

# Occupancy dynamics of escaped farmed Atlantic salmon in Canadian Pacific coastal salmon streams: implications for sustained invasions

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**Abstract** Farmed non-native Atlantic salmon (*Salmo salar*) is the largest agriculture export product of British Columbia, Canada. Chronic low-volume escapes of salmon from farms into Pacific waters (“leakage”) are typically undetectable (Britton et al. 2011). Analysis of escape-reporting from farmers indicates that reports greatly underestimate the true number of Atlantic salmon inadvertently released from open-net pen rearing sites (Morton and Volpe 2002). To quantify the spatial extent of escaped Atlantic salmon in Canadian Pacific rivers, we systematically snorkel-surveyed 41 known Pacific salmon (*Oncorhynchus* spp.)-supporting rivers and creeks on Vancouver Island over a span of 3 years. We estimated and accounted for imperfect detections using multi-season occupancy models. We detected Atlantic salmon in 36.6 % of surveyed rivers. After accounting for imperfect detection, occupancy models estimated that over half of surveyed streams across the study area contained Atlantic salmon, and that 97 % of streams with high native salmon diversity were occupied by Atlantic salmon. Even in intensive

snorkel surveys, Atlantic salmon are detected in occupied streams only 2/3 the time, suggesting abundance and distribution of non-native salmon is greater than indicated by the only existing data. Further, Atlantic salmon are more likely to occupy streams with high native Pacific salmon diversity—and more likely to maintain occupancy across years—potentially increasing competitive pressure on native salmonids. Understanding local biotic and abiotic predictors of Atlantic salmon occupancy, stream colonization, and local extinction requires more data; the same is true for the effects of escaped Atlantic salmon on local salmon diversity and sustainability. These data for the first time show that Atlantic salmon occupy Pacific coastal rivers for multiple years. The impact of Atlantic salmon occupancy in British Columbia rivers must be factored into policy decisions regarding the future of salmon farming in the provincial waters.

**Keywords** Atlantic salmon · Pacific salmon · *Salmo* · *Oncorhynchus* · Occupancy · Aquaculture · Invasion

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## Introduction

Salmon farming is a major economic activity in coastal British Columbia (BC). In BC, three kilograms of farm salmon are brought to market for each

kilogram of wild salmon (BC Ministry of Environment 2010 data). Commercial salmon culture in BC is dominated by non-native Atlantic salmon (*Salmo salar*) which comprises approximately 95 % of total farm salmon production (BC Ministry of Environment 2010 data). Globally, salmon farming has increased over 50-fold since the 1980s (Porter 2003) while annual compounded growth of global aquaculture has been 9.2 %, more than three times that of terrestrial meat agriculture (2.8 %) (Lubchenco 2003). Contrasting to this rampant growth, Sumaila et al. (2005) observed declining wild salmon landings in BC while wild salmon landings in adjacent Alaska, where salmon farming is banned, increased over the same period—though multiple differential factors such as logging and salmon harvest policies likely contribute.

The ecological impacts of industrial-scale aquaculture, and salmon farming in particular, have drawn significant attention of late. In BC, the almost total reliance of the salmon farming industry on an exotic species has clear implications. There exists significant potential for farm escapees to negatively affect native species, and permanent colonization of Atlantic salmon in the Pacific Ocean cannot be discounted (Volpe et al. 2000, 2001a, 2001b; Morton and Volpe 2002). While the risk of escape can be reduced and even eliminated with alternative production techniques (e.g. closed containment) the economic constraints resulting from the commoditization of salmon currently limits large-scale implementation of such technologies (Volpe and Shaw 2008).

Virtually all farmed salmon produced around the world are grown in *open-net pens*, the most cost-effective method of production. However, such production systems are prone to fish escape events, either as chronic low-volume “leakage” or episodic high-volume net pen failures. Farm-level assessments of escapes have been shown to consistently underestimate escapes (Morton and Volpe 2002), since detection is impossible below threshold levels (Britton et al. 2011). Further, discrete high-volume escape events often go unreported until Atlantic salmon appear in commercial Pacific salmon fishermen’s nets (Sumaila et al. 2005). Such haphazard reporting represent the only data on Atlantic salmon occurrence in Pacific waters. Ad-hoc and passive reporting mechanisms greatly underestimate Atlantic salmon presence in the wild (Morton and Volpe 2002). Moreover, despite identical farm infrastructure and operating procedures,

the reported rate of escapes from BC salmon farms is orders of magnitudes less than in all other salmon farming countries, casting significant doubt on the veracity of BC data. These and other irregularities in the BC reporting system (Volpe et al. 2010) make the current status of Atlantic salmon in BC unknowable, as is by extension the impact on native Pacific salmon.

Despite a decade of virtually no monitoring of escaped farm salmon in British Columbia, the potential magnitude and biological impact of invasion has not diminished. The lack of attention, effort and data cannot be construed as the issue of escaped salmon being resolved. The vast majority of BC rivers flow through wilderness and the potential for colonization to occur without documentation is considerable. Our data set, collected over three years, 1997–1999, from standardized and repeated Atlantic salmon surveys on the Pacific coast (including the rest of BC, Alaska and Washington) is the only scientific survey in existence despite  $\gg 100,000$  reported escapes. These data revealed numerous rivers inhabited by Atlantic salmon, but until recently there was no method by which to estimate the degree to which salmon may have been missed in these surveys, nor any robust estimate of the fraction of Pacific salmon streams occupied by escaped Atlantic salmon. New and powerful hierarchical modelling techniques have since come to the fore that allow us to examine the probability of detecting escaped salmon, and estimate the occupancy rate of Atlantic salmon in Pacific coast streams, to help contextualize the invasion risk.

A notable problem in species surveys, particularly with rare, elusive, or uncommon species, is that of false absences. When a species is not detected at a site, one cannot be sure whether a species is (1) truly absent from a site, or (2) present but undetected (Mackenzie 2005; Mackenzie et al. 2002, 2006). This is particularly germane to Atlantic salmon, since population sizes below a threshold level have proven undetectable (Britton et al. 2011). Mackenzie et al. (2002) formulated this basic problem and illustrated that species occupancy at a site must be modelled in conjunction with the probability of detecting that species when it is, in fact, present. This probability of detection ( $p$ ) is often less than one (Mackenzie et al. 2002), meaning that unadjusted or naive counts of occurrence are negatively biased. Estimating  $p$  provides key information to more accurately estimate species occupancy at sites across a study landscape.

Mackenzie et al. (2003) further demonstrate that occupancy dynamics can be modeled through time, providing estimates of local extinction and invasion. We applied these multi-year occupancy models to the dataset on escaped Atlantic salmon in BC streams. We modelled serial detections/non-detections in an occupancy framework to estimate the probability of detecting an Atlantic salmon, given it is there; the probability of Atlantic salmon occupancy within Pacific rivers; extinction rates of occupied rivers; invasion rates of unoccupied rivers; and rates of change of occupancy across years. We tested whether Atlantic salmon were more or less likely to occupy streams already inhabited by native Pacific salmon, and whether Atlantic salmon occupancy changed or stayed stable throughout the 3 years of surveys.

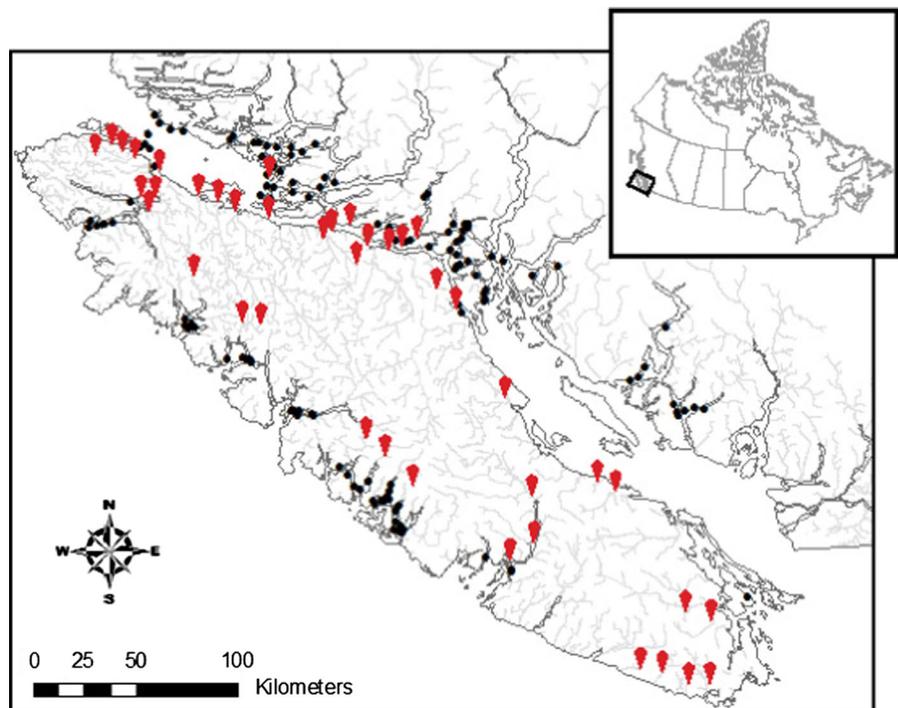
## Methods

Forty-one rivers on Vancouver Island were surveyed by snorkel surveys in 1997, 1998, and 1999 (Fig. 1). Candidate rivers for survey were restricted to systems known to support migratory Pacific salmon populations. Streams were distributed across Vancouver

Island. Salmon farms are aggregated in sounds across Vancouver Island and lower mainland British Columbia (Living Oceans Society 2013). Depending on the length of the river system, snorkel surveys ranged from 0.5 to 9.0 km in length. The number of repeat surveys conducted in each stream in each year ranged from 1 to 5. Not all rivers were surveyed in each year, but occupancy models are robust to missing dependent data (Mackenzie et al. 2006). Species identity and age-class were recorded of all individual salmonids identified during each survey. Atlantic salmon are morphologically and behaviourally distinct from Pacific species and so are readily identifiable in snorkel surveys. We also recorded the presence of Pacific salmonids, including Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon in addition to anadromous steelhead trout (*O. mykiss*).

We created hierarchical models in the program *Presence* (ver. 41; Hines 2006) informed by Atlantic salmon detection histories for each river. Hierarchical occupancy models can be considered as simultaneous generalized linear models (GLMs) of serial detection data, applied to each component of the model, with binomial errors (logistic link). *Presence* fits the GLM

**Fig. 1** We surveyed the occurrence of Atlantic salmon that had escaped from fish farms (*black dots*), and native Pacific salmon, in 41 Pacific coast rivers and creeks (*red diamonds*) between 1997 and 1999 on Vancouver Island and the adjacent mainland of British Columbia, Canada. Map courtesy of Living Oceans Society



models using maximum likelihood methods. Models best supported by data are selected via an information-theoretic framework using Akaike's Information Criterion (AIC) scores, normalised across each candidate set to produce AIC weights ( $AIC_w$ ; Burnham and Anderson 2002). We then calculated evidence ratios (ER), the ratio of AIC weights of all those candidate models that included a specific variable, versus those excluding that variable. For example,  $ER > 2$  suggests there is twice the evidence for including that explanatory variable as than for excluding it.

We assumed rivers were closed to species-level changes in occupancy within each season (MacKenzie et al. 2006)—a model assumption that fits salmon biology. Occupancy, local extinction and invasion at each site were estimated from models using a first-order Markov process wherein the probability of occupancy at a site in year 2 is contingent on occupancy in year 1, and:

- $\psi_1$  = probability a river is occupied in year 1
- $\varepsilon_t$  = probability a river becomes unoccupied between years  $t$  and  $t + 1$
- $\gamma_t$  = probability a river becomes occupied between years  $t$  and  $t + 1$
- $p_{t,j}$  = probability that Atlantic salmon is detected at a river in survey  $j$  of season  $t$  (given presence)

We examined model sets hierarchically. In an exploratory analysis, we tested several hypotheses about the relationship between Atlantic salmon occupancy and native salmon: (1) Atlantic salmon occupancy might be explained by the occurrence of steelhead (*O. mykiss*), based on observations made during the surveys. (2) The occurrence of coho or Chinook salmon might explain Atlantic occurrence, as the juveniles of both are river resident, as are Atlantic salmon juveniles, and so are all subject to the same environmental effects. (3) The occurrence of pink and chum salmon might negatively predict Atlantic occurrence, as both juvenile pink and chum salmon migrate to marine waters early in life, shortly following emergence. (4) The occurrence of Atlantics might be related to native salmon diversity, and indicative of the potential of a stream in general for salmon-bearing.

We ran competing models and used the covariate with the most support (salmon diversity) in subsequent models with different parameterizations to estimate occupancy, invasion, and extinction of Atlantic salmon within Pacific coastal rivers, following

MacKenzie et al. (2003). We ran multiple competing models to assess the weight of evidence that (1) probability of detection was constant or varied among YEARS; (2) probability of occupancy was constant or varied with native salmon DIVERSITY; (3) probability of extinction and probability of invasion were either constant or varied among YEARS. We explored using length of stream surveyed as a covariate for  $p$ , but not all streams were surveyed on all occasions, yielding missing covariates, to which occupancy models are not robust (Mackenzie et al. 2006). We tested for differences in detectability among years, and differences in invasion rates among years, and whether these parameters varied with Pacific salmon diversity.

## Results

Atlantic salmon were detected in 15 of the 41 sampled streams (36.6 %) with a mean diversity of three Pacific salmon species per stream (Table 1). In exploratory analysis, native salmon diversity was the best predictor of Atlantic salmon occurrence, compared to steelhead, coho/Chinook, or chum/pink salmon. Atlantic salmon were more likely to occupy streams with high native salmon diversity; this model was supported by 96 % of the weight of evidence ( $\Sigma AIC_w = 0.96$ ;  $ER = 24$ ; Table 2). We then modeled occupancy, colonization, and extinction as varying with DIVERSITY or held constant.

**Table 1** Summary of Atlantic salmon (*Salmo salar*) and Pacific salmon (*Oncorhynchus* spp.) found within sampled streams ( $n = 41$ )

	Present in number of streams	Mean	SD
Length of reach surveyed per survey (km)		2.76	1.94
Diversity of Pacific Salmon species	35	3	1.76
Abundance			
Chinook ( <i>O. tshawytscha</i> )	20	71	217
Coho ( <i>O. kisutch</i> )	23	45	92
Sockeye ( <i>O. nerka</i> )	19	1,726	7,282
Pink ( <i>O. gorbuscha</i> )	19	3,095	11,794
Chum ( <i>O. keta</i> )	23	1,691	7,672
Atlantic Salmon	15	11.10	38.82

**Table 2** Occupancy models of escaped Atlantic salmon in Pacific coast rivers (n = 41), 1997–1999

Model#	Model parameterization	AIC score	$\Delta$ AIC	AIC weight	ML <sup>a</sup>	#para <sup>b</sup>	2LL <sup>c</sup>
1	$\psi(\text{DIVERSITY}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	120.94	0.00	0.96	1	5	110.94
2	$\psi(\text{STEEL}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	128.35	7.41	0.02	0.02	5	119.35
3	$\psi(\text{CHIN-COHO}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	130.30	9.36	0.009	0.009	5	120.30
4	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	131.22	10.28	0.006	0.006	4	123.22
5	$\psi(\text{PINK-CHUM}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	133.38	12.94	0.002	0.002	5	123.88

Occupancy ( $\psi$ ) was modeled over time and was assumed to be either constant ( $\cdot$ ) or to vary with the repeat occurrence of steelhead (STEEL); the occurrence of chinook or coho salmon (CHIN-COHO); the occurrence of pink and chum salmon (PINK-CHUM); or to vary with total native salmon DIVERSITY. Detectability, colonization, and extinction were held constant

<sup>a</sup> Model likelihood, based on AIC weights

<sup>b</sup> Number of parameters in the model

<sup>c</sup>  $-2 \log$  likelihood of the model

The best-supported model (Model 1, Table 3) estimated initial occupancy ( $\psi$ ), invasion ( $\gamma$ ), extinction ( $\varepsilon$ ), and detectability ( $p$ ), and used reciprocal equations to derive yearly  $\psi$  and rates of change ( $\lambda$ ). In multi-season models, Atlantic salmon were more likely to occupy streams with high native salmon diversity; the best-supported models included DIVERSITY, supported by 80 % of the weight of evidence ( $\Sigma \text{AIC}_w = 0.80$ ; ER = 4.1; Table 3). Native salmon diversity also explained variation in Atlantic salmon extinction rates ( $\Sigma \text{AIC}_w = 0.64$ ; ER = 2.9; Table 3). There was no evidential support that colonization rates varied with salmon diversity (ER = 0.61), nor any evidence that colonization rates (ER = 0.37) or extinction rates (ER = 0.44) varied among years. Likewise, there was no evidence that detectability differed among years (ER = 0.36), lending confidence that inter-annual changes in occupancy were an ecological signal, not an artifact of sampling.

The two best-supported models (Models 1 and 2, Table 3) estimated  $p = 0.64$  (SE = 0.068) across surveys and years. Intensive snorkel surveys detected escaped Atlantic salmon—when they were present in Pacific coast rivers—only about 2/3 of the time, and thus missed detecting them about 1/3 of the time. Naïve estimates of occurrence and abundance of Atlantic salmon in Pacific rivers are therefore negatively biased. The probability of false absences ( $pfa$ ) for a given survey is  $[1 - p]^k$ , where  $k$  = number of independent sampling occasions. For Atlantic salmon snorkel surveys,  $pfa$  approached 5 % after three repeated surveys, and approached zero only after 5 repeated surveys each season (Fig. 2).

Initial occupancy ( $\psi_{1997}$ ) varied between 0.97 (95 % CI 0.03–0.99) and 0.07 (95 % CI 0.004–0.61) depending on native salmon diversity (Fig. 3), meaning almost all high-diversity streams are estimated to be occupied by Atlantic salmon, and low-diversity streams were not likely to be occupied. The third model, which assumed constant occupancy irrespective of native salmon diversity, estimated  $\psi = 0.53$  (SE = 0.13) across the study area, meaning that over half of the surveyed rivers are estimated to be occupied by Atlantic salmon.

Extinction probabilities of occupied rivers decreased with increasing native salmon diversity, meaning that Atlantic salmon were more likely to occupy a river consistently across successive fall migratory periods if that river supported a greater diversity of native Pacific salmon (Fig. 4). Invasion probabilities were not stable in these models and could not be accurately estimated; in occupancy models where estimates approach boundary conditions (those close to 0 or 1), algorithms can fail to find a maximum likelihood, and so produce an unstable estimate with confidence intervals of 0.0–1.0.

Based on estimated  $\varepsilon$  and  $\gamma$ , mean occupancy in subsequent years varied with native salmon diversity (Fig. 5). Although Atlantic salmon diversity in medium-diversity streams seemed to decline, a significant difference between initial and final occupancy probabilities was not indicated by the data, as 95 % confidence intervals overlap (95 % CI $_{\psi_{1997}} = 0.29$ –0.96; 95 % CI $_{\psi_{1999}} = 0.008$ –0.71).

**Table 3** Occupancy models of escaped Atlantic salmon in Pacific coast rivers (n = 41), 1997–1999

Model#	Model parameterization	AIC score	$\Delta$ AIC	AIC weight	ML <sup>a</sup>	#para <sup>b</sup>	2LL <sup>c</sup>
1	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\text{DIV}), p(\cdot)$	129.3	0	0.250	1	6	117.3
2	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	130.87	1.57	0.114	0.456	5	120.87
3	$\psi, \gamma(\text{DIV}), \varepsilon(\text{DIV}), p(\cdot)$	131.28	1.98	0.092	0.372	6	119.28
4	$\psi(\text{DIV}), \gamma(\text{DIV}), \varepsilon(\text{DIV}), p(\cdot)$	131.3	2	0.092	0.368	7	117.3
5	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\text{DIV}), p(\text{YEAR})$	131.43	2.13	0.086	0.344	8	115.43
6	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\text{YEAR}), p(\cdot)$	132.57	3.27	0.049	0.195	6	120.57
7	$\psi(\text{DIV}), \gamma(\text{DIV}), \varepsilon(\cdot), p(\cdot)$	132.87	3.57	0.042	0.168	6	120.87
8	$\psi(\text{DIV}), \gamma(\text{YEAR}), \varepsilon(\cdot), p(\cdot)$	132.87	3.57	0.042	0.168	6	120.87
9	$\psi, \gamma(\text{DIV}), \varepsilon(\text{DIV}), p(\text{YEAR})$	132.96	3.66	0.040	0.160	8	116.96
10	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\cdot), p(\text{YEAR})$	133.32	4.02	0.034	0.134	7	119.32
11	$\psi(\text{DIV}), \gamma(\text{DIV}), \varepsilon(\text{DIV}), p(\text{YEAR})$	133.43	4.13	0.032	0.127	9	115.43
12	$\psi, \gamma(\cdot), \varepsilon(\text{DIV}), p(\cdot)$	133.97	4.67	0.024	0.097	5	123.97
13	$\psi, \gamma(\cdot), \varepsilon(\text{DIV}), p(\text{YEAR})$	134.11	4.81	0.023	0.090	7	120.11
14	$\psi(\text{DIV}), \gamma(\text{YEAR}), \varepsilon(\text{YEAR}), p(\cdot)$	134.57	5.27	0.018	0.072	7	120.57
15	$\psi(\text{DIV}), \gamma(\cdot), \varepsilon(\text{YEAR}), p(\text{YEAR})$	134.71	5.41	0.017	0.067	8	118.71
16	$\psi(\text{DIV}), \gamma(\text{DIV}), \varepsilon(\cdot), p(\text{YEAR})$	135.32	6.02	0.012	0.049	8	119.32
17	$\psi(\text{DIV}), \gamma(\text{YEAR}), \varepsilon(\cdot), p(\text{YEAR})$	135.32	6.02	0.012	0.049	8	119.32
18	$\psi, \gamma(\text{DIV}), \varepsilon(\cdot), p(\cdot)$	135.59	6.29	0.011	0.043	5	125.59
19	$\psi(\text{DIV}), \gamma(\text{YEAR}), \varepsilon(\text{YEAR}), p(\text{YEAR})$	136.71	7.41	0.006	0.025	9	118.71
20	$\psi, \gamma(\text{DIV}), \varepsilon(\cdot), p(\text{YEAR})$	138.23	8.93	0.003	0.011	7	124.23
21	$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	140.56	11.26	0.001	0.004	4	132.56
22	$\psi, \gamma(\cdot), \varepsilon(\text{YEAR}), p(\cdot)$	142.36	13.06	0.0004	0.002	5	132.36
23	$\psi, \gamma(\text{YEAR}), \varepsilon(\cdot), p(\cdot)$	142.44	13.14	0.0003	0.001	5	132.44
24	$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\text{YEAR})$	142.76	13.46	0.0003	0.001	6	130.76
25	$\psi, \gamma(\cdot), \varepsilon(\text{YEAR}), p(\text{YEAR})$	144.09	14.79	0.0002	0.001	7	130.09
26	$\psi, \gamma(\text{YEAR}), \varepsilon(\cdot), p(\text{YEAR})$	144.21	14.91	0.0001	0.001	7	130.21
27	$\psi, \gamma(\text{YEAR}), \varepsilon(\text{YEAR}), p(\cdot)$	144.32	15.02	0.0001	0.001	6	132.32
28	$\psi, \gamma(\text{YEAR}), \varepsilon(\text{YEAR}), p(\text{YEAR})$	145.67	16.37	0.0001	0.000	8	129.67

Occupancy ( $\psi$ ) was modeled over time with estimates of river recolonization ( $\gamma$ ) and extinction ( $\varepsilon$ ), which were either constant ( $\cdot$ ), varied among YEARS, or varied with native salmon DIVERSITY. Probability of detection ( $p$ ) was constant ( $\cdot$ ) or varied by YEAR. The different model parameterizations follow Mackenzie et al. (2003)

<sup>a</sup> Model likelihood, based on AIC weights

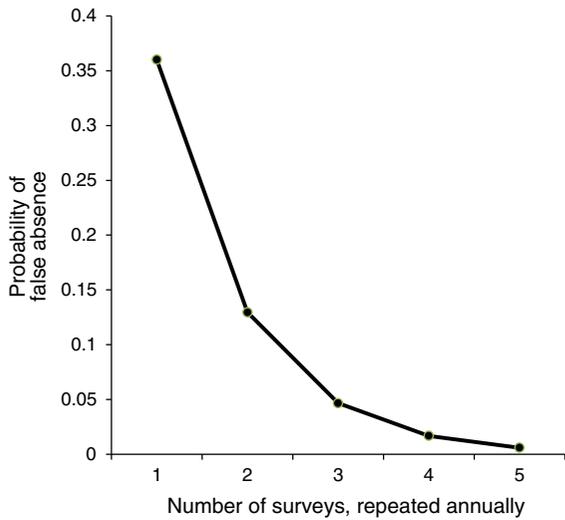
<sup>b</sup> Number of parameters in the model

<sup>c</sup>  $-2$  log likelihood of the model

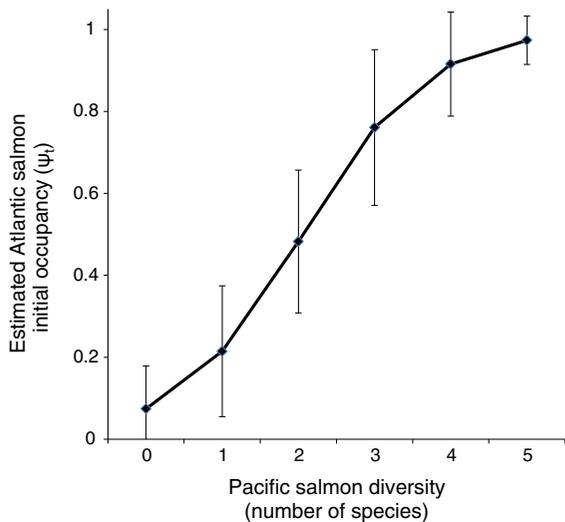
## Discussion

Atlantic salmon are estimated to have occupied over half of the surveyed rivers across the study area: as much as 97 % of streams with high native salmon diversity, and as little as 7 % of streams with few or no native salmon. As surveyed streams are ecologically and biologically representative of salmon-bearing streams from Washington State to Alaska, USA, the degree to which escaped farmed salmon may have

infiltrated native ecosystems is marked. The spatial distribution of the invasion changed among years, with Atlantic salmon disappearing from some streams and appearing in others. However, existing data suggest a high probability that occupancy probabilities within these streams did not differ from year to year across the study area. This is in part owing to very large confidence intervals around occupancy estimates. More data are needed to reduce this error and produce more precise estimates and to better understand



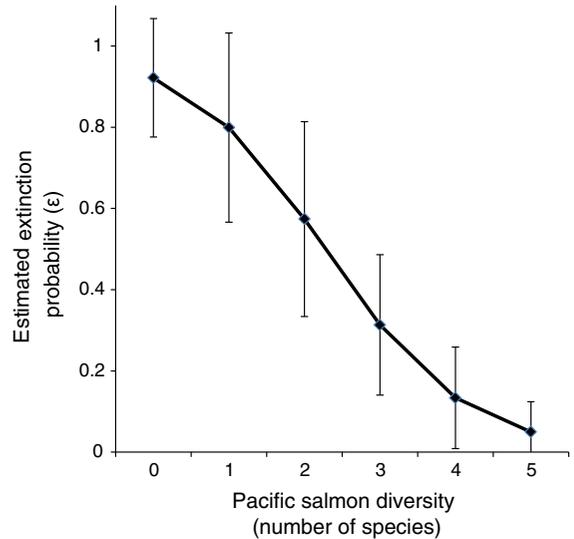
**Fig. 2** The per-survey probability of false absence in Atlantic salmon snorkel surveys approached zero after 5 surveys



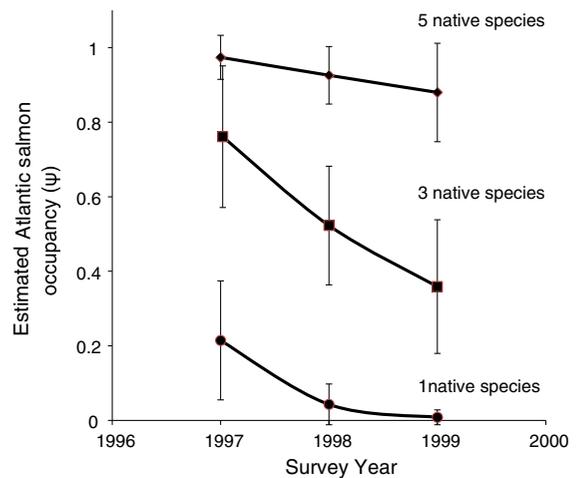
**Fig. 3** Initial probability of occupancy ( $\psi_i$ ) of escaped Atlantic salmon in Pacific coast rivers increased with the number of native salmon species in that river. Bars represent SE

interannual dynamics of escaped farmed salmon. Based on this analysis and the only existing data on Atlantic salmon occurrence in Pacific streams, the scale of the invasion remained extensive throughout the survey period between 1997 and 1999.

Detectability in Atlantic salmon surveys is imperfect, as has been demonstrated for surveys of myriad other vertebrate species (Mackenzie et al. 2002, 2006), including salamanders (Bailey et al. 2004), frogs



**Fig. 4** The probability of local extinction ( $\epsilon$ ) of exotic Atlantic salmon from 41 Canadian Pacific coastal streams (1997–1999) decreased with native Pacific salmon diversity. Bars represent SE



**Fig. 5** Estimated occupancy of exotic Atlantic salmon in 41 Canadian Pacific coastal streams between 1997 and 1999 for streams with 5, 3, and 1 native salmon species. Bars represent SE. Between 1997 and 1999 95 % confidence intervals (not shown) of annual occupancy estimates overlap

(Mazerolle et al. 2005), bats (Weller 2008), Wolverines (Fisher et al. 2013) and grizzly bears (Fisher et al. in press). Estimating for imperfect detections through occupancy models has recently been applied to fish assemblages (Falke et al. 2010; Cosentino et al. 2011). Ours is one of the few applications of the technique to the problem of fish invasions (see Britton et al. 2011)

and the first to examine invasion of coastal streams by exotic salmonids. Based on this approach, we conclude that in a single intensive snorkel survey, Atlantic salmon are detected only 2/3 the time when present in occupied streams, with a *pfa* of 36 %. Repeated intensive surveys replicated at least three times within a season are needed to reduce *pfa* to approximately 5 %. However, despite significant industry expansion there has not been, nor is there currently, any active monitoring of Atlantic salmon in Pacific waters despite recent evidence of continued range expansion of farm escapees (Piccolo and Orlikowska 2012). Further, there remains no response plan to mitigate potential invasions should widespread colonization be detected.

This analysis challenges the prevalent assumption that steelhead occurrence is a reliable proxy for Atlantic salmon occurrence (Volpe et al. 2001b). Rather, diversity of native Pacific salmon species was the most reliable predictor of Atlantic salmon presence in Pacific coastal rivers. Though this study is the first to survey Pacific rivers for Atlantic salmon presence over multiple years, further investigation is needed to discern whether steelhead or native salmon consistently co-occur with Atlantic salmon, as well as what other biological and ecological predictors of Atlantic salmon presence may exist. For now, our study indicates that a more active monitoring and management approach is necessary. Atlantic salmon are not only present in the same rivers for multiple years, but also selectively occupy more salmon-diverse systems, and therefore may be more of a conservation threat to native salmon than is currently assumed. Further, once occupying a stream, Atlantic salmon are less likely to go locally extinct from highly salmon-diverse streams than from less salmon-diverse streams. Residency time by exotic Atlantic salmon is longer in streams with more native salmon, thus compounding the potential threat to native species.

Current data do not provide precise estimates of invasion rates, but the fact that data do not support a significant difference between initial and final occupancy probabilities—despite some degree of local extinction—illustrates that invasions continued throughout the study period. With a significant increase in overall production but no change in on-farm practice since the survey period (1997–1999), it is logical to conclude that invasion continues to occur. Two scenarios may explain this result: (1) Atlantic

salmon had stable self-sustaining populations with a relatively equal degree of local extinction and immigration from other source rivers; or (2) there were enough Atlantic salmon escaping farm systems to allow a near-constant replacement of local extinctions of previous escapees. We cannot discern between these two possible conclusions, however the ramifications are significant in either case.

The first case implies that Atlantic salmon effectively naturalized, even though current policy (absent data) of Fisheries and Oceans Canada maintains that naturalization is biologically impossible despite empirical evidence to the contrary (Volpe et al. 2000, 2001a, 2001b). Piccolo and Orlikowska's (2012) risk assessment suggests the greatest risk of a widespread Atlantic salmon invasion in Pacific waters would be spreading from locally-adapted naturalized populations in BC. Given that Atlantic salmon remain at sea for 2–4 years prior to returning to their natal streams (see Schaffer and Elson (1975)), it is possible for a river to support a wild stock of Atlantic salmon but have adult Atlantic salmon absent from that river for up to three of every 4 years. Further research is needed to assess if this may contribute false absences to survey data, and how this affects estimates of annual occupancy.

The second case suggests a source-sink relationship (sensu Pulliam 1988; Pulliam and Danielson 1991), wherein sink populations do not reproduce sufficiently to offset mortality, but rely on immigration from source populations of dispersers—in this case, escaped farm fish. Source-sink dynamics are key processes in maintaining and facilitating invasive species in other systems (reviewed in Hull et al. 2011; Haddad et al. 2011) and may do the same in Pacific coastal rivers. The management implication in the source-sink scenario is thus: if Atlantic salmon farms were removed, then Atlantic salmon abundance would decline to zero in Pacific watersheds. If, however, Atlantic salmon populations have naturalized, then eradication becomes a complex and costly affair.

We present strong evidence to warrant more aggressive monitoring and policy development for Atlantic salmon farms on the Canadian Pacific coast. This analysis of the only systematically-collected Atlantic salmon surveys clearly reveals that widespread survey effort over time—generating a large spatial and temporal sample size—is required to track Atlantic salmon occurrence with any accuracy or

precision. We strongly recommend that streams be regularly surveyed several times annually in a standardized framework. The current Fisheries and Oceans Canada escapes-reporting system—the Atlantic Salmon Watch Program—has been effectively abandoned and was shown to under-represent Atlantic salmon encounters by at least 40 % when it was operational (Morton and Volpe 2002). The lack of monitoring of salmon escapes and invasions indicates a failure of current management practices and a lack of oversight of escapes in British Columbia, with unknown consequences for populations of native Pacific salmon in coastal rivers. The case for prevention of exotic species colonization is well known, yet there has been no concerted effort to document the extent of invasion by Atlantic salmon, and no scientific study made of their potential ecological effects. Atlantic salmon appear to be favouring more diverse systems, thus they may be more of a conservation threat to native Pacific salmon than if they favoured less-diverse rivers. Their current distribution, and the potential effects on Pacific ecosystems and native Pacific salmon, is a conservation priority that has been neglected in the push for economic return.

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