FW	
		2001	0	2	2	100	FW	SA
		2002	5	6	11	55	FW	
		2003	1	0	1	0	FW	
		2004	2	0	2	0	FW	SA
		2005	0	4	4	100	FW	SA
		2006		0		0		
Unknown	ME	1991, 1992		Few				
		2005		Many				

Note: Question marks (???) in the Year column indicate that a source did not report the year but provided data on numbers of farmed salmon, and we could not find a way to assign the values to a specific year. A single question mark (?) means that the sources were difficult to interpret but ambiguously suggested the presence of farmed salmon in a river in a particular year. The 116 references, as well as footnotes and 1SW/MSW (1 sea winter/multiple sea winters) salmon numbers, are found in Supplementary Table S1. Parr and smolt information is in Supplementary Tables S2–S3 (available online from NRC Data Depository).

in the secondary source was assumed to be accurate. Note that secondary sources are not differentiated from primary sources in Table 1 and the supplementary tables.

If a literature source only provided limited information on a certain river, such as the total number of salmon caught in a particular year and the percentage of those that were of farmed origin, we calculated and reported estimates of the number of farmed and wild salmon from the information presented. These estimates are indicated by a "~" in front of the salmon numbers in Table 1 and in the supplementary information. If a source did not report the year but provided

data on numbers of farmed salmon and we could not find a way to assign the values to a specific year, we placed a "???" in the date column. If the reports indicated only that farmed salmon were taken but not the actual numbers caught, we scored this as "detected" in the farmed salmon column. Some sources speculated on the presence of farmed salmon in a particular river based on anecdotal evidence; in such cases, the river was mentioned and the term "suspected" was placed in the farmed salmon column. Quotes of the speculations from the source reference are provided in a supplementary footnote (Supplementary Appendix S1,

[&]quot;Province (P) or state (S): NS, Nova Scotia; NB, New Brunswick; NL, Newfoundland and Labrador; ME, Maine.

^bA, angling; CF, counting fence; D, driftnet; EF, electrofishing; FW, fishway; GN, gill net; HT, monitoring-harvest trap; M&R, mark and recapture; S, seining; SC, snorkel count; SH, shore count; W, weir.

^{&#}x27;Method used to identify farmed or wild origins of salmon: BF, body form; EX, external characteristics; FE, fin erosion; FL, fork length; G, genetics; I, isotopes; SA, scale analysis.

available online from NRC Data Depository²). In a few instances, the sources were difficult to interpret but ambiguously suggested the presence of farmed salmon in a river in a particular year; this was indicated by "?" under the farmed salmon column and the appropriate quote was again footnoted.

If researchers specifically mentioned the presence or absence of farmed salmon in a river in a given year, that river was classified as "investigated" for that particular year. Investigated rivers included rivers in which trained personnel verified that no farmed salmon were present. All investigated rivers were included in Table 1 and Supplementary Tables S1–S3 (available online from NRC Data Depository²). If researchers did not mention the presence or absence of farmed salmon in a river in a given year, it was assumed that there were no trained personnel present to identify farmed salmon at that river and the river was classified as "uninvestigated" for that particular year. Uninvestigated rivers were not included in Table 1 or the supplementary tables, with the exception of the "suspected" rivers as defined above.

Farmed salmon were distinguished from wild salmon in the literature based on the following methods: (*i*) body morphology and fin erosion (reviewed in Jonsson and Jonsson 2006), (*ii*) scale analysis (as per Lund and Hansen 1991; Stokesbury et al. 2001; Lacroix and Stokesbury 2004), (*iii*) genetic screening (Skaala et al. 2004; O'Reilly et al. 2006), (*iv*) isotope analysis (Dempson and Power 2004), and (*v*) age at smolting (Carr 2005). These methods, when known, are identified in Table 1 and the supplementary tables.

For the purposes of this paper, a salmon "adult" is defined as any salmon above the smolt life stage, including immature postsmolts. The term "parr" is used in reference to the posthatch freshwater juvenile phase of the salmon life cycle, and "smolts" are postparr salmon that have undergone physiological changes prior to seaward migration. "Farmed" adults are salmon that (i) escaped directly from sea cages, (ii) escaped from freshwater aquaculture hatcheries as parr or smolts and survived to adulthood, or (iii) were the adult offspring of sea cage or hatchery escapees that spawned in the wild. The first type of farmed adult is likely the type most commonly referenced in Table 1; type ii fish could only be identified by scale, isotope, or genetic analyses and type iii fish could only be identified by genetic or isotope analyses. Any adult visually identified as farmed could only be, if correctly classified, a sea cage escapee. Farmed parr and farmed smolts were, unless otherwise noted, escapees from freshwater aquaculture hatcheries situated along the rivers in which they were found; the few exceptions include the offspring of farmed salmon that had successfully spawned in the wild.

In many wild salmon rivers, salmon are reared in hatcheries and released to supplement the wild population. If a source identified a salmon adult as "hatchery origin", they were grouped with the wild salmon (Table 1; with the notable exception of the Little River, NL, reports in which "hatchery" was a euphemism for farmed escapee). This decision was made in part because farmed salmon are often moved to geographic locations that contain genetically divergent wild salmon populations, whereas hatchery salmon

are generally raised along their ancestral rivers (Hutchings and Fraser 2008). Also, unlike hatchery salmon, farmed salmon undergo several generations of artificial selection (Roberge et al. 2006), further diverging farmed salmon from wild salmon. Our decision to group hatchery origin salmon with wild salmon met its greatest challenge in the Saint John River (NB) in which wild, farmed and hatchery fish are all of Saint John River origin and thus cannot be positively identified based on genetic screening (P. O'Reilly, Fisheries and Oceans Canada, 1 Challenger Drive, Bedford Institute of Oceanography, Dartmouth, NS B2Y 4A2, Canada, personal communications). However, in this river, hatchery and farmed salmon could be distinguished from wild salmon based on fin erosion and scale analysis, and farmed salmon could further be distinguished from hatchery salmon based on scale analysis and the presence of an adipose fin, as all hatchery fish were fin-clipped (Jones et al. 2004). Hatchery-released fish are also adipose fin clipped in the Magaguadavic River, NB (Carr 2005). Although these methods may not always correctly classify the salmon as "farmed" or "hatchery-wild", they are accurate to a high degree and we accepted the reports of the field researchers as accurate with some potential caveats (see Discussion).

The total number of salmon found in a river in a particular year was based, whenever possible, on actual counts of the salmon spawning run. In some circumstances, salmon abundance was estimated using mark-recapture techniques. In those cases, the number of farmed salmon was sometimes based on an estimate provided by the mark-recapture study and sometimes was a minimum estimate based on the actual number found. The minimum values probably underestimate the true numbers of farmed salmon present. The use of mark-recapture data is indicated (Table 1). There were also some instances (such as with the Conne River, NL) where a subset of the total run was sampled and the proportion of farmed salmon within that sample was recorded. In these cases, the sample size and not the spawning run size was included in the table; this is indicated by a footnote in the supplementary information.

Statistics and figures

Some simple summary statistics of the information presented in Table 1 and the supplementary tables are provided in the Results section and accompanying figures. These calculations include the following: mean proportions of farmed salmon by region, river, and year; the proportion of investigated rivers that contained farmed salmon; the "detection rate", defined as the percentage of investigations that detected farmed salmon; and search effort, defined as the number of rivers that were investigated in a particular year. Because many data points were incomplete (a "data point" being a row in Table 1), some had to be excluded from these calculations.

The mean proportions of adult farmed salmon were calculated from the proportions of farmed salmon within individual rivers for individual years. Only those data points for which proportions and years were given were used (Table 1). All bays (Belle Isle, Cobscott, Cobscook, St. Ann's, and Whycocomagh) were excluded from these calculations, as were suspected or questionable rivers. For the LaHave, Liscomb, Margaree, Miramichi, Sackville, and St. Mary's riv-

ers, each year in which no farmed salmon were found was considered an independent data point, with an equal number of wild salmon assumed for each year. The Miramichi data were assumed to begin in 1989, and only one data point was assumed for the Bear River. All other data points that encompassed multiple years were excluded. In some instances, several data points were available for a single river for the same year; Table 1 has been constructed such that the data point used in these calculations is the first one mentioned. Data points that covered an entire year were favoured over those that encompassed only a few days. If a range of possible proportions was provided, the highest proportion was used. Finally, all data points were excluded from the proportion calculations for which the numbers of both wild and farmed salmon were zero, as they could not properly be said to be a proportion. Thus, although the East Machias was investigated for three years, only the one year in which any salmon were found is included in these calculations. Six data points were excluded for this reason.

The regional (province or state and salmon fishing area) and yearly mean proportions of farmed salmon in the salmon spawning run were calculated using a modified version of Freeman and Tukey's (1950) arcsine transformation (Anscombe 1948; Zar 1999). This transformation corrected for differences in the numbers of farmed and wild salmon found among rivers and accounted for the high frequency of proportion values in our data set that approached either 0 or 1 (see Zar 1999). The range (the lowest and highest proportions in the untransformed data set) was provided along with the transformed means. Only those data points (n = 196) that fulfilled the above conditions and contained both the number of wild salmon and farmed salmon were used.

The proportion of rivers that contained farmed salmon were calculated by adding all of the investigated rivers that contained farmed salmon in at least one year and dividing by the total number of investigated rivers. Suspected and questionable rivers were excluded from these calculations, as were Cobscook Bay (because farmed salmon were intentionally released into it) and Bras D'Or Lakes (as it is not separate from Whycocomagh Bay). All other water systems were included. Rivers for which the exact number of farmed salmon or the year in which they were found was unknown were also included in these calculations, as long as the presence of farmed salmon had been confirmed. Rivers that contained farmed salmon in multiple years were only counted once.

For detection rate and search effort calculations, all data points that included a year and either the number of farmed salmon or the confirmed presence of farmed salmon were included. A data point that had a proportion of farmed salmon greater than zero was scored as a "success". Again, the Bear River was treated as one data point, the Miramichi data were assumed to begin in 1989, and all of the years included in the LaHave, Liscomb, Margaree, Miramichi, Sackville, and St. Mary's rivers data sets were counted as independent data points. All other data points that encompassed multiple years were excluded, including those years scored as "detected" in the East Machias River. Cobscook Bay and Bras D'Or Lakes were excluded, but all other bays were included. If two methods were used to identify farmed salmon in the same year and one method detected farmed

salmon and the other did not, the one that detected farmed salmon was used as a data point, providing all other conditions were met.

There were several cases in which information from one document conflicted with information from another. In those cases, the primary or peer-reviewed source is displayed in Table 1 and the supplementary tables. If no primary source was found (or if primary sources conflicted), the source that contained more data (e.g., the number of farmed salmon and the total number of salmon, as opposed to only the percentage of farmed salmon) was used. All conflicting information is indicated in footnotes in the supplementary tables. If possible, explanations are suggested to explain the conflicting data. The figures and calculations that follow in our review use the data from Table 1 and exclude any conflicting information cited in the supplementary footnotes.

Results

Frequency and magnitude of farmed salmon escapes in eastern North America

We found 27 reports of documented farmed salmon escapes from sea cages and aquaculture hatcheries in eastern NA since 1980 (Table 2). The main causes of farmed salmon escapes (when reported) were storms (n = 8) and vandalism (n = 8), followed by gear failure (n = 2), boating accidents (n = 1), and handling error (n = 1). Although three of these escapes were very large $(n = >100\,000)$, even the smallest (n = 200) was over half the size of the spawning run of wild salmon in the adjacent river for that year.

We hypothesized that the frequency and magnitude of farmed salmon escapes increased as aquaculture production increased in eastern NA, but there was no evidence of such a relationship (Fig. 1; Table 2). Although farmed salmon production has steadily increased since 1984, and the frequency of escape events and the estimated number of farmed salmon escapees in 1994 and 2000 were comparatively higher than in 1984, the intervening years show no consistent pattern. This could be due to data deficiencies; it is likely that there were more escapes than documented.

Importantly, escape events often coincided with peaks in the numbers and proportions of farmed salmon recorded in neighboring river systems (Figs. 2, 3). For example, the escape of 20 000–40 000 salmon from a sea cage in NB in 1994 led to the highest recorded catch of farmed salmon in any river in eastern NA — nearly 1200 farmed salmon were caught in the Magaguadavic River (NB) in 1994, up from 154 in 1993. However, not every peak coincided with reported escape events. The 1997 peak for the Dennys (ME) and St. Croix (NB) rivers, the 1999 peaks for the Union (ME), St. Croix (NB), and Narraguagus (ME) rivers, and the 1995 peak for the Saint John River (NB) could not be linked to any particular reported escape event.

The proportions of adult farmed salmon within the salmon spawning run in rivers varied considerably among years (Fig. 2), with the Magaguadavic River (NB) being a notable exception. This river exhibited slight peaks; however, salmon returns to the river from the sea have been consistently dominated by farmed fish (Fig. 2).

Table 2. Documented escapes of farmed Atlantic salmon (Salmo salar) adults and juveniles from sea cages and aquaculture hatcheries.

Year	Number	Life stage	Location	Cause	Reference ^a
1984	5 000	1.5-3 kg	East Dover, NS	Vandalism	99
1994	20 000-40 000		SW NB	Storm	43, 96
1994			Eastport, ME		37
Feb. 1995	100 000	Parr	NL	Storm	38
June 1995	20 000		Cape Breton, NS	Vandalism	38
1996			Cape Breton, NS	Vandalism	71
1996			Libby Island, ME	Storm	45
1998	8 000		Annapolis Basin, NS		43, 96
1998	63 300	Parr	Jeddore Lake, NL		115
1999	50 000		Annapolis Basin, NS		43, 115
1999	200		Vyse Cove, NL	Handling error	115
1999	6300	Smolts	May Cove	Gear failure	115
2000	30 000 maximum		Tinkers Island, NB	Gear failure	115
2000	100 000-170 000	5 lb	Stone Island, ME	Storm	29, 45, 115
2000	13 000	2-2.5 lb	Eastport, ME	Boat crash	115
Dec. 2000	15 000	800 g	Nantucket Island, NB	Storm	115
2000 total	175 000 minimum in six escape events	Salmon and rainbow trout	Eastern NA	Storms (3), vandalism (1), boat crash (1), unknown (1)	48, 49
2001	3 000-5 000		Eastport, ME		29
2001	6	Smolts	Deblois Hatchery, ME		45
2003	2 000		Birch Cove, ME	Storm	45, 115
May 2003	6 5 0 0	Adults	NL		
2004		800 g	ME	Storm	83
April-May 2005	26 300	1.5 and 2.4 kg	Deer Island, NB	Vandalism	84, 115
Aug. 2005	20 000	400–500 g	St. Andrew's, NB	Vandalism	84, 114, 115
Summer 2005	Tens of thousands	Adults	Cooke's Aquaculture, NB	Vandalisms (3)	20
Nov. 9, 2005	100 000	4–5 kg	Cooke's Aquaculture, NB	Vandalism	21, 84, 114

"See Appendix S4 in Supplementary data for references (available online from NRC Data Depository).

Incidence of escaped farmed salmon in eastern North American rivers

From 1984-2006, escaped farmed salmon juveniles and (or) adults have been documented in 54 of 62 (87%) rivers investigated within a 300 km radius of the aquaculture industry in ME, NL, NB, and NS (Figs. 4, 5; Table 1; Supplementary Tables S1-S3, available online from NRC Data Depository²). Of these 62 rivers, adult salmon were investigated in 50; farmed adult salmon were found in 42 (84%) of these 50 rivers (Tables 1, 3). Of these 42 rivers with adult farmed salmon, estimates for 15 were based on data obtained over a period of five or more years; adult farmed salmon were detected in multiple years in 12 of 15 (80%) of these rivers. Nineteen of 22 rivers (86%) in which parr were screened had parr of farmed origin (Table 3; Supplementary Table S2, available online from NRC Data Depository²) and 4 of 4 rivers searched contained farmed smolts (Table 3; Supplementary Table 3, available online from NRC Data Depository²). Farmed salmon were not detected in eight investigated rivers (Androscoggin, Grand, Liscomb, Margaree, Miramichi, St. Mary's, and Sackville rivers, and Buckman's Creek; Figs. 4, 5; Tables 1, 3; supplementary tables). They were also suspected to occur in an additional three rivers or bays (Skye River, St. Ann's Bay, and the endangered Harrington River; Fig. 4; Table 1; see supplementary footnotes for Table 1, available online from NRC Data Depository²).

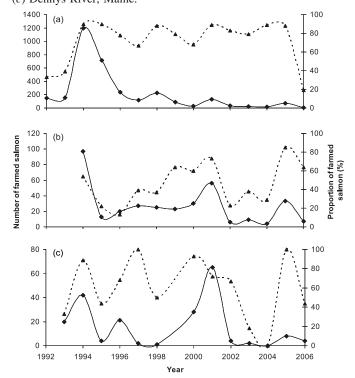
Within regions (NS, NB, NL, ME), farmed salmon adults have been identified in 13 of 14 rivers investigated in NB (for the purpose of this paper, the St. Croix River is consid-

ered part of NB because the monitoring station was in the NB portion of the river), 16 of 21 NS rivers, 2 of 2 NL rivers, and 11 of 13 ME rivers (Tables 1, 3). Farmed parr have been detected in 10 of 13 NB rivers and 9 of 9 ME rivers (Table 3; Supplementary Table 2, available online from NRC Data Depository²). The presence of farmed parr has not been reported for any NL or NS river, nor were any reports found indicating that their presence had been investigated. Similarly, farmed smolts have been documented in two NB rivers, one NL river, and one ME river, with no published results for NS (Table 3; Supplementary Table 2).

In total, whenever the presence or absence of adult farmed salmon has been investigated, there has been a detection rate of 49%, or 114 out of 235 searches conducted (i.e., the sum of the total number of years searched per river). By region, farmed salmon adults were detected 32% (8/25) of the time in NL, 43% (26/61) in ME, 39% (28/71) in NS, and 68% (53/78) in NB (Tables 1, 3).

The number of rivers in which adult farmed salmon were found in a particular year closely reflected the search effort (Fig. 6), defined here as the total number of rivers investigated in a particular year. Thus, years in which few rivers contained adult farmed salmon appeared to also be years in which few rivers were searched, and vice versa (Fig. 6). For example, in 2000, 13 rivers were found to contain adult farmed salmon out of 20 that had been searched. In 2005, adult farmed salmon were found in only half as many rivers (n = 7), but only about half as many rivers (n = 11) had been searched. An outlier year was 1997, in which effort was high (n = 18) but the presence of adult farmed

Fig. 2. Numbers (solid line) and proportions (broken line) of farmed Atlantic salmon (*Salmo salar*) over time in three river systems. Note that the numbers and proportions fluctuate from year to year, possibly correlating to mass escape events. (*a*) Magaguadavic River, New Brunswick; (*b*) St. Croix River, New Brunswick; (*c*) Dennys River, Maine.



salmon was low (n = 5). This may, however, be attributable to the fact that several rivers previously known to have contained farmed salmon were not searched in 1997 (Table 1).

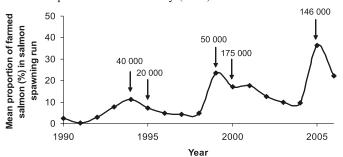
Escaped farmed salmon in rivers harbouring endangered salmon populations

Farmed salmon have been documented in 11 rivers that harbour endangered wild salmon populations as defined under the US ESA or Canada's SARA, including six of eight endangered rivers in ME (Dennys, East Machias, Machias, Narraguagus, Pleasant, and Sheepscot) that have been deemed to contain salmon that genetically correspond to historic populations. Of the approximately 40 rivers with SARA-listed endangered salmon in the Inner Bay of Fundy, Canada, all five that have been searched have been found to contain farmed salmon (Big Salmon, Gaspereau, Parrsboro, Stewiacke, and Upper Salmon rivers; see supplementary footnotes² for Table 1 for the Parrsboro and Harrington rivers). The endangered population with the highest reported proportions of escaped farmed salmon was the Dennys River, ME, with farmed salmon comprising 100% of the salmon spawning run in 1997 and possibly again in 2005 (only farmed salmon were found, but adult counts may have been incomplete).

Proportions and counts of escaped farmed salmon

To date, adult farmed salmon have been found in 42 rivers within a 300 km radius of the aquaculture industry in

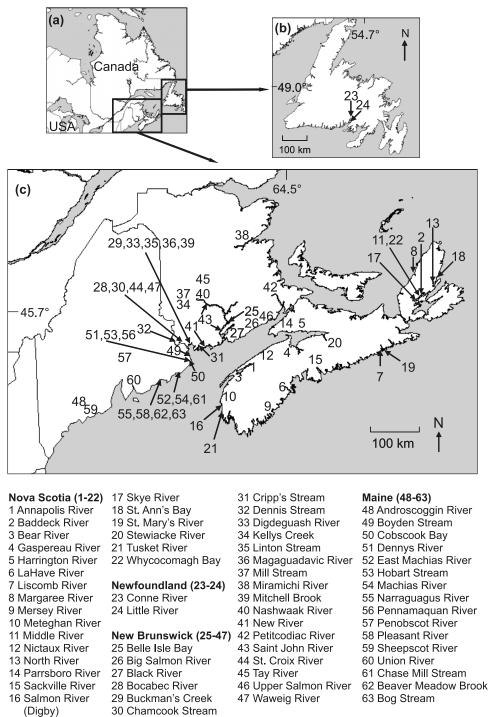
Fig. 3. Yearly mean proportions of escaped farmed Atlantic salmon (*Salmo salar*) within the salmon spawning run, averaged over all eastern North America rivers. Peaks may correspond to mass episodic escape events. The 5 years in which it is known that more than 10 000 adult farmed salmon escaped are indicated by arrows, with the estimated number of escapees noted. Data were arcsine-transformed as per Freeman and Tukey (1950).



eastern NA (Table 1). Just over half of these rivers (22) had counts or estimates of both wild and farmed salmon returns. In these investigated rivers, for at least one year, farmed salmon contributed ≥10% of the total salmon spawning run in 12 (54%), \geq 20% of the run in 9 (41%), \geq 80% of the run in 5 (23%), and 100% of the run in 3 (14%) of the rivers (Table 1). Importantly, although the proportion of farmed salmon in rivers was high in some years, it fluctuated greatly from year to year, often peaking after mass escapes (Figs. 2, 3). For example, farmed salmon proportions in the Dennys River, ME, increased from 0% to 100% over consecutive years (Fig. 2). In NS, the highest recorded proportion of farmed salmon in a river occurred in the Nictaux River in 2000 when 12 of 17 (71%) of the salmon caught in the fishway were of farmed origin. The second highest was from a partial count in 1995 in the now-endangered Stewiacke River, where farmed salmon comprised 33% of the total that had been sampled. Only two rivers in NL (Conne and Little) have been examined for the presence of farmed salmon, with the higher proportion comprising just over 2% of the run. By contrast, ME and NB were characterized by the highest farmed salmon proportions, attaining 100% in ME's Dennys River (1997 and possibly 2005) and Union River (2001 and 2005) and in NB's Bocabec River (1999). Farmed salmon have contributed to more than 80% of the run in NB's Magaguadavic River in 7 of 15 years in which counts have been made, and only once since 1994 has this proportion declined below 60% (Fig. 2c).

Collectively, for all investigations, the mean proportion of adult farmed salmon among returning wild salmon, based on Freeman and Tukey's (1950) arcsine transformation, was 0.4% (range 0% to 2.3%) in NL, 1.8% (range 0% to 71%) in NS, 20.2% (range 0% to 100%) in ME, and 16.8% (range 0% to 100%) in NB (Table 3; Fig. 5). The overall mean proportion of adult farmed salmon in eastern NA, for all investigations, was 9.2% (range 0% to 100%). For the period of 1990–2006, the mean per year for all of eastern NA fell within the range of 0.2% (1991) to 36.3% (2005) (Fig. 3). Taken another way, the sum of the number of farmed salmon from all investigations, divided by the sum of the number of all wild and farmed salmon, yielded a proportion of escaped farmed salmon of 3.0%. However, in removing two

Fig. 4. Maps of (a) northeastern North America, (b) rivers in Newfoundland (NL) mentioned in Table 1, and (c) rivers in Maine, New Brunswick, and Nova Scotia mentioned in Table 1.



rivers (Saint John and Penobscot) that accounted for a very large fraction of the total number of wild salmon in all investigations (73.4%), the proportion of farmed salmon changed to 9.8%. This is similar to our reported mean of 9.2% using the proportions of farmed salmon within individual rivers, an approach that accounts for the small size of many wild salmon populations in the region.

In Canada, the provinces containing Atlantic salmon are

partitioned into salmon fishing areas (SFAs) for management purposes. SFAs located in principal aquaculture regions include SFA 19 (eastern Cape Breton region), SFA 22 (inner Bay of Fundy), and SFA 23 (inner and outer Bay of Fundy). Investigations in these SFAs yielded mean adult farmed salmon proportions of 1.7% (range 0% to 11%), 11.1% (range 0% to 71%), and 22.6% (range 0% to 100%), respectively. For the few rivers that had been searched in

Fig. 5. Mean proportions and numbers of adult, farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers (excluding Newfoundland and Labrador): Maine, ME; Nova Scotia, NS; New Brunswick, NB. In the charts, the mean proportion of farmed salmon within the spawning run of a river for all years of available data is indicated by solid areas in each pie chart; the proportion of wild–hatchery adult salmon is indicated by open areas. The numbers above each pie chart indicate the number of years in which data were collected for a river system, and the numbers below indicate the mean number of farmed salmon found in the river system for the investigated years. Inset: location of aquaculture sites (triangles). This may include other salmonids and some sites that are not currently in operation. Inset adapted from COSEWIC (2006), Nova Scotia Fisheries and Aquaculture (2008), and Anderson (2007).

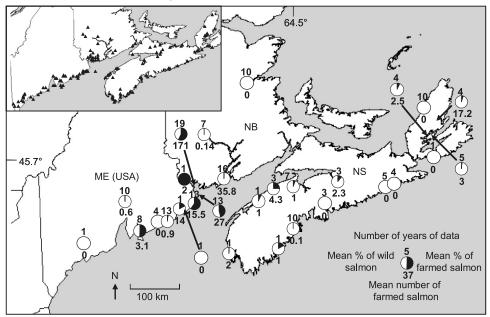


Table 3. Regional summary of information on the prevalence of escaped farmed Atlantic salmon (*Salmo salar*) in investigated eastern North American rivers.

Region	Mean % of adult farmed salmon	No. of rivers with adult farmed salmon	No. of rivers with farmed smolts	No. of rivers with farmed parr	Total no. of rivers with farmed salmon	Detection rate (no. of successful searches/total)
ME	20.2	11 of 13	1 of 1	9 of 9	16 of 17	26/61
NB	16.8	13 of 14	2 of 2	10 of 13	20 of 21	53/78
NL	0.4	2 of 2	1 of 1	N/A	2 of 2	8/25
NS	1.8	16 of 21	N/A	N/A	16 of 21	28/71
All	9.2	42 of 50	4 of 4	19 of 22	54 of 62	114/235

SFAs 16 (Miramichi and southwestern Gulf of St. Lawrence, NB), 18 (Northumberland Strait and western Cape Breton, NS), and 20 (eastern shore NS), no farmed salmon were reported. SFA 21 (southern shore NS) had a mean adult farmed salmon proportion of 0.9% (range 0% to 17%).

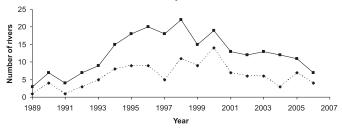
The highest number of farmed salmon counted in a river in a single year occurred in NB's Magaguadavic River in which nearly 1200 farmed salmon were captured in the fishway in 1994. Although the numbers have decreased dramatically since then, the proportion has remained relatively stable because of declining wild stocks (Fig. 2). The highest counts of farmed salmon detected in ME occurred in the Dennys River in 2001 (65 found) and 1994 (42 found). In NS, the highest counts of farmed salmon were 55 in the North River (1998) and 23 in the Baddeck River (1995), both of which are located in Cape Breton. In 1997, 10 farmed salmon were reported in NL's Conne River, the highest recorded count for a river in that province. Given

that this count was based on a subset of a sample, the true number of farmed salmon was almost certainly higher.

Discussion

Our review supports the contention that escaped farmed salmon are prevalent in rivers of eastern NA. Specifically, escaped farmed salmon have been reported in 54 rivers and bays in the region, or 87% of the watersheds that have been investigated since the inception of the salmon aquaculture industry in 1980. Most of the investigated rivers are located in the heart of the salmon aquaculture industry (Quoddy region, ME and NB), so this percentage would likely be lower if more wild salmon rivers outside of the aquaculture region were investigated. Nevertheless, escaped farmed salmon have been found continuously in appreciable numbers in the region extending from ME to Cape Breton, and this includes some rivers that are not in the primary aquaculture region

Fig. 6. Effort used in detecting farmed Atlantic salmon (*Salmo salar*) on an annual basis versus success in finding farmed salmon. The solid line represents the total number of investigated rivers in any given year; the broken line represents the number of rivers in which farmed salmon were actually found.



(e.g., Stewiacke River, NS; North River, Cape Breton, NS; Nictaux River, NS). Furthermore, the overall mean proportion of adult farmed salmon relative to wild salmon in investigated rivers over investigated years in eastern NA is estimated to be 9.2%. The proportion of farmed salmon entering rivers with annual adult runs of wild salmon has also been high (>20%) in at least one year in nearly half of the investigated rivers for which proportions were known. These proportions have fluctuated temporally, possibly peaking during mass escape events. The presence of farmed salmon in a river is often not limited to one event; that is, 80% of investigated rivers contained adult farmed salmon in multiple years. Finally, the number of rivers in which farmed salmon are detected in any given year closely reflects the search effort allocated. Collectively, the spatially broad occurrence of escaped farmed salmon in rivers of eastern NA should be cause for concern, given the conservation status of many wild salmon populations in the region (World Wildlife Fund (WWF) 2001; COSEWIC 2006) and the potentially negative impacts of such intrusions on the persistence of wild salmon (Hindar et al. 1991; Weir and Grant 2005; Hutchings and Fraser 2008).

Escape events

In eastern NA, the number of recorded escapes of farmed salmon from sea cages and freshwater hatcheries that we documented (n = 27) is most certainly an underestimate. Since 2003, aquaculture facilities in ME have been required to report escapes of 50 or more 2+ kg salmon; currently, there are no similar government regulations in eastern Canada (Naylor et al. 2005). Interestingly, reported escape events in our review coincided with peaks in annual mean farmed salmon proportions for most years. It is, therefore, possible that unexplained peaks in the numbers of farmed salmon entering rivers result from unreported escapes. The presence of sea cage farmed salmon in rivers in other, "non-peak" years could also be attributed to returning farmed salmon that were able to survive the winter at sea, or to the unreported "leaking" of farmed salmon from sea cages and hatcheries (Stokesbury et al. 2001; Naylor et al. 2005). In the context of managing the risk posed to wild salmon, these patterns, albeit speculative, suggest a means to reduce farmed-wild salmon interactions. With regards to catastrophic, large-scale escapes, "clean-ups" could be planned for nearby rivers to remove as many of these fish as possible during the next spawning run (e.g., Porter 2005). The planning and implementation of farm operation procedures with the aim of reducing such escapes could reduce or possibly eliminate "trickle losses". In Maine, growers have implemented a Hazard Assessment Critical Control Point process (HAACP) to specifically address this issue for both sea cage sites and freshwater hatcheries (Goode and Whoriskey 2003). The public reporting of escape event data would help mobilize the resources to mitigate escape events, engage a broader audience in thinking about solutions for problems, and bolster public confidence in the sustainability of the industry and wild fisheries. For these practical reasons, it is highly advisable that Canadian aquaculture facilities be required to report escapes to governmental agencies with that information then being made accessible to the public.

Incidence of farmed salmon in eastern North America and comparisons with Europe

Our documentation of 54 rivers containing escaped farmed salmon is significantly higher than 14 rivers reported by Ritter et al. (1999) and the estimate of 25 rivers documented by the North American Commission of NASCO (O'Neil et al. 2005). Our literature search found past records that had been missed by previous authors and new records from field teams investigating new sites. Nonetheless, our estimate of 54 rivers should be considered an underestimate, given that some rivers near aquaculture facilities have never been investigated or have been inadequately searched either spatially or temporally. Of the 15 rivers for which there were five years or more of data, we found that 80% contained escaped farmed salmon in multiple years, but not in every year.

The overall mean proportion of adult farmed salmon, across all years, for all investigated eastern NA rivers, was 9.2% of the wild spawning run, with a yearly range from 1990-2006 of 0.2% to 36.3%. This range is similar to that reported for rivers in Norway (yearly mean from 1989-2000: 11%-35%; Fiske and Lund 1999; Fiske et al. 2001, 2006). Alternatively, the United Kingdom, which produces approximately three times more farmed salmon than eastern NA (primarily on the west coast of Scotland), has reported the incidence of farmed salmon in the spawning runs of wild populations to be only 0.5% in Northern Ireland, 4.4% in Scotland (Walker et al. 2006), and 3.2% in England (Milner and Evans 2003). Escapees from these regions may be entrained by prevailing ocean currents (e.g., Whoriskey et al. 2006) and moved north to the coast of Norway (Hansen 2006). If this is true, available data in Europe may underestimate escapes in the UK and overestimate those in Norway.

Fate of escaped farmed salmon

Although the numbers of farmed salmon in rivers often peaked after large-scale escape events, the percentages of escaped fish that have been recovered has always been low and seems to be decreasing with time. For example, in 2000, approximately 128 000 adult salmon escaped from ME and NB aquaculture sites; in 2000–2001, 0.3% (n = 367) of the total number of escapees were recovered in rivers. A similar pattern was noted for 2005 and 2006 (0.5%). In contrast, after an escape event of 20000–40000 salmon in 1994, 5.5%–11% (n = 2200) of the farmed salmon were recovered

in ME and NB rivers in 1994–1995, despite lower search effort than in 2005–2006. There has been a general trend towards lowered farmed salmon numbers in the St. Croix, Saint John, and Dennys rivers as well.

The apparent decrease in the recovery of escaped salmon in rivers could be attributable to several factors. First, it is likely that more escapes occurred in 1994 than were reported; however, to achieve the same recapture rate as 2000-2001 and 2005-2006, 730 000 salmon would have had to have escaped, a number considerably higher than that of any other year. A second possibility is that farmed salmon are experiencing the same high mortalities at sea that are currently threatening wild salmon populations (ASF 2006). This could be evidenced by the relative stability of the proportion of farmed salmon in the Magaguadavic River despite decreasing wild stocks and large escape events. Third, farmed salmon may be less equipped to cope with the natural environment now than they were 10 years ago due to successive generations of domestic breeding (Fleming et al. 2000; Roberge et al. 2006). Fourth, predation rates of farmed salmon could have increased if predators have learned to target the escaped fish (e.g., Whoriskey et al. 2006). Fifth, the 1994 escape event occurred immediately prior to the spawning period, increasing the probability that farmed salmon would return to the rivers and again highlighting the need for aquaculture companies to report escape events immediately. Sixth, in 1994, >50% of the salmon aquaculture industry's smolts were raised in the Magaguadavic watershed, potentially imprinting the farmed smolts to the Magaguadavic and increasing their likelihood to home in to it (e.g., Whoriskey and Carr 2001). Whatever the causes, more studies such as that undertaken by Whoriskey et al. (2006) are needed to establish the fate of farmed salmon at sea

Potential caveats and data deficiencies

Although the numbers and proportions of farmed salmon may be somewhat biased, any potential biases could not be accounted for in our calculations. Biases could be caused by, for example, the time period during which the salmon run counts were made. Those counts that persisted over a longer time have a greater chance of being accurate, as the numbers of farmed salmon returning to rivers can vary considerably from month to month (Carr et al. 1997; Fiske et al. 2006). The counting method can also affect the proportions and numbers of farmed salmon that are recorded (mark-recapture studies are estimates, swim and shore counts only visually identify salmon, weirs do not capture every salmon going upriver). The method used to determine the origins of the salmon could also bias farmed salmon counts, as identification based on external characteristics (fin erosion, body size, etc.) has led to an underestimation of adult farmed salmon in the past (e.g., Union River, ME, in 2001), and before 2004, there was not a reliable way to identify farmed salmon adults that had escaped as juveniles (Lacroix and Stokesbury 2004). Also, there is the problem of misclassifying a hatchery-released salmon as a farmed escapee, and vice versa. Scale analyses and genetic testing are the most reliable means of identifying farmed salmon but have not been employed in every investigated river. All of these potential biases highlight the need for a standardized way of investigating rivers for the presence or absence of farmed salmon.

Our review also identifies gaps in the spatial distribution of data and thus areas in which further investigation for farmed salmon in eastern NA is merited. Effort was highest in existing major areas of salmon farming in NB, ME, and Cape Breton (NS), but was low along the South Shore of Nova Scotia. This is despite the fact that Nova Scotia's salmon aquaculture industry has experienced a 900% increase in production from 1995 to 2005 (Statistics Canada 2006), with the majority of salmon farming activity occurring along the South Shore. Effort was also low in areas located considerable distances from salmon farming and was almost entirely absent east of the Saint John River, NB. Overall, search effort peaked in 1998 but has been steadily decreasing ever since, despite an increase in farmed salmon production in eastern Canada and several mass episodic escapes.

On a temporal scale, ME, NB, and NL have the most complete data set for certain rivers, having continuous counts for approximately one decade beginning in the mid-1990s for nine rivers (Dennys, Narraguagus, Penobscot, and Union rivers in ME; Magaguadavic, Saint John, and St. Croix rivers in NB; Conne and Little rivers in NL). These long-term ecological data sets are vital to determining the potential impact of farmed—wild salmon interactions (Hutchings 1991; Hindar et al. 2006). Although there are no continuous data sets for any river in NS, despite the presence of farmed salmon in more rivers than ME, NB, or NL, the effort in NS has, in terms of numbers of rivers searched, been greater than that expended in any other region.

There is also a bias in the data with respect to age class. Almost all the reported data are based on adult counts; very little effort has been directed towards the detection of farmed parr and smolts (but see Stokesbury and Lacroix 1997; Stokesbury et al. 2001; Carr and Whoriskey 2006). This relative lack of effort is unfortunate given the observation that farmed juvenile escapees in Europe have a tendency to return to their river of origin as adults (Hansen and Jonsson 1991), whereas adult escapees tend to disperse widely (Hansen 2006), and given that juvenile escapees appear to be more reproductively successful as adults than adult escapees (Fleming et al. 1997). Although episodic escapes of farmed parr and smolts may not be frequent, mass escapes can still occur, e.g., the escape of 100 000 farmed parr during a storm in NL in 1995 (Fisheries and Oceans Canada 1996). Until 2004, standard scale analyses were unable to identify farmed salmon adults that had escaped as juveniles (Lacroix and Stokesbury 2004); thus there has been ample time for farmed-wild introgression to be initiated in wild salmon populations. A comprehensive evaluation of the true impact of such introgression in eastern NA is difficult to undertake given that so little data have been collected on the incidence of farmed salmon in rivers and the effects of farmed-wild interbreeding on wild salmon fitness.

It should also be noted that although this paper focuses exclusively on Atlantic salmon, there are other nonindigenous salmonid species that are being farmed and are escaping in eastern NA. Escaped farmed rainbow trout (*Oncorhynchus mykiss*) have been recorded in 35 NL rivers alone (O'Neil et al. 2005), in addition to several other rivers in NB and NS.

Implications for risk assessment

Our review provides a comprehensive first step in assessing the scale and scope of the impact that escaped farmed salmon may have on wild salmon populations in eastern NA. Limited work has been done on farmed-wild salmon interactions, with most of it being done in Europe (e.g., Fleming et al. 1997; McGinnity et al. 1997, 2003). Results suggest that farmed salmon can exhibit lower genetic variability than wild salmon (Norris et al. 1999) and that the introgression of farmed salmon genes into a wild population can be comparatively rapid (Garant et al. 2003; Weir et al. 2004). This combination can result in a form of genetic "homogenization" (Fleming et al. 2000), such that the limited genetic variability of the farmed salmon accounts for an increasing proportion of the total population variability (Tufto and Hindar 2003). The consequences of this genetic introgression on fitness, in addition to ecological factors such as competition and disease, are hypothesized to be, in general, negative (reviewed in Jonsson and Jonsson 2006; Hutchings and Fraser 2008; Thorstad et al. 2008). Despite this body of research, little has been done to date to determine whether the consequences of farmed salmon to wild salmon fitness in eastern NA are likely to be similar to those documented in Europe.

What is known in eastern NA is that farmed salmon are appearing in rivers at an overall mean of 9.2% of the spawning run, but occurring in some rivers in some years at proportions exceeding 80%. It is also known that large episodic escapes of farmed salmon occur and that farmed salmon are often found in the same river over multiple years. Furthermore, the successful spawning of farmed salmon has been recorded in several eastern NA rivers (Carr et al. 1997; Lage and Kornfield 2006). Roberge et al. (2006) showed that the farmed salmon strain originating from the Saint John River (NB) exhibited heritable changes in gene expression after five to seven generations of domestication. Most recently, Fraser et al. (2008) showed that crossing Saint John River farmed salmon with wild salmon from one NS population resulted in outbreeding depression in first-generation (F1) farmed-wild hybrid progeny under wild-like conditions. Complexities in the fitness rebound of later generation farmed-wild hybrids (e.g., F2, backcrosses) suggested that divergent mechanisms affect the performance of different farmed-wild hybrids (Fraser et al. 2008). Thus, although limited, available data in eastern NA suggest that the potential risk of both genetic homogenization and a loss of local adaptation in NA wild Atlantic salmon populations due to introgression with farmed fish should be considered high.

Given the implications of our findings from a risk-assessment perspective, we offer the following recommendations (see also Hansen and Windsor 2006). First, escapes of farmed salmon must be immediately reported by aquaculture companies to the government in regions where this is not already done, and this information should be made available to the public. This is an essential step in that those rivers in which the escaped farmed salmon are likely to appear can be monitored and the escapees recovered before they have the opportunity to spawn. This information will provide an empirical basis for the parameterization of ecological impact models. The report should include the numbers of salmon that escaped, the date and time of the escape, the size and life stage (including maturity status) of the salmon, and their

health status (Hansen and Windsor 2006). Second, farmed salmon should be marked in such a way that they can be traced back to the aquaculture site of origin, and initiatives to favor continued improvements in containment at farms should be initiated. These initiatives could include improvements in sea cage technologies and sites and in the formation of a clear regulatory environment. Third, methods need to be developed and implemented to identify commercially produced juvenile salmon that escape to fresh water and the offspring of farmed or farmed-wild hybrids in fresh water. Methods are also needed to distinguish farm-origin juveniles from endangered juvenile salmon that have been reared for varying periods in hatcheries before being released to the wild as part of restoration efforts. Identification methods need to be standardized and consistently used in all investigated rivers.

The declining abundance of wild Atlantic salmon, coupled with the ever-increasing production of salmon of aquaculture origin, draws attention to the fundamental need for empirically rigorous assessments of potential risks associated with interactions between wild and farmed individuals. Our compilation of all existing data on escaped farmed salmon in eastern NA is intended to contribute to such a process.

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References

- Anderson, J.M. 2007. The salmon connection the development of Atlantic salmon aquaculture in Canada. Glen Margaret Publishing, Tantallon, N.S.
- Anscombe, F.J. 1948. The transformation of Poisson, binomial, and negative binomial data. Biometrika, **35**: 246–254.
- Atlantic Salmon Federation. 2006. Status of North American wild Atlantic salmon in 2006: Atlantic salmon at the balancing point — an urgency to understand mortality at sea [online]. Available at www.asf.ca/docs/media/ASFstate.pdf [accessed 13 August 2008].
- Baum, E.T. 1998. History and description of the Atlantic salmon aquaculture industry in Maine. Canadian Stock Assessment Secretariat Research Document 98/152 Revised, Fisheries and Oceans Canada, Ottawa, Ont.
- Carr, J.W. 2005. Restoration of western Fundy Atlantic salmon final report to NB Environmental Trust Fund, April 2005. Atlantic Salmon Federation, St. Andrews, N.B.
- Carr, J.W., and Whoriskey, F.G. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. ICES J. Mar. Sci. 63: 1263–1268. doi:10.1016/j.icesjms.2006.03.020.
- Carr, J.W., Anderson, J.M., Whoriskey, F.G., and Dilworth, T. 1997.
 The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES J. Mar. Sci. 54: 1064–1073.
- Committee on the Status of Endangered Wildlife in Canada. 2006. COSEWIC assessment and update status report on the Atlantic salmon *Salmo salar* (inner Bay of Fundy populations) in Canada [online]. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont. Available at http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_atlantic_salmon_inner_bay_e.pdf [accessed 13 August 2008].
- Crozier, W.W. 2000. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. Fish. Manag. Ecol. **7**(5): 437–446. doi:10.1046/j.1365-2400.2000.00219.x.
- Dempson, J.B., and Power, M. 2004. Use of stable isotopes to distinguish farmed from wild Atlantic salmon, *Salmo salar*. Ecol. Freshwat. Fish, **13**: 176–184. doi:10.1111/j.1600-0633.2004. 00057.x.
- Fisheries and Oceans Canada. 1996. Report on the status of Atlantic salmon stocks in eastern Canada in 1995. DFO Atlantic Fisheries Stock Status Report 96/80, Atlantic Stock Assessment Secretariat, Fisheries Research Branch, Fisheries and Oceans Canada, Ottawa, Ont. Available at www.meds-sdmm.dfo-mpo. gc.ca/csas/applications/Requests/Request_e.asp.
- Fiske, P., and Lund, R.A. 1999. Rømt oppdrettslaks i sjø- og elvefisket i årene 1989–1998. NINA Oppdragsmelding, **603**: 1–23. [With English abstract.]
- Fiske, P., Lund, R.A., Østborg, G.M., and Fløystad, L. 2001. Rømt oppdrettslaks i sjø- og elvefisket i årene 1989–2000. NINA Oppdragsmelding, **704**: 1–26. [With English abstract.]
- Fiske, P., Lund, R.A., and Hansen, L.P. 2006. Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989–2004. ICES J. Mar. Sci. 63(7): 1182–1189. doi:10.1016/j.icesjms.2006.04.006.
- Fleming, I.A., Jonsson, B., Gross, M.R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). J. Appl. Ecol. 33(4): 893–905. doi:10.2307/2404960.
- Fleming, I.A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behav. Ecol. **8**(5): 470–480. doi:10.1093/beheco/8.5.470.

- Fleming, I.A., Hindar, K., Mjølnerød, I.B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proc. R. Soc. Lond. B, Biol. Sci. 267: 1517–1523. doi:10.1098/rspb.2000.1173.
- Fraser, D.J., Jones, M.W., McParland, T.L., and Hutchings, J.A. 2007a. Loss of historical immigration and the unsuccessful rehabilitation of extirpated salmon populations. Conserv. Genet. 8: 527–546. doi:10.1007/s10592-006-9188-8.
- Fraser, D.J., Weir, L.K., Darwish, T.L., Eddington, J.D., and Hutchings, J.A. 2007b. Divergent compensatory growth responses within species: linked to contrasting migrations in salmon? Oecologia (Berl.), 153: 543–553. doi:10.1007/s00442-007-0763-6.
- Fraser, D.J., Cook, A.M., Eddington, J.D., Bentzen, P., and Hutchings, J.A. 2008. Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. Evol. Appl. 1: 501–512. doi:10.1111/j.1752-4571.2008.00037.x.
- Freeman, M.F., and Tukey, J.W. 1950. Transformations related to the angular and the square root. Ann. Math. Stat. 21: 607–611. doi:10.1214/aoms/1177729756.
- Garant, D., Fleming, I.A., Einum, S., and Bernatchez, L. 2003. Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. Ecol. Lett. 6(6): 541–549. doi:10.1046/j.1461-0248.2003.00462. x.
- Garcia de Leaniz, C., Fleming, I., Einum, S., Verspoor, E., Jordan, W.C., Consuegra, S., Aubin-Horth, N., Lanjus, D., Lecher, B.H., Youngson, A.F., Webb, J.H., Vøllestad, L.A., Villanueva, B., Ferguson, A., and Quinn, T.P. 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biol. Rev. Camb. Philos. Soc. 82: 173–211. doi:10. 1111/j.1469-185X.2006.00004.x. PMID:17437557.
- Gausen, D., and Moen, V. 1991. Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Can. J. Fish. Aquat. Sci. **48**(3): 426–428. doi:10.1139/f91-055.
- Goode, A., and Whoriskey, F. 2003. Finding resolution to farmed salmon issues in Eastern North America. *In Salmon at the Edge. Edited by Derek Mills. Blackwell Science*, Oxford, UK. pp. 144–158.
- Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 131–144. doi:10.1139/cjfas-55-S1-131.
- Gudjonsson, S. 1991. Occurrence of reared salmon in natural salmon rivers in Iceland. Aquaculture, 98: 133–142. doi:10.1016/0044-8486(91)90378-K.
- Hansen, L.P. 2006. Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. ICES J. Mar. Sci. 63(7): 1211–1217. doi:10.1016/j.icesjms.2006. 04 022
- Hansen, L.P., and Jacobsen, J.A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar L.*, in oceanic areas north of the Faroe Islands. ICES J. Mar. Sci. **60**(1): 110–119. doi:10.1006/jmsc.2002.1324.
- Hansen, L.P., and Jonsson, B. 1991. The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult return. Aquaculture, **98**: 61–67. doi:10.1016/0044-8486(91)90371-D.
- Hansen, L.P., and Windsor, M. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. Convener's Report. NINA Special Report No. 34, Trondheim, Norway.

- Hansen, L.P., Reddin, D.G., and Lund, R.A. 1997. The incidence of reared Atlantic salmon (*Salmo salar L.*) of fish farm origin at West Greenland. ICES J. Mar. Sci. 54(1): 152–155. doi:10. 1006/jmsc.1996.0178.
- Hansen, L.P., Jacobsen, J.A., and Lund, R.A. 1999. The incidence of escaped farmed Atlantic salmon, *Salmo salar L.*, in the Faroese fishery and estimates of catches of wild salmon. ICES J. Mar. Sci. 56(2): 200–206. doi:10.1006/jmsc.1998.0437.
- Hindar, K., Ryman, N., and Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. 48: 945–957. doi:10.1139/f91-111.
- Hindar, K., Fleming, I.A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES J. Mar. Sci. 63: 1234–1247. doi:10.1016/j.icesjms.2006.04.025.
- Hutchings, J.A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. Aquaculture, 98: 119–132. doi:10.1016/0044-8486(91)90377-J.
- Hutchings, J.A., and Fraser, D.J. 2008. The nature of fisheries- and farming-induced evolutionary change. Mol. Ecol. 17: 294–313. doi:10.1111/j.1365-294X.2007.03485.x. PMID:17784924.
- Innal, D., and Erk'akan, F. 2006. Effects of exotic and translocated fish species in the inland waters of Turkey. Rev. Fish Biol. Fish. **16**: 39–50. doi:10.1007/s11160-006-9005-y.
- International Council for the Exploration of the Sea. 2007. Report of the Working Group on North Atlantic salmon (WGNAS) [online]. ICES WGNAS Report 2007, ICES CM 2007/ACFM:13, Advisory Committee on Fishery Management, International Council for the Exploration of the Sea, Copenhagen, Denmark. Available at www.ices.dk/reports/ACOM/ 2007/WGNAS/WGNAS07.pdf [accessed 13 August 2008].
- Jones, R.A., Anderson, L., and Goff, T. 2004. Assessments of Atlantic salmon stocks in southwest New Brunswick, an update to 2003. Canadian Science Advisory Secretariat Research Document 2004/019, Fisheries and Oceans Canada, Ottawa, Ont. Available at www.dfo-mpo.gc.ca/csas/Csas/DocREC/2004/ RES2004_019_e.pdf [accessed 13 August 2008].
- Jonsson, B., and Jonsson, N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. ICES J. Mar. Sci. 63: 1162–1181. doi:10.1016/j.icesjms.2006. 03.004.
- King, T.L., Kalinowski, S.T., Schill, W.B., Spidle, A.P., and Lubinski, B.A. 2001. Population structure of Atlantic salmon (*Salmo salar L.*): a range-wide perspective from microsatellite DNA variation. Mol. Ecol. 10: 807–821. doi:10.1046/j.1365-294X.2001.01231.x. PMID:11348491.
- Lacroix, G.L., and Stokesbury, M.J. 2004. Adult return of farmed Atlantic salmon escaped as juveniles into freshwater. Trans. Am. Fish. Soc. 133: 484–490. doi:10.1577/03-022.
- Lage, C., and Kornfield, I. 2006. Reduced genetic diversity and effective population size in an endangered Atlantic salmon (*Salmo salar*) population from Maine, USA. Conserv. Genet. 7: 91–104. doi:10.1007/s10592-005-8669-5.
- Lund, R.A., and Hansen, L.P. 1991. Identification of wild and reared Atlantic salmon, *Salmo salar L.*, using scale characters. Aquacult. Fish. Manage. 22: 499–508.
- Lund, R.A., Økland, F., and Hansen, L.P. 1991. Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. Aquaculture, 98: 143–150. doi:10.1016/0044-8486(91)90379-L.
- Lura, H., and Sægrov, H. 1991. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture, **98**: 151–159. doi:10. 1016/0044-8486(91)90380-P.
- Maine Department of Marine Resources. 2006. Aquaculture lease

- inventory [online]. Available from the Maine Department of Marine Resources at www.maine.gov/dmr/aquaculture/leaseinventory2006/index.htm [accessed 13 August 2008].
- McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D.,
 Hynes, R., McCamley, C., Cross, T., and Ferguson, A. 1997.
 Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J. Mar. Sci. 54: 998–1008.
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Ó Maoiléidigh, N., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., and Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc. R. Soc. Lond. Ser. B Biol. Sci. 270: 2443–2450. doi:10. 1098/rspb.2003.2520.
- McVicar, A.H. 1997. Disease and parasite implications of the coexistence of wild and cultured Atlantic salmon populations. ICES J. Mar. Sci. **54**(6): 1093–1103.
- Milner, N.J., and Evans, R. 2003. The incidence of escaped Irish farmed salmon in English and Welsh rivers. Fish. Manag. Ecol. **10**: 403–406. doi:10.1111/j.1365-2400.2003.00348.x.
- Mjølnerød, I.B., Refseth, U.H., Karlsen, E., Balstad, T., Jakobsen, K.S., and Hindar, K. 1997. Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. Hereditas, 127: 239–248. doi:10.1111/j.1601-5223.1997.t01-1-00239.x.
- Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Mooney, H., and Troell, M. 2000. Effect of aquaculture on world fish supplies. Nature (London), 405: 1017–1024. doi:10.1038/35016500. PMID:10890435.
- Naylor, R., Hindar, K., Fleming, I.A., Goldburg, R., Williams, S., Volpe, J., Whoriskey, F., Eagle, J., Kelso, D., and Mangel, M. 2005. Fugitive salmon: assessing the risks of escaped fish from net-pen aquaculture. Bioscience, 55(5): 427–437. doi:10.1641/0006-3568(2005)055[0427:FSATRO]2.0.CO;2.
- Newfoundland and Labrador Department of Fisheries and Aquaculture. 2006. Fact sheet: aquaculture highlights Newfoundland and Labrador 2005 [online]. Available from the Newfoundland and Labrador Department of Fisheries and Aquaculture at www. fishaq.gov.nl.ca/statistics/fact%20sheet%202005%20mar%20o6. pdf [accessed 2 March 2007].
- Norris, A.T., Bradley, D.G., and Cunningham, E.P. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. Aquaculture, **180**(3–4): 247–264. doi:10.1016/S0044-8486(99)00212-4.
- Nova Scotia Fisheries and Aquaculture. 2008. Salmonid aquaculture sites map [online]. Available from Nova Scotia Fisheries and Aquaculture at www.gov.ns.ca/fish/aquaculture/aquamap. shtml [accessed 13 August 2008].
- O'Neil, S.F., Olivier, G., Colligan, M., and Bean, D. 2005. NAC Scientific Working Group on Salmonid Introductions and Transfers report of activities 2004/2005. Report of the 22nd Annual Meeting of the Commission. North American Commission NAC(05), North Atlantic Salmon Conservation Organization, Vichy, France.
- O'Reilly, P.T., Carr, J.W., Whoriskey, F.G., and Verspoor, E. 2006. Detection of European ancestry in escaped farmed Atlantic salmon, *Salmo salar* L., in the Magaguadavic River and Chamcook Stream, New Brunswick, Canada. ICES J. Mar. Sci. 63: 1256–1262. doi:10.1016/j.icesjms.2006.04.013.
- Porter, G. 2005. Protecting wild Atlantic salmon from impacts of salmon aquaculture: a country-by-country progress report, 2nd

- report, 2005 [online]. Available from the Atlantic Salmon Federation and World Wildlife Fund at www.asf.ca/docs/issues/impacts2005.pdf [accessed 13 August 2008].
- Ritter, J., Stewart, J.E., and Lacroix, G.L. 1999. Interaction between wild and farmed Atlantic salmon in the Maritime provinces [online]. DFO Maritimes Regional Habitat Status Report 99/1E. Available from Fisheries and Oceans Canada, Dartmouth, N.S., at www.mar.dfo-mpo.gc.ca/science/rap/internet/hsr99-1e. pdf [accessed 13 August 2008].
- Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Mol. Ecol. 15: 9–20. doi:10. 1111/j.1365-294X.2005.02807.x. PMID:16367826.
- Schiermeier, Q. 2003. Fish farms' threat to salmon stocks exposed [online]. Nature (London), **425**: 753. Available at www.nature. com/nature/journal/v425/n6960/full/425753a.html [accessed 13 August 2008].
- Skaala, Ø., Høyheim, B., Glover, K., and Dahle, G. 2004. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. Aquaculture, 240(1–4): 131–143. doi:10.1016/j.aquaculture. 2004.07.009.
- Soto, D., Jara, F., and Moreno, C. 2001. Escaped salmon in the inner seas, southern Chile: facing ecological and social conflicts. Ecol. Appl. 11(6): 1750–1762. doi:10.1890/1051-0761(2001) 011[1750:ESITIS]2.0.CO;2.
- Statistics Canada. 2006. Aquaculture statistics 2005 [online]. Cat. No. 23-222-XIE. Available at www.statcan.ca/english/freepub/23-222-XIE/23-222-XIE2005000.pdf [accessed 13 August 2008].
- Stokesbury, M.J., and Lacroix, G.L. 1997. High incidence of hatchery origin Atlantic salmon in the smolt output of a Canadian river. ICES J. Mar. Sci. 54: 1074–1081.
- Stokesbury, M.J., Lacroix, G.L., Price, E.L., Knox, D., and Dadswell, M.J. 2001. Identification by scale analysis of farmed Atlantic salmon juveniles in southwestern New Brunswick rivers. Trans. Am. Fish. Soc. 130: 815–822. doi:10.1577/1548-8659(2001)130<0815:IBSAOF>2.0.CO;2.
- The Australian. June 14, 2007. Salmon escape sparks fishing frenzy [online]. News Limited. Available at www.theaustralian.news. com.au/story/0,20867,21904536-5006788,00.html [accessed 2 July 2007].
- Thorstad, E.B., Fleming, I.A., McGinnity, P., Soto, D., Wennevik, V., and Whoriskey, F. 2008. Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. Report from the Technical Working Group on Escapes of the Salmon Aquaculture Dialogue. Available online from the Atlantic Salmon Federation at www.asf.ca/docs/media/impacts-escapes-2008.pdf [accessed 5 December 2008].
- Tufto, J., and Hindar, K. 2003. Effective size in management and conservation of subdivided populations. J. Theor. Biol. **222**: 273–281. doi:10.1016/S0022-5193(03)00018-3. PMID:12732474.

- UN Food and Agriculture Organization. 2006. World review of fisheries and aquaculture 2006 [online]. Available at ftp.fao.org/ docrep/fao/009/a0699e/a0699e01.pdf [accessed 13 August 2008].
- US Atlantic Salmon Assessment Committee. 2006. Annual report of the U.S. Atlantic Salmon Assessment Committee Report No. 18-2005 activities. US Atlantic Salmon Assessment Committee, Gloucester, Mass.
- Volpe, J.P., Taylor, E.B., Rimmer, D.W., and Glickman, B.W. 2000. Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. Conserv. Biol. **14**(3): 899–903. doi:10.1046/j.1523-1739.2000.99194.x.
- Walker, A.M., Beveridge, M.C.M., Crozier, W., Ó Maoiléidigh, N., and Milner, N. 2006. Monitoring the incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in rivers and fisheries of the United Kingdom and Ireland: current progress and recommendations for future programmes. ICES J. Mar. Sci. 63: 1201– 1210. doi:10.1016/j.icesjms.2006.04.018.
- Webb, J.H., McLaren, I.S., Donaghy, M.J., and Youngson, A.F. 1993. Spawning of farmed Atlantic salmon, *Salmo salar L.*, in the second year after their escape. Aquacult. Fish. Manage. **24**(4): 557–561.
- Weir, L.K., and Grant, J.W. 2005. Effects of aquaculture on wild fish populations: a synthesis of data. Environ. Rev. 13(4): 145– 168. doi:10.1139/a05-012.
- Weir, L.K., Hutchings, J.A., Fleming, I.A., and Einum, S. 2004. Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. J. Anim. Ecol. **73**(6): 1069–1079. doi:10.1111/j. 0021-8790.2004.00876.x.
- Whoriskey, F., and Carr, J.W. 2001. Returns of transplanted adult, escaped, cultured Atlantic salmon to the Magaguadavic River, New Brunswick. ICES J. Mar. Sci. **58**(2): 504–509. doi:10. 1006/jmsc.2000.1031.
- Whoriskey, F.G., Brooking, P., Doucette, G., Tinker, S., and Carr, J.W. 2006. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES J. Mar. Sci. 63: 1218–1223. doi:10.1016/j.icesjms.2006.04.002.
- World Wildlife Fund. 2001. The status of wild Atlantic salmon—
 a river by river assessment [online]. Available from the World
 Wildlife Fund at www.panda.org/about_wwf/what_we_do/
 marine/publications/index.cfm?uNewsID=3729 [accessed 13 August 2008].
- Youngson, A.F., Webb, J.H., MacLean, J.C., and Whyte, B.M. 1997. Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. ICES J. Mar. Sci. 54(6): 1216–1220. doi:10.1016/S1054-3139(97)80028-8.
- Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, N.J.