REVIEW

Wild Salmon Sustain the Effectiveness of Parasite Control on Salmon Farms: Conservation Implications from an Evolutionary Ecosystem Service

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Abstract

Rapid evolution can increase or maintain the provision of ecosystem services, motivating the conservation of wild species and communities. We detail one such *contemporary evosystem service* by synthesizing theoretical evidence that rapid evolution can sustain parasiticide efficacy in salmon aquaculture, thus creating an added incentive for salmon conservation. Globally, wild and farmed salmon share native parasites: sea lice. In most major salmon farming areas sea lice have evolved resistance to parasiticides, but in the North Pacific, where farmed salmon coexist with large wild salmon populations, resistance has not emerged. We present a model to show that flow of susceptible genes from lice hosted on wild salmon to those hosted on farmed salmon can delay or preclude resistance. This theoretical and observational data suggests that wild salmon (both oceanic populations that function as a refuge and local migratory populations that connect this refuge to domesticated environments) provide an evosystem service by prolonging parasiticide efficacy. To preserve this service, aquaculture managers could avoid production quantities that exceed wild salmon abundances, and sustain wild salmon populations through regional and oceanic scale conservation. The evosystem service of resistance mitigation is one example of how a contemporary evolutionary process that benefits people can strengthen the case for conservation of intrinsically important wild species.

Introduction

The ecosystem services concept provides a utilitarian framework accounting for nature's contributions to human well-being (Daily 1997), thereby adding practical motivations on top of more traditional, intrinsic ones for conserving species and ecosystems. Recently, authors have sought to explicitly integrate evolutionary thinking into the ecosystem services concept using the term *evosystem services*. Some have noted that historical evolution has generated the diversity of life and thus all ecosystem services (Faith *et al.* 2010), while others have focused on

the idea that contemporary, rapid evolution can generate or maintain specific ecosystem services in the present day (Rudman *et al.* 2017). While numerous examples of putative contemporary evosystem services have been suggested (Rudman *et al.* 2017), there are few examples where rapid evolution provides quantifiable benefits to humans. Detailed study of contemporary evosystem services might internalize externalized benefits and motivate more sustainable management and conservation of biological resources.

To demonstrate the evosystem services concept and explore its conservation implications, we discuss a case study involving rapid evolution and gene flow in salmon (*Oncorhynchus* spp. and *Salmo* spp.) and their sea louse parasites. We synthesize theoretical research from agricultural and aquatic systems, present broad global observations, and develop our own model to suggest that the presence of natural populations of wild salmon near farms may slow the evolution of parasiticide resistance in sea lice, thereby benefitting salmon farmers. We frame this evolutionary process in an ecosystem services context, and draw lessons for the sustainable conservation and management of wild salmon.

The case of salmon aquaculture and sea lice

Globally, farm production of Atlantic salmon (*Salmo salar*) has grown 400-fold since 1980 (FAO 2015a), and by the 2000s it was outpacing wild salmon capture (Goldburg & Naylor 2005). Salmon farming takes place in the Atlantic Ocean (primarily Norway, Scotland, Ireland, and Atlantic Canada) and Pacific Ocean (primarily Chile, Pacific Canada, and Japan). Farmed salmon are typically raised in protected coastal waters, in net-pens that allow nutrients, chemicals, pathogens, and parasites to transfer freely between the farm and wild environments (Burridge *et al.* 2010).

Sea lice (*Lepeophtheirus* and *Caligus* spp.; Figure 1a) are examples of parasites shared by wild and farmed salmon. These ectoparasitic copepods feed on the epidermis and other tissues of marine fish, including salmonids, causing a variety of lethal and sublethal effects in their hosts (Costello 2006). Globally, sea lice are a major parasite affecting fish health in aquaculture (Costello 2006), and infestation on farms is subject to substantial management efforts (Costello 2009). Parasiticides, including emamectin benzoate (EB; trade name Slice®), are primary tools in the management of sea lice on salmon farms, but their efficacy has declined with the evolution of resistance in the most common sea louse species in many salmon-farming areas (i.e., *L. salmonis* in

the Northern Hemisphere, and *C. rogercresseyi* in Chile). *L. salmonis*, the primary parasite in the Northern Hemisphere, does not have nonsalmonid hosts (Costello 2006). In contrast, *C. rogercresseyi* (in Chile), *C. elongatus* (common in the North Atlantic), and *C. clemensii* (common in the North Pacific) can be hosted by nonsalmonids (Revie *et al.* 2002). The former has developed resistance and become a major concern for the industry in Chile, while the latter two are relatively of lower concern, and thus the subject of less research than *L. salmonis* (Revie *et al.* 2002; Aaen *et al.* 2015). We are not aware of any studies of possible EB resistance in *C. elongatus*. British Columbia (BC) (Saksida *et al.* 2013; Aaen *et al.* 2015), Japan, and Russia (Nagasawa 2004) are now the only major salmon-farming areas where sea lice are present and where parasiticide resistance is not consistently detected in the common sea louse species (Supplementary Table S1).

We propose that the reason for the lack of EB resistance in BC, Japanese, and Russian sea lice may be that the evolution of resistance is mitigated by migrations of wild salmon that connect louse subpopulations on farms with a large population of wild sea lice that infects wild salmon in the North Pacific Ocean (Figure 2). By way of contrast, in countries where resistance has evolved—Chile, Norway, Scotland, Ireland, and Atlantic Canada—farmed salmon outnumber wild salmon. In these latter areas, most hosts for sea lice live in coastal net pens where selection for EB resistance is intense and the size of the wild refuges for parasites is small relative to the domesticated environment. While wild catch data (Figure 2; Supplementary Table S1) are not strictly localized, the fact that wild salmonids are much more abundant in the North Pacific than in the North Atlantic or Chile is not controversial (Ruggerone *et al.* 2010; Chaput 2012; FAO 2015b). Sea lice control problems and the presence of resistance seem to be correlated to both size and location of the industry (Supplementary Material A).

In BC, *L. salmonis* is the primary sea louse infesting salmon farms. *L. salmonis* found in farms are part of a larger panmictic population, characterized by high migration and low genetic differentiation (Messmer *et al.* 2011). In the fall, salmon farms receive an influx of sea lice from migrating adult wild salmon that carry lice from the open ocean into coastal waters (Figure 1b). Some of these sea lice infest salmon farms, survive, and reproduce on farms throughout the winter (Figure 1b). Selection for EB resistance occurs when farms apply EB, often in winter (Peacock *et al.* 2013). In the spring (Figure 1b), the farm-bred lice can infest outmigrating wild salmon smolts, elevating mortality in populations of some salmon species near to farms (Krkošek *et al.* 2006). As a result, sea lice amplified on salmon farms can depress some nearby wild salmon populations and thereby reduce mi-
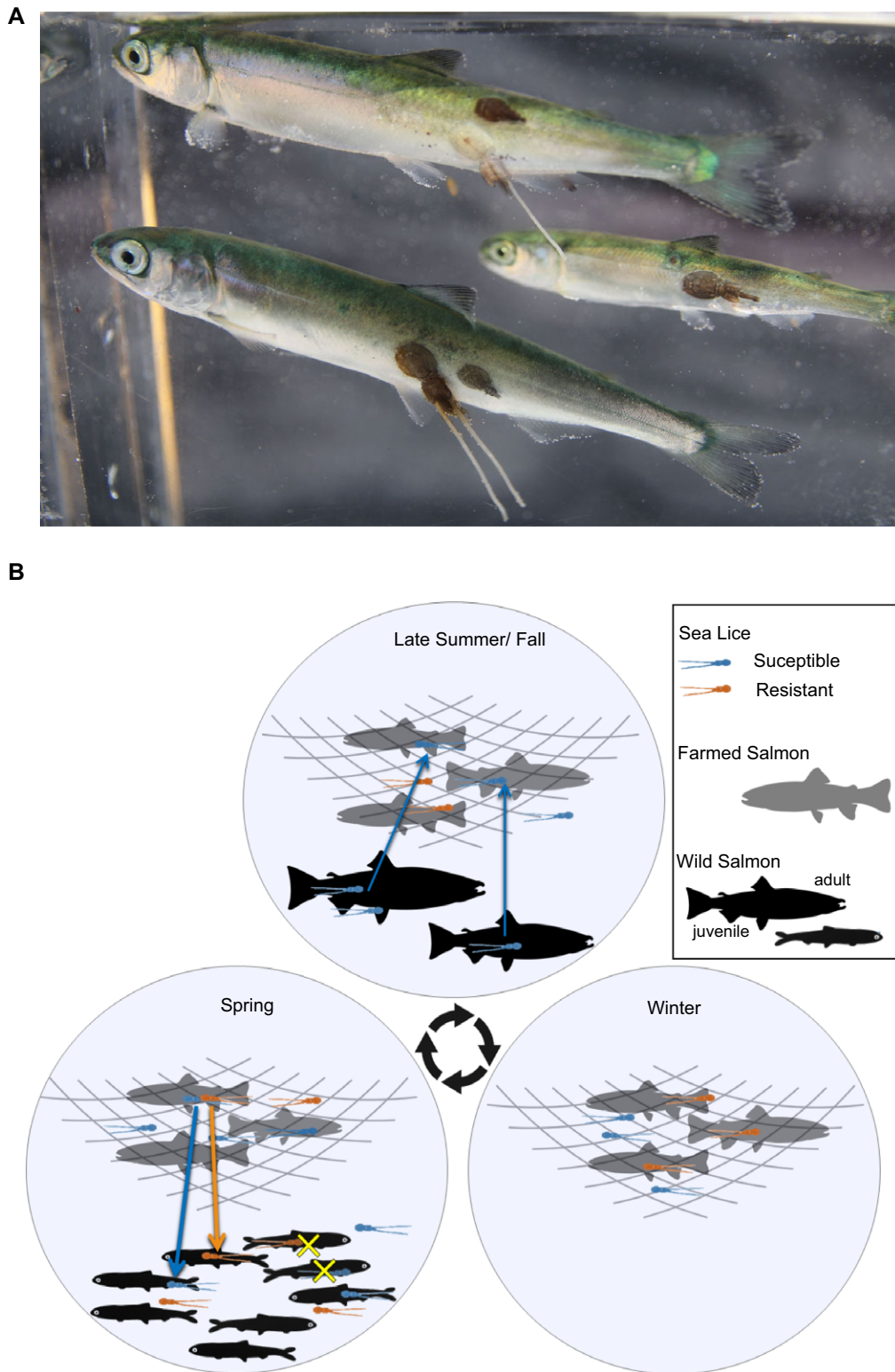
Figure 1 The life history of salmon and sea lice. (a) Adult *Lepeophtheirus salmonis* infesting juvenile pink salmon, *Oncorhynchus gorbuscha* (photo: Alexandra Morton). (b) When wild adult salmon migrate past salmon farms in late summer or fall they bring immigrant homozygous susceptible lice (blue) to farms. In winter, the farm population of lice is isolated and subjected to selection for EB resistant sea lice (orange). Migrating wild juveniles move past farms in spring, receiving sea lice infection from farms that cause wild salmon population declines, indicated by juveniles with an X.
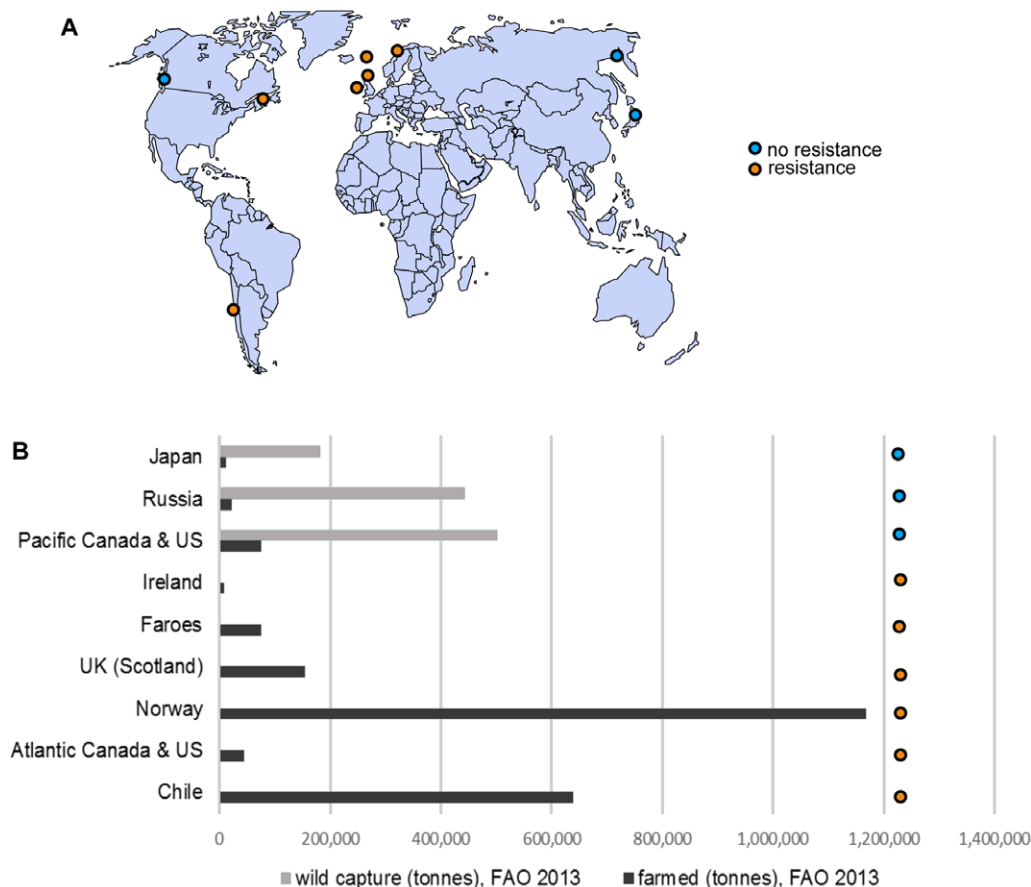
Figure 2 Global trends in sea lice resistance and wild salmon abundance. (a) Locations of resistant and nonresistant sea lice populations in salmon aquaculture areas around the world, from Aaen *et al.* (2015). (b) Farmed salmon production and wild capture (all species) on the same scale, for 2013 (FAO 2015a, 2015b). The areas with the greatest wild capture are in the North Pacific, where sea lice on farms have not evolved resistance to sea lice treatment. Note that wild capture is not a proxy for stock assessments in Pacific Canada, U.S., Japan, and Russia, but still demonstrates the existence of substantial wild salmon biomass in the North Pacific.

gration of sea lice between wild and farm subpopulations (Vollset *et al.* 2016).

Processes at several spatial scales play important roles in the lice salmon system. At the farm scale, application of parasiticides imposes selective pressure for the evolution of resistance (Aaen *et al.* 2015). At the regional scale, a wild salmon run brings sea lice from the open ocean to the farm or farms near its migration route (Costello 2009), thereby connecting the louse population on those farms to the population of susceptible sea lice in the ocean basin (conceptual model, Figure 1). In addition, sea lice on several farms may form a single population (Jansen *et al.* 2012; Rogers *et al.* 2013), within which alleles can be exchanged. Also at the regional scale, breeding populations from different species of salmon and multiple subpopulations of particular salmon species use the same estuaries and primary river channels for rearing and migration, making this scale critical for the protection and

Table 1 Notation of salmon and sea lice populations at different scales

	Salmon	Lice
Farm	S_F	N_F
Regional	S_W	N_W
Ocean basin	S_O	N_O

restoration of wild salmon habitat (Nehlsen 1997). At the oceanic scale, sea lice form a single panmictic population (Messmer *et al.* 2011). While in the Pacific, wild salmon are abundant at the oceanic scale, providing a large refuge from on-farm treatment, this is not the case in the Atlantic, where local wild populations are usually small relative to the abundance of farmed salmon. We will use the notation in Table 1 to discuss the populations and processes at these different scales in the next section.

In BC, wild salmon are an important food and cultural resource but have also served as a nuisance to the

salmon farming industry, both as a source of naturally occurring pathogens like sea lice (Costello 2009) and as a source of economic competition and negative publicity (Rayner & Howlett 2007). However, theoretical models, reviewed and presented below, suggest that wild salmon might offer a substantial evosystem service by connecting farm-scale sea louse populations with an open-ocean population that provides a refuge from selection for EB resistance. The existence of this evosystem service for the salmon farming industry might gain wild salmon populations an important conservation ally.

Evolutionary models of the salmon sea lice system

Although there have been many studies of treatment-free refuges in agriculture (Tabashnik *et al.* 2013; Box 1), the idea is much newer in aquaculture. Two recent modeling studies of the lice salmon system (Murray 2011; McEwan *et al.* 2015) examined how connectivity between wild and farm louse subpopulations affects resistance evolution. The models of Murray (2011) and McEwan *et al.* (2015) do not consider oceanic lice N_O, which are not directly connected to the farm lice N_F. Thus, these models represent settings, such as the Atlantic coast of North America, Norway, or Great Britain, where farms share coastal waters with small populations of wild salmonids that are not connected with a large oceanic wild refuge population.

Box 1: Terrestrial refuges and the mitigation of pesticide resistance

Nuisance evolution, such as the accumulation of antibiotic and pesticide resistance, has justifiably received much attention since it was first reported more than a century ago (Melander 1914). Fundamentally, stronger treatments impose stronger selection for resistance. But, ecosystem components and processes can sometimes slow such nuisance evolution, thereby providing an evosystem service. Theory has shown that patches of untreated habitat, "treatment-free refuges," slow down or stall evolution of chemical resistance (Comins 1977). This is because refuges permit mixing between the pest or parasite subpopulation in the selective environment (exposed to pesticide) and that in the refuge (not exposed to pesticide), diluting resistance genes in the population that is under selection for resistance (Comins 1977; Georghiou & Taylor 1977). Under this theory, the expected time for resistance to emerge, by reaching a threshold frequency, is influ-

enced by the size of the refuge, the rate of migration between refuge and treated area, and the genetic dominance of resistance genes (Comins 1977). Dominance is important because when resistance alleles are rare they occur almost exclusively in heterozygous individuals. If high doses of treatment can overcome the resistance of heterozygotes, then stronger doses of chemicals could eliminate resistant alleles from the population, and thus counterintuitively delay resistance. The proposed approach of combining refuges with high levels of treatment is known as the "high-dose refuge" (HDR) strategy (Gould 1998).

Empirical studies on many species of crop pests, faced with multiple types of transgenic *Bacillus thuringiensis* (Bt) crops, have borne out the theoretical predictions of refuge-based resistance management, in particular the HDR strategy (Tabashnik *et al.* 2013). This empirical support has led to regulators mandating refuge-based management (U.S. EPA 2015). While compliance with associated regulations can be challenging due to a mismatch between the private cost and the collective benefit of correct resistance management (Marsh *et al.* 2006), the importance of refuges in resistance mitigation is widely accepted. Nonetheless, most theory on refuges has focused on measuring stationary, biophysical habitat, rather than wild animal hosts (mobile "link" organisms, which also provide other types of ecosystem services; e.g., Kremen *et al.* 2007). One system where wild animals provide refuges is that of farmed salmon, wild salmon, and their shared native parasites.

While the two studies take different approaches, they both showed that connectivity between farm lice N_F and wild lice N_W is important. In the absence of any connectivity between the farm and wild environment, susceptible lice dominated on farms at low treatment levels, and resistant lice reached 100% at high treatment levels (Murray 2011). Similarly, McEwan *et al.* (2015) showed that resistance evolved more slowly when connectivity increased. Both studies also showed that in the presence of connectivity, the relative size of farm lice N_F and wild lice N_W affects resistance evolution: McEwan *et al.* (2015) showed resistance might not evolve when wild hosts equal or outnumbered farm hosts, even with no cost of resistance. Similarly, Murray (2011) showed that when farms are large relative to wild populations, resistance emerged quickly.

These existing model results do not correspond exactly to coastal BC, where the abundance of wild populations in the North Pacific relative to farmed salmon is high,

and lice from farms negatively impact nearby populations of some wild salmon species (Krkošek *et al.* 2007; Vollset *et al.* 2016). This means that many oceanic lice N_O may never interact directly with farm lice N_F. To understand the dynamics of resistance in situations such as coastal BC, we present a model that differs from previous work in that (1) it draws a distinction between the oceanic S_O and the regional migratory population S_W of salmon and associated lice, (2) it can be simply formulated and solved analytically, and (3) it considers the empirically backed decline of the migratory wild salmon S_W that link treated N_F and untreated N_O populations of sea lice.

Our model (Box 2) reflects the multiscale populations of sea lice in the North Pacific, but is simple in that it only represents N_F and N_W explicitly. It analytically models resistance emergence at different levels of connectivity, defined as immigrant lice/farm resident lice/year (N_W/N_F). We assume that all lice immigrating to farms from the oceanic population, N_O, are susceptible. This is reasonable in two situations: (1) if the oceanic population is very large (so that selection is efficient) and there is a small cost to resistance in the wild, or (2) if the population is not so large, but the cost to resistance is high in the nonselective environment. The first situation is more likely because experiments testing the survival and fecundity of resistant and wild-type sea lice in the absence of EB have failed to find costs to resistance (Espedal *et al.* 2013; Aaen *et al.* 2015). The model is presented in Box 2, and more details are provided in Supplementary Material B.

Box 2: Resistance emergence with connectivity to a large, susceptible wild population

We model the frequency of chemical resistance, p_i, in a population of $N_F(i)$ farm lice which receive $N_W(i) \geq 0$ lice from the oceanic population of lice at each time i, due to a regional migratory population of wild salmon. We define connectivity between oceanic and farm sea lice as $N_W(i)/N_F(i)$, and assume that all lice immigrating to farms from the oceanic population are susceptible. Under this assumption, immigration dilutes resistance and greater connectivity implies greater dilution: resistance frequency decreases as $p_{i+1} = p_i/(N_W(i)/N_F(i) + 1)$.

We model resistance as controlled by a diallelic locus in a randomly mating, sexual population of nonoverlapping generations. The frequency p of the resistant allele R increases with treatment p (and the frequency $1 - p$ of the susceptible allele S decreases). According to standard population genetics (e.g., equation B2.2.3 of Charlesworth &

Charlesworth 2010) the allele frequency p changes in proportion to the product of the variance in its frequency and its effect on mean relative fitness so that when resistance is rare, as it must be if a resistant strain first arises by mutation, treatment increases p by the ratio of the heterozygote's fitness w_{RS} to that of the susceptible homozygote w_{SS}. That is, the frequency dynamics are $p_{i+1} \approx \frac{w_{RS}}{w_{SS}} p_i$. (This is from a Taylor approximation for small p; see Supplementary Material B).

The *heterozygote advantage*, $\frac{w_{RS}}{w_{SS}}$, which depends on treatment status, strength of selection, and genetic dominance of resistance, thus determines the dynamics of p when resistance is rare. We parameterize the heterozygote advantage by strength of treatment (i.e., selection) $0 \leq s \leq 1$ and dominance $0 \leq \beta \leq 1$, where 1 is complete dominance and 0 is complete recessiveness. Then, relative genotypic fitness during treatment is $w_{SS} = 1 - s$, $w_{RS} = (1 - s)^{1-\beta}$, and $w_{RR} = 1$. Unless resistance is completely recessive, heterozygote advantage exceeds one during treatment and resistance frequency increases. Without treatment, we assume there is no advantage so resistance remains at a constant frequency; this could occur if there is no cost to resistance in an untreated farm.

Along with the heterozygote advantage, the connectivity then determines the time to resistance. In general, the value of connectivity $N_W(i)/N_F(i)$ depends on the size of the farm parasite population and number of immigrating wild parasites, both of which can change over time. But, if connectivity is the same each year (due, e.g., to farm management and stable population sizes of wild hosts), we can derive the time to resistance emergence (see Supplementary Material B). With k treatments, each of strength s, applied in each year to a population where the dominance of resistance is β and which maintains a constant connectivity N_W/N_F (analogous to Comins 1977, equation 6, who derived a similar formula but with no immigration) the time to resistance in years is

$$T_R = \frac{\log\left(\frac{p_e}{p_0}\right)}{k\beta\log\left(\frac{1}{1-s}\right) - \log\left(\frac{N_W}{N_F} + 1\right)}, \quad (1)$$

where the initial frequency of resistance is p_0 and the emergence threshold is p_e.

The key insight from our simple model is that the speed of evolution for resistance depends strongly on both the

Figure 3 Effects of connectivity on the time to resistance. (a) Predictions for resistance on farms plotted against connectivity (immigrant lice per resident lice per year) between the lice populations in farms and the wild. Large connectivity values represent small farms or intensive control of farm lice. Predictions depend on the dominance of resistance (varying grayscale, full dominance = 1; see equation (1)). Resistance does not emerge with high connectivity, even with full dominance. Resistance emergence is defined as resistance frequency = 0.1. (b) Predicted resistance frequency when connectivity is constant (solid lines) or decreases by 10% per year (dashed lines). Dominance = 0.5. In both panels, initial resistance frequency = 0.001 in the farm, and zero in refuge.
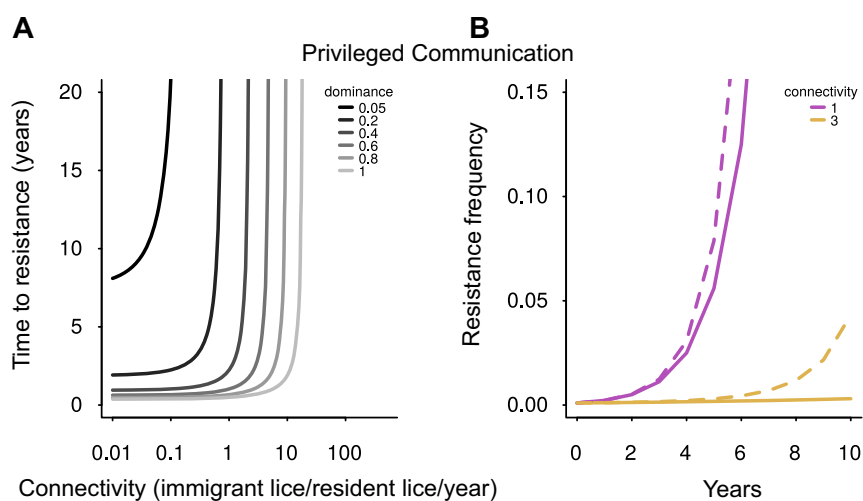
dominance of resistance genes and on the connectivity between wild and farmed populations (equation (1); Figure 3a). Some combinations of connectivity and dominance prevent emergence of resistant genotypes altogether, for example, a connectivity above one immigrant louse per farm-resident louse per year and a dominance of resistance less than 0.5 (Figure 3a).

If connectivity decreases over time, as may occur if effects from farms reduce wild salmon populations (Ford & Myers 2008), resistance-emergence times decrease dramatically. To see this, we calculated the time to resistance if connectivity decreased by 10% each year (compare dashed lines with decreasing connectivity to solid lines with constant connectivity in Figure 3b; see Box 1). The work of Ashander (2010), upon which our model is based, also considered a dynamical model in which the connectivity reduction resulted from farm-induced declines of juvenile wild salmon. Within the model, this linked the size and management of salmon farms to the size of the connective populations in a manner consistent with empirical findings (Krkošek *et al.* 2007; Ford & Myers 2008). Whether connectivity decreases as a parameter (Figure 3b) or as a dynamic variable (Ashander 2010), resistance emerges faster when the sensitivity of juvenile wild salmon to sea lice from farms is taken into account.

Our model offers a compact equation for the effect on resistance when a regional population of wild salmon N_W provides connectivity to an oceanic population N_O that is large enough to be considered 100% susceptible. Our analysis (Figure 3b) also describes the realistic case where regional connective populations near salmon farms decline over time.

Our model has several limitations. It does not include possible spillover of resistant genes into the oceanic refuge, which would reduce the time to resistance in the absence of costs. A limitation of both our model and previous work is the absence of stochastic effects, especially because even advantageous alleles can be lost to such effects when they are still rare (Orr & Unckless 2014). Importantly, several parameters that influence emergence of resistance in all the models remain largely unknown for sea lice. These include the genetic dominance of the gene—or genes—responsible (Heumann *et al.* 2012; Igboeli *et al.* 2012) and whether resistance carries a fitness cost (Espedal *et al.* 2013). Further, violation of the population genetics assumptions of our model (e.g., no assortative mating by resistance status) would drastically change our results: the immigrating susceptible individuals would no longer dilute resistance, but the resistant population would grow more slowly. In addition, to connect changes in population size of wild salmon, e.g., S_W, to lice N_W requires that we assume the total number of lice brought near farms by migratory wild fish is proportional to the abundance of those migratory fish.

Previous results (Murray 2011; McEwan *et al.* 2015) agree that large wild salmon populations connected to farms will slow, or possibly preclude, the emergence of EB resistance. Our model shows that even assuming the existence of large wild salmon populations is not enough to avoid resistance if regional migrating populations are small or in decline. Taken together, these results point to two features of the salmon/sea lice system that have critical conservation and management implications: (1) the ratio of total wild salmon to total farmed salmon biomass and (2) the flow of susceptible alleles from the refuge to the farm. We will explore these in detail in the "Conservation and management implications" section, below.

Evosystem services, ecosystem services, and resistance mitigation

Early ecosystem services literature typically treated evolutionary processes as relevant for having produced ecosystem service providers (e.g., genetic diversity), but not for directly generating services themselves (de Groot et al. 2002; MEA 2005). More recently, there have been calls for a more explicit accounting of evolutionary processes that provide benefit to people (Faith et al. 2010). Faith et al. (2010) coined the term *evosystem services* to mean "all of the uses or services to humans that are produced from the evolutionary process." This definition includes both the legacy of evolution in the form of all biodiversity and the contemporary role of evolution as a continuing process that can generate new services. Rudman et al. (2017) proposed several examples of possible contemporary evosystem services in systems where they might buffer against undesired effects of human harvesting or accelerate recovery from pollution, disturbance, or invasion. Yet, the characterization of evosystem services resulting from contemporary evolution has been theoretical and (excepting one example involving *Daphnia* spp.; Rudman et al. 2017) lacking in case studies. In our example of resistance mitigation, a genetic resource (the genotypes of nonselected parasites) and the ecological process of migration between subpopulations, combine to maintain pesticide efficacy in a continuing, contemporary evolutionary process.

In concrete terms, the BC salmon farming industry likely derives an economic benefit from the maintenance of EB susceptibility, by avoiding costs associated with resistance. The need for treatments results in direct costs (e.g., purchase costs of parasiticides) and indirect costs (e.g., production losses). Economic costs would therefore be expected to accrue with increases in the frequency of treatments and/or amount of parasiticides used in treatments. Available information suggests that the BC salmon farming industry uses less parasiticide per unit production (Bridson 2014) and has lower associated costs than other major salmon farming areas. While a variety of factors may influence patterns of parasiticide use and associated economic and environmental costs, the introduction of EB resistance to the BC salmon farming industry would likely reduce BC's advantages. An estimate of this economic benefit is a potential subject for future research.

Further analysis of the ecosystem services provided by wild salmon would be needed to fully assess trade-offs among management approaches on the BC coast. As a cultural keystone species, wild salmon provides a long list of valuable ecosystem services including nutrient cycling value for forests (Helfield & Naiman 2001), commercial value, subsistence value, spiritual value, and recreation value (Turner & Garibaldi 2004). To these, we can now add the value of mitigating pesticide resistance on salmon farms. A comprehensive ecosystem services analysis of salmon would account both for externalized benefits that are nonmaterial, collective, or long-term and for internalized benefits that have immediate economic impacts. To date, there is no comprehensive ecosystem services assessment of salmon to allow for comparison of trade-offs in future scenarios involving aquaculture development, status quo, or intensive restoration.

Conservation and management implications

Our synthesis of evolutionary models of pesticide resistance for the sea lice salmon system indicates two related but distinct mechanisms for delaying resistance, both of which have implications for the conservation of wild salmon and for the management of aquaculture. The first mechanism involves changes in the ratio of total wild salmon to total farmed salmon biomass. When the wild sea louse population shrinks relative to the farm population, resistance emerges faster (Murray 2011; McEwan et al. 2015). The second mechanism is the flow of susceptible sea louse alleles from the refuge to the farm through salmon populations that migrate past salmon farms (Figure 3). This mechanism is critical for managers, because the connectivity of farm louse subpopulations to the refuge louse population at the ocean basin scale depends on the abundance, survival, and migration of regional salmon populations (Figure 3), over which farms appear to have influence (Krkošek et al. 2011). Even if total wild salmon (and lice) are abundant at the ocean basin scale, declines in wild salmon populations near to farms are likely to threaten the evosystem service of resistance mitigation. In the following sections, we discuss management and conservation actions (numbered 1–6) related to the two above-mentioned mechanisms.

Total refuge- and farm-population sizes: ocean basin scale conservation and management

Because multiple farming regions within an ocean basin may all interact with a refuge population of wild salmon at the ocean basin scale, large scales are most pertinent to evaluating and managing the ratio of total wild salmon to total farmed salmon biomass. Intensified farm production can reduce the resistance-mitigating effects of wild salmon on an ocean basin scale, first, by directly increasing the number of farmed fish, meaning more treated hosts which select for resistance, and second, by depressing total wild fish stocks via parasite

transmission to juveniles or other ecological interactions (Krkošek *et al.* 2007; Ford & Myers 2008). If abundance of farmed salmon greatly exceeds that of wild salmon, as it does in some areas of the Northern Atlantic, resistance delays mediated by wild salmon will likely be weak or absent. Thus, aquaculture management might sustainably mitigate louse evolution by (1) scaling the intensity of aquaculture production on the ocean basin scale so that it does not exceed total wild salmon abundance.

On the wild salmon side, efforts to maintain the evosystem service would benefit from (2) rebuilding wild salmon abundance at the ocean basin scale, particularly in the North Atlantic, toward historical levels that are 1–2 orders of magnitude higher than at present (Limburg & Waldman 2009). While the biomass of salmon in the North Pacific has fluctuated depending on species (Irvine & Fukuwaka 2011), the total wild:farmed ratio is still much higher than the 1:1 that is theoretically needed to preclude resistance according to the model of McEwan *et al.* (2015). However, as we discuss in the next section, a large enough population at the ocean basin scale does not ensure the continued provision of this evosystem service.

Connectivity: regional and farm-scale conservation and management

The service that farms derive from being connected to ocean basin scale salmon populations suggests a previously unrecognized motivation to conserve regional salmon runs. The importance of these connective populations to resistance mitigation suggests that even small or at-risk salmon runs of little apparent commercial fisheries value may provide crucial connectivity which, if lost, could isolate sea lice on farms from the oceanic sea louse pool, leaving them in a selective environment favoring rapid evolution of treatment resistance. Numerous studies have demonstrated the considerable risks of salmon farms on wild runs (Krkošek *et al.* 2007; Krkošek 2010; Peacock *et al.* 2013; Rogers *et al.* 2013; Vollset *et al.* 2016). Our study indicates that reducing these may ultimately be in the best interest of farms, as the loss of regional wild salmon runs would represent a loss of the connectivity that is required for the resistance mitigation evosystem service. Enhancing connectivity can be approached via aquaculture management and direct wild salmon conservation.

In aquaculture management, louse evolution management might entail (3) identifying farms that are at high risk for resistance evolution due to declining or absent connectivity to wild populations, and more closely monitoring frequency of resistance on these farms. In addition, (4) modifying the scheduling and intensity of sea lice treatments on all farms to sustain regional migratory salmon (Peacock *et al.* 2013) could help maintain connectivity (Ashander 2010; Rogers *et al.* 2013). Management action 4 would be most effective if implemented on a regional (multifarm) scale. This is because multiple spawning populations of wild salmon often migrate past multiple farms, and sea lice on multiple farms likely form a single population (Jansen *et al.* 2012; Rogers *et al.* 2013).

The regional management of sea lice aligns with previous calls for larger-scale management, based on total numbers of lice, instead of average lice per farmed fish (e.g., Frazer *et al.* 2012; Jansen *et al.* 2012). This recommendation contrasts with many current practices, as sea louse management practices in BC (Rogers *et al.* 2013) and (until recently) in Norway (Jansen *et al.* 2012) have involved monitoring louse abundance per fish and treating individual farms when on-farm average density exceeds a threshold (Fisheries and Oceans Canada 2014). In contrast, regional management would entail coordinated production intensity, treatment timing, and treatment thresholds on multiple farms within a region (Bjørn *et al.* 2011; Rogers *et al.* 2013; Jones *et al.* 2015). Although coordination at subregional scales may also reduce effects of lice on wild fish (Bjørn *et al.* 2011), Norway has recently moved toward regional management, instituting a "traffic light" system that allows for regional aquaculture expansion, maintenance of the status quo, or contraction, depending on impacts on wild salmonids (Undercurrent News 2015).

For wild salmon, this evosystem service would benefit from (5) restoring, rebuilding, and maintaining populations that spawn in river systems with nearby salmon-aquaculture operations. In a restoration context, our definition of the regional scale must reach inland to include the watersheds that support regional wild salmon populations. The headwater tributaries and mainstem reaches of a river provide the spawning, rearing, and migrating habitat for multiple species of salmon; the watersheds surrounding them contribute to the hydrological, biological, and geological processes that sustain the entire ecosystem (Nehlsen 1997). An ecosystem-based approach to restoration encompasses processes in the river basin and its subwatersheds that support many species, including salmon (Nehlsen 1997). Ecosystem-based restoration does not characteristically include species-specific efforts such as hatcheries or ladders for example. Although hatchery enhancement programs could in principle increase regional connectivity, such programs have downsides. While reviewing these is beyond the scope of this article, one study showed that hatchery wild hybrids had lower reproductive success in subsequent generations, suggesting that even brief periods of captivity can have negative evolutionary effects (Araki *et al.* 2007).

It is important to note that by recognizing the benefit of wild salmon migrations close to aquaculture operations we do not mean to imply that new salmon farms *should* be located near abundant wild salmon runs. Selecting sites for salmon farms involves economic, social, and ecological considerations, including the risk that regional wild salmon will decline (Ford & Myers 2008). The role of connectivity between wild and farmed salmon in the context of resistance is only one factor informing management.

Linking wild salmon conservation and aquaculture management

The management goal of mitigating resistance and the conservation goal of sustaining wild salmon near existing farms are highly related: if connectivity declines, resistance increases, and on-farm louse treatment fails, infection of juveniles would increase further and a negative feedback cycle could cause regional wild salmon to go extinct. Therefore, thriving wild salmon populations on both the ocean basin scale and the regional scale that potentially mitigate resistance benefit aquaculture and, indirectly, themselves. But, even in the functional scenario (like the current situation in North Pacific, where neither resistance nor dramatic total wild salmon declines have occurred), the costs and benefits are not reciprocal: while both farms and nearby wild salmon reap benefits from avoided resistance, wild salmon alone bear costs associated with proximity to salmon farms (Ford & Myers 2008; Krkošek *et al.* 2011). This cost combined with other stressors means that the stability of the current situation in North Pacific is not assured, and requires proactive and cooperative actions. The insight that aquaculture benefits from an evosystem service that depends on wild salmon contrasts to the status quo whereby wild and farmed salmon are frequently at odds (Rayner & Howlett 2007), perhaps creating political and economic opportunities for this necessary cooperation.

One practical mechanism for cooperative action would be (6) to create a payment for ecosystem services (PES) program where existing farms pay for wild salmon habitat restoration or enhancement, thereby buffering the system from regional salmon declines that could lead to a negative feedback cycle. Such programs have been employed in the agricultural sector (Wunder *et al.* 2008), and have high potential in marine contexts as well. Bladon *et al.* (2014) describe designs and conditions for marine PES; while their case studies involve PES from wild catch industries, the principles for accommodating economic externalities in marine environments are applicable to net-pen aquaculture as well. The case of resistance mitigation is unique in the sense that the same entity (the aquaculture industry) may be both directly benefiting from the ecosystem service and actively eroding it. The directness of this link may enable a simple PES design in comparison to PES schemes for ecosystem services where the costs and benefits accrue to different groups of people on different scales. In this case, aquaculture companies would recognize the benefit they receive from regional wild salmon runs, identify local partners to do watershed conservation/habitat restoration work, and pay them according to an estimate of benefit. Such a PES program is one mechanism for a win-win scenario where the industry sustains and stabilizes the provision of an evosystem service it needs by supporting the conservation and restoration of wild salmon.

Management actions (1–6) suggest that integration of knowledge between aquaculture and wild fisheries managers is necessary. Because resistance emergence depends on both wild and farmed salmon at multiple scales, there is a need for the sharing of knowledge and data across regulatory agencies, and for cooperation among regulators, stakeholders, titleholders, and industry. One example is the Broughton Archipelago Monitoring Plan (BAMP; http://www.bamp.ca), a now-defunct program that brought together agencies, NGOs, industry, and academics. This illustrates the difficulties of collaborative marine spatial planning at larger scales; while promising, policies that attempt such large-scale planning have had mixed results (e.g., see discussion of the Pacific Salmon Forum; Krkošek 2010), or they are in the early stages of implementation (in the United States, the National Ocean Policy; Torres *et al.* 2015).

Conclusion

The relationship between salmon and their sea louse parasites demonstrates the importance of identifying—and protecting—the evosystem services afforded by contemporary evolution. Wild salmon have functioned as a nuisance to the salmon aquaculture industry, in part due to their role as a source of parasites—sea lice and others (Hamouda *et al.* 2005; Rayner & Howlett 2007; Gudjonsson & Scarnecchia 2009). However, an evosystem service perspective suggests that the existence of large oceanic populations of wild salmon and their connectivity to salmon farms via regional salmon runs has provided an unappreciated service by slowing or stopping the evolution of parasiticide resistance in sea lice on farms. The flow of susceptible genes means the presence of wild salmon runs near salmon farms may effectively subsidize the salmon aquaculture industry through avoided costs of parasite management.

Management that accounts for this evosystem service must consider the relative abundances of wild versus

farmed salmon on an ocean basin scale, as well as connectivity between them on a regional scale. We suggest that actions both on the side of aquaculture management and on the side of wild salmon conservation can contribute to the sustainable provision of this evosystem service. Organizations that are capable of implementing decisions at the regional scale, and perhaps even larger scales, are necessary to implement such actions. Furthermore, we suggest that a narrative of interdependence rather than conflict may animate the forums for marine management and link the two sides together in creating stabilizing solutions such as PES.

Contemporary evolutionary processes can provide benefits to people (Faith *et al.* 2010; Rudman *et al.* 2017). These evosystem services are situated at the interface of evolution, ecology, and conservation science. As our case study illustrates, a fuller accounting of the interacting forces involved may allow effective pursuit of more sustainable conservation management at evolution-relevant scales. As such, evosystem services may be of interest to conservationists, as species and ecosystems adapt and respond to a rapidly changing environment, sometimes in beneficial ways.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supplementary Material A. A complete list of aquaculture production and sea lice control.

Supplementary Material B. Details of model for resistance emergence with immigration.

Table S1. Showing for all countries from Costello (2009): farmed and wild salmon production, native wild salmon presence, sea lice control problems, and presence of resistance.

Figure S1. Summary of modeling results from McEwan *et al.* (2015) and Murray (2011).

References

Aaen, S.M., Helgesen, K.O., Bakke, M.J., Kaur, K. & Horsberg, T.E. (2015). Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends Parasitol.*, **31**, 72-81.

Araki, H., Cooper, B. & Blouin, M.S. (2009). Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters*, **5**, 621–624.

Ashander, J. (2010). *Effects of parasite exchange between wild and farmed salmon.* https://doi.org/10.6084/m9.figshare. 1584651. http:/hdl.handle.net/10048/1292 (visited May 15, 2017).

Bjørn, S.R., Finstad, B., Nilsen, R., Serra-Llinares, R.M. & Kristoffersen, R. (2011). Area protection may reduce salmon louse infection risk to wild salmonids. *Aquaculture Environ. Interactions*, **1**, 223-244.

Bladon, A.J., Short, K.M., Mohammed, E.Y. & Milner-Gulland, E.J. (2014). Payments for ecosystem services in developing world fisheries. *Fish Fish.*, **17**, 839-859.

Bridson, P. (2014). *Monterey Bay Seafood Watch Four Region Summary Document (Atlantic Salmon, Coho Salmon) for Norway, Chile, Scotland, British Columbia.* Monterey Bay Aquarium Seafood Watch Program.

Burridge, L., Weis, J.S., Cabello, F., Pizarro, J. & Bostick, K. (2010). Chemical use in salmon aquaculture: a review of current practices and possible environmental effects. *Aquaculture*, **306**, 7-23.

Chaput, G. (2012). Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES J. Mar. Sci. J. Cons.*, **69**, 1538-1548.

Charlesworth, B., & Charlesworth, D. (2010). *Elements of evolutionary genetics.* Roberts; Company Publishers, Greenwood Village, CO, USA.

Comins, H.N. (1977). The development of insecticide resistance in the presence of migration. *J. Theor. Biol.*, **64**, 177-197.

Costello, M.J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol.*, **22**, 475-483.

Costello, M.J. (2009). The global economic cost of sea lice to the salmonid farming industry. *J. Fish Dis.*, **32**, 115-118.

Daily, G. (1997). *Nature's services: societal dependence on natural ecosystems.* Island Press, Washington, D.C.

De Groot, R.S., Wilson, M.A. & Boumans, R.M.J. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecol. Econ.*, **41**, 393-408.

Espedal, P.G., Glover, K.A., Horsberg, T.E. & Nilsen, F. (2013). Emamectin benzoate resistance and fitness in laboratory reared salmon lice (Lepeophtheirus salmonis). *Aquaculture*, **416-417**, 111-118.

Faith, D.P., Magallón, S., Hendry, A.P., Conti, E., Yahara, T. & Donoghue, M.J. (2010). Evosystem services: an evolutionary perspective on the links between biodiversity and human well-being. *Curr. Opin. Environ. Sustain.*, **2**, 66-74.

FAO (Food and Agriculture Organization, United Nations). (2015a). FAO Global Aquaculture Production database updated to 2013. http://www.fao.org/fishery/statistics/global-aquaculture-production/query/en (visited April 15, 2016).

FAO (Food and Agriculture Organization, United Nations). (2015b). FAO Global Capture Production database updated to 2013. http://www.fao.org/fishery/statistics/global-capture-production/query/en (visited April 15, 2016).

Fisheries and Oceans Canada. (2014). Use of SLICE®. http://www.pac.dfo-mpo.gc.ca/aquaculture/reporting-rapports/health-sante/slice-eng.html (visited July 13, 2016).

Ford, J.S. & Myers, R.A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLOS Biol.*, **6**, e33.

Frazer, L.N., Morton, A. & Krkošek, M. (2012). Critical thresholds in sea lice epidemics: evidence, sensitivity and subcritical estimation. *Proc. R. Soc. Lond. B Biol. Sci.*, **279**, 1950-1958.

Georghiou, G.P. & Taylor, C.E. (1977). Operational influences in the evolution of insecticide resistance. *J. Econ. Entomol.*, **70**, 653-658.

Goldburg, R. & Naylor, R. (2005). Future seascapes, fishing, and fish farming. *Front. Ecol. Environ.*, **3**, 21-28.

Gould, F. (1998). Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annu. Rev. Entomol.*, **43**, 701-726.

Gudjonsson, S. & Scarnecchia, D.L. (2009). "Even the Evil Need a Place to Live": wild salmon, salmon farming, and zoning of the Icelandic coastline. *Fisheries*, **34**, 477-486.

Hamouda, L., Hipel, K.W., Kilgour, M.D., Noakes, D.J., Fang, L. & McDaniels, T. (2005). The salmon aquaculture conflict in British Columbia: a graph model analysis. *Ocean Coast. Manage.*, **48**, 571-587.

Helfield, J.M. & Naiman, R.J. (2001). Effects of salmon-derived nitrogen on Riparian forest growth and implications for stream productivity. *Ecology*, **82**, 2403-2409.

Heumann, J., Carmichael, S., Bron, J.E., Tildesley, A. & Sturm, A. (2012). Molecular cloning and characterisation of a novel P-glycoprotein in the salmon louse Lepeophtheirus salmonis. *Comp. Biochem. Physiol. Part C Toxicol. Pharmacol.*, **155**, 198-205.

Igboeli, O.O., Fast, M.D., Heumann, J. & Burka, J.F. (2012). Role of P-glycoprotein in emamectin benzoate (SLICE®) resistance in sea lice, Lepeophtheirus salmonis. *Aquaculture*, **344-349**, 40-47.

Irvine, J.R. & Fukuwaka, M. (2011). Pacific salmon abundance trends and climate change. *ICES J. Mar. Sci.*, **68**, 1122-1130.

Jansen, P.A., Kristoffersen, A.B., Viljugrein, H., Jimenez, D., Aldrin, M. & Stien, A. (2012). Sea lice as a density-dependent constraint to salmonid farming. *Proc. R. Soc. Lond. B Biol. Sci.*, **279**, 2330-2338.

Jones, S.R.M., Bruno, D.W., Madsen, L. & Peeler, E.J. (2015). Disease management mitigates risk of pathogen transmission from maricultured salmonids. *Aquaculture Environ. Interactions*, **6**, 119-134.

Kremen, C., Williams, N.M., Aizen, M.A., *et al.* (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.*, **10**, 299-314.

Krkošek, M. (2010). Sea lice and salmon in Pacific Canada: ecology and policy. *Front. Ecol. Environ.*, **8**, 201-209.

Krkošek, M., Ford, J.S., Morton, A., Lele, S., Myers, R.A. & Lewis, M.A. (2007). Declining wild salmon populations in relation to parasites from farm salmon. *Science*, **318**, 1772-1775.

Krkošek, M., Lewis, M.A., Morton, A., Frazer, L.N. & Volpe, J.P. (2006). Epizootics of wild fish induced by farm fish. *Proc. Natl. Acad. Sci.*, **103**, 15506-15510.

Krkošek, M., Connors, B.M., Morton, A., Lewis, M.A., Dill, L.M. & Hilborn, R. (2011). Effects of parasites from salmon farms on productivity of wild salmon. *PNAS*, **108**, 14700–14704.

Limburg, K.E. & Waldman, J.R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, **59**, 955-965.

Marsh, S.P., Llewellyn, R.S. & Powles, S.B. (2006). Social costs of herbicide resistance: the case of resistance to glyphosate. In: *Proceeding Annu. Meet. Int. Assoc. Agric. Econ.* International Association of Agricultural Economists, Queensland, Australia.

McEwan, G.F., Groner, M.L., Fast, M.D., Gettinby, G. & Revie, C.W. (2015). Using agent-based modelling to predict the role of wild refugia in the evolution of resistance of sea lice to chemotherapeutants. *PLOS ONE*, **10**, e0139128.

Melander, A.L. (1914). Can insects become resistant to sprays? *J. Econ. Entomol.*, **7**, 167-173.

Messmer, A.M., Rondeau, E.B., Jantzen, S.G., Lubieniecki, K.P., Davidson, W.S. & Koop, B.F. (2011). Assessment of population structure in Pacific Lepeophtheirus salmonis (Krøyer) using single nucleotide polymorphism and microsatellite genetic markers. *Aquaculture*, Sea Lice 2010, Proceedings of the 8th International Sea Lice Conference, Victoria, BC, Canada, May 9–12, 2010, **320**, 183-192.

Millennium Ecosystem Assessment (MEA). (2005). *Ecosystem and human wellbeing: synthesis*. United Nations, Washington, D.C.

Murray, A.G. (2011). A simple model to assess selection for treatment-resistant sea lice. *Ecol. Model.*, **222**, 1854-1862.

Nagasawa, K. (2004). Sea lice, Lepeophtheirus salmonis and Caligus orientalis (Copepoda: Caligidae), of wild and farmed fish in sea and brackish waters of Japan and adjacent regions: a review. *Zoolog. Stud.*, **43**, 173-178.

Nehlsen, W. (1997). Prioritizing Watersheds in Oregon for Salmon Restoration. *Restoration Ecology*, **5**, 25–33.

Orr, H.A. & Unckless, R.L. (2014). The population genetics of evolutionary rescue. *PLOS Genet*, **10**, e1004551.

Peacock, S.J., Krkošek, M., Proboszcz, S., Orr, C. & Lewis, M.A. (2013). Cessation of a salmon decline with control of parasites. *Ecol. Appl.*, **23**, 606-620.

Rayner, J. & Howlett, M. (2007). Towards a post-staples future? New products and new directions in Canada's resource industries caught in a staples vise: the political economy of Canadian aquaculture. *Policy Soc.*, **26**, 49-69.

Revie, C.W., Gettinby, G., Treasurer, J.W. & Rae, G.H. (2002). The epidemiology of the sea lice, Caligus elongatus Nordmann, in marine aquaculture of Atlantic salmon, Salmo salar L., in Scotland. *J. Fish. Dis.*, **25**, 391-399.

Rogers, L.A., Peacock, S.J., McKenzie, P., *et al.* (2013). Modeling parasite dynamics on farmed salmon for precautionary conservation management of wild salmon. *PLoS ONE*, **8**, e60096.

Rudman, S.M., Kreitzman, M., Chan, K.M.A. & Schluter, D. (2017). Evosystem services: the role of contemporary evolution in maintaining and providing ecosystem services. *Trends Ecol. Evol.*, **32**, 403-415.

Ruggerone, G.T., Peterman, R.M., Dorner, B. & Myers, K.W. (2010). Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Mar. Coast. Fish.*, **2**, 306-328.

Saksida, S.M., Morrison, D., McKenzie, P., *et al.* (2013). Use of Atlantic salmon, Salmo salar L., farm treatment data and bioassays to assess for resistance of sea lice, Lepeophtheirus salmonis, to emamectin benzoate (SLICE®) in British Columbia, Canada. *J. Fish Dis.*, **36**, 515-520.

Tabashnik, B.E., Brévault, T. & Carrière, Y. (2013). Insect resistance to Bt crops: lessons from the first billion acres. *Nat. Biotechnol.*, **31**, 510-521.

Torres, H., Muller-Karger, F., Keys, D., Thornton, H., Luther, M. & Alsharif, K. (2015). Whither the U.S. National Ocean Policy Implementation Plan? *Mar. Policy*, **53**, 198-212.

Turner, N. & Garibaldi, A. (2004). Cultural keystone species: implications for ecological conservation and restoration. *Ecol. Soc.*, http://www.ecologyandsociety.org/vol9/iss3/art1/.

Undercurrent News. (2015). Norway unveils plan for 5% aquaculture growth; tied to lice levels, "traffic light" system. https://www.undercurrentnews.com/2015/03/23/norway-unveils-proposal-for-5-aquaculture-growth-tied-to-traffic-light-system/ (visited Jan. 31, 2017).

U.S. EPA. (2015). Insect Resistance Management Fact Sheet for Bacillus thuringiensis (Bt) Corn Products. http://www.epa.gov/oppbppd1/biopesticides/pips/bt_corn_refuge_2006.htm (visited Aug. 8, 2015).

Vollset, K.W., Krontveit, R.I., Jansen, P.A., *et al.* (2016). Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. *Fish Fish*, **17**, 714-730.

Wunder, S., Engel, S. & Pagiola, S. (2008). Taking stock: A comparative analysis of payments for environmental services programs in developed and developing countries. *Ecol. Econ.*, Payments for Environmental Services in Developing and Developed Countries, **65**, 834-852.