Ecological Economics 142 (2017) 228–237

Contents lists available at ScienceDirect

Ecological Economics

journal homepage: www.elsevier.com/locate/ecolecon

ANALYSIS

Managing the Risks of Sea Lice Transmission Between Salmon Aquaculture and Wild Pink Salmon Fishery

Biao Huang [a,*], Charles Perrings [b]

[a] School of Life and Environmental Science, Centre for Integrative Ecology, Deakin University, Victoria 3125, Australia
[b] EcoSERVICES Group, School of Life Sciences, Arizona State University, Tempe, AZ, United States

ARTICLE INFO

Article history:
Received 26 August 2016
Received in revised form 2 March 2017
Accepted 5 March 2017
Available online 6 July 2017

Keywords:
Infectious wildlife disease
Sea lice
Externality
Marine salmon aquaculture
Binary control

ABSTRACT

A common external effect of aquaculture is the transmission of infectious diseases to wild fish stocks. A frequently cited example of this is the infection of wild salmon by sea lice from salmon farms. Management of the disease risk to wild salmon populations requires an understanding both of the disease transmission mechanisms and the control incentives faced by fish farmers. In this paper we develop a bioeconomic model that integrates sea lice population dynamics, fish population dynamics, aquaculture, and wild capture salmon fisheries. Using an optimal control framework, we investigate options for managing the sea lice infection externality. We pay particular attention to the role of sea lice management on the stability of wild stocks, and the sensitivity of sea lice effects on wild fisheries. We find that the stability of wild stocks is related to sea-lice-induced mortality (inversely) and the value of wild fishery.

© 2017 Published by Elsevier B.V.

1. Introduction

Aquaculture is a rapidly growing industry that has become a major supplier of fish and shellfish to the global market (FAO, 2014). Concern about the environmental effects of aquaculture is also growing. The production of shrimp and salmon, two of the most lucrative and widely traded aquaculture products, is responsible for a range of environmental impacts due to the off-site effects of disease transmission, waste discharge, escapees, the use of chemicals and drugs, and the consumption of fishmeal and fish oil (Naylor et al., 1998). The most important of the environmental externalities of salmon farming is the transmission of sea lice to wild fish stocks (Asche et al., 2009; Taranger et al., 2015; Lafferty et al., 2015).

In this paper we focus on a particular disease externality of coastal salmon farms— the effect of sea lice on wild fish stocks. This effect has been debated extensively. Researchers agree that sea lice are one of many factors that affect wild stock levels. However, there is disagreement about the size of the effect. Some argue that lice are not instrumental in wild stock population decline (Marty et al., 2010). Others claim that where salmon net-pens provide ideal conditions for sea lice, they are the primary threat to vulnerable migrating wild juveniles (Krkošek et al., 2006, 2007). In both Norway and Canada, sea lice are argued to be a major threat to the sustainability of marine aquaculture and the viability of wild fisheries, and are subject to strict regulations (Torrissen et al., 2013).

The generic problem in the management of wildlife disease externalities of aquaculture is the regulation of transmission risks due to contact between infected farmed stocks and susceptible wild stocks (Conrad and Rondeau, 2015; Fischer et al., 2015, 2016). The mitigation of disease risk requires reduction in either the infection rate of farmed stocks or contact between farmed and wild stocks. In the case of marine salmon aquaculture, the infection rate of farmed fish may be reduced by chemical controls. Since farmed fish stocks have a reservoir-host effect on disease transmission, this also affects disease transmission to wild fish stocks.

From a social perspective, salmon farmers should ideally take account of the costs incurred by wild capture fisheries when deciding how much in-farm disease control to apply. Nor is the disease of wild salmon the only off-site effect to consider. It may, for instance, change the structure and distribution of other species within the system (Burge et al., 2014). Since disease is an external cost of salmon production, however, it will not be considered in the absence of regulatory, property-rights, or tax-based initiatives by a fishery authority.

This study focuses on the optimal management of sea lice externalities between salmon aquaculture and wild salmon fisheries that run in both directions. Sea lice are native ectoparasite copepods, common on wild adult salmon. The salmon louse (*L. salmonis*) has a free-living phase and a parasitic phase in its approximately 2-month life cycle (Frazer, 2009). Once attached to salmon, lice feed on mucous, blood, and skin which causes both morbidity and mortality of salmon (Costello, 2006). When wild stocks migrate to a fresh water environment in the fall for spawning, lice from wild stocks disperse into fish farms located on the migration route of wild stocks and infest the

* Corresponding author.
E-mail address: b.huang@deakin.edu.au (B. Huang).

http://dx.doi.org/10.1016/j.ecolecon.2017.03.012
0921-8009/© 2017 Published by Elsevier B.V.

farmed fish. If not treated in the farms, the lice grow rapidly and re-infest wild juveniles when they emigrate into marine environment in the early summer. Although the disease problem associated with fish farms is widely recognized, there are few estimates of the ecological and economic impacts on both farmed and wild fisheries. One estimate is that sea lice may cost the salmon industry US$480 million a year or 6% of product value (Costello, 2009). Currently, salmon farms control lice with in-food chemical such as emamectin benzoate (SLICE) with high efficacy to control all stages of sea lice (Stone et al., 2000), and with cleaner fish such as wrasse or lumpfish. These controls have different cost effectiveness (Liu and Bjelland, 2014), also sea lice may develop resistance to SLICE (McEwan et al., 2015).

To analyze this problem we develop a bioeconomic model that incorporates epidemiological, ecological, and economic elements. As in prior studies of wildlife disease management that employ an optimal control framework (Gramig et al., 2009; Horan et al., 2010), we treat the level of disease control as endogenous. Specifically, we integrate sea lice population dynamics in an economic model of salmon production to determine the optimal control policy—first from the perspective of salmon aquaculture producer, and then from the perspective of a joint fisheries manager. By taking account of the complex relationship between sea lice populations in farmed and wild fisheries, we are able to assess the economic impact of salmon aquaculture on the wild fishery due to sea lice transmission. While our model is calibrated on the pink salmon fishery in Pacific Canada, our approach can readily be applied to the management of the disease effects of aquaculture on wild fisheries more generally.

The structure of the paper is as follows. Section 2 describes various components of sea lice-salmon interactions in aquaculture. Section 3 presents a bioeconomic model of farmed and wild fisheries. The main results and the outcome of numerical simulations are presented in Section 4. This is followed by sensitivity analysis provided in Section 5. Finally, Section 6 discusses the results and draws conclusions.

2. A Model of Sea Lice-salmon Interactions in Aquaculture

2.1. Sea Lice Dynamics

We consider a coastal area in which an Atlantic salmon (*Salmo salar*) farm (or a coordinated aquaculture industry consisting of many farms) is connected by the free-living stage of sea lice transmission with wild pink salmon stocks when they migrate into or out of spawning rivers. The farm manager releases salmon smolts ($F_{f,0}$) into fish farms just before wild adults head home for spawning. Fish farmers either employ batch harvesting at fixed intervals to target specific markets, or employ graded harvesting during the whole grow-out season. Aquaculture salmon production has a production cycle between 1.5 and 2.5 years (Asche et al., 2009). In this study we assume that production involves fixed interval batch harvesting-all fish are harvested 24 months after being released.

We divide sea lice growth into a free-living copepodite phase and an adult lice phase. Sea lice cannot survive in a fresh water environment. Due to the relatively brief spawning migration (August and September) of wild pink salmon from marine environment to fresh water environment, gravid lice from homecoming wild adult stocks would infest farmed stocks by spreading copepodite produced by gravid lice ($L_{w,t}$). Copepodites have a probability of ρ to attach to farmed ($F_{f,t}$) or wild ($F_{w,t}$) hosts if present in coastal waters. They then survive to adult lice stage with probability ψ_t depending on environmental factors, such as salinity and water temperature (Tucker et al., 2000). Settlement success ψ_t is assumed to be periodically forced, and takes the form,

$$\psi_t = \varepsilon_1 + \varepsilon_2 \sin\left(\frac{2\pi}{12}t\right) \quad (1)$$

This simple sinusoidal function generates a 12 month periodicity to infections, $t = 1, 2\ldots12$, and has a seasonal force impact coefficient of ε_2 and a base settlement success of ε_1.

When migrating wild juveniles pass by fish farms close to wild migratory routes from May to July they are subject to lice infestation. Wild juveniles are vulnerable because of their small size, and also because that they are subject to the environmental stress caused by the transition from fresh water to marine environment. We assume that the chemical treatment u_t, if applied, kills both adult sea lice and copepodites on farmed fish. The mortality rate associated with chemical treatment for copepodites and adult sea lice is denoted by k and z, respectively.

2.2. A Well-mixed Coastal Environment

The hydrodynamic environment is one of the main factors affecting the dynamics of sea lice transmission (Adams et al., 2012). Two different environments are considered here. First, we consider a coastal environment in which copepodites are well-mixed (Ashander et al., 2012), implying that copepodite density is the same across the whole area including the farm system. In what follows, subscript f denotes farmed stock, subscript w denotes wild stock, and subscript t denotes time (measured in months). If X_t denotes total copepodite abundance in the coastal area at time t, and $L_{f,t}$ denotes lice abundance in the farm, then a discrete model for sea lice dynamics in farm is,

$$X_{t+1} = \lambda\left(L_{f,t} + L_{w,t}\right) + X_t\left(1-\rho\left(F_{f,t} + F_{w,t}\right)\right)(1-\xi)f_c(u_{t-2}, u_{t-1}, u_t) \quad (2)$$

$$L_{f,t+1} = \rho\psi_t X_t F_{f,t} + L_{f,t}(1-\nu)\left(F_{f,t+1}/F_{f,t}\right)f_l(u_{t-2}, u_{t-1}, u_t) \quad (3)$$

The dynamics of copepodite and lice populations are described by Eqs. (2) and (3). They are similar to a discrete-time version of the canonical Anderson-May host parasite model (Anderson and May, 1978). Eq. (2) describes the dynamics of copepodites in the coastal area. The first term on the right hand side (RHS) is the number of copepodites produced by lice on farmed $L_{f,t}$ and gravid lice $L_{w,t}$ which is equal to zero when there are no adult wild stocks in the coastal area. Copepodite production is taken to be at the constant rate, λ. $F_{w,t}$ denotes the abundance of wild juveniles at the end of month t. The second term has three components. The first component, $X_t(1-\rho(F_{f,t}+F_{w,t}))$, is total copepodite abundance after dispersal and attachment to fish host. Copepodites are assumed to attach to hosts at the rate ρ. The second component is the surviving proportion after natural mortality of ξ and the third component is copepodite mortality due to chemical treatment, $f_c(u_{t-2}, u_{t-1}, u_t)$, the control being included in feed. Copepodite transmission between farmed and wild fish only happens during the spawning migration of wild adults and the emigration of juvenile wild stocks. Because sea lice cannot survive in a fresh water environment we assume that in this well-mixed system copepodites do not attach to wild spawning adults. However, wild juveniles will be infested when they migrate into the ocean.

Eq. (3) gives the total lice abundance in the farm at the beginning of each time unit (month) as the sum of the newly mature adults and the lice remaining from last period after natural mortality and the effects of chemical control. The first term on the RHS of Eq. (3) is the number of copepodites attached to hosts that become adult, the survival rate being ψ_t. The second term on the RHS is the number of lice remaining from last period. There are four components in this term. The first component is the total lice number at the beginning of the period, the second component $(1 - \nu)$ is the proportion surviving after natural mortality ν. The third one is the proportional change in the lice due to mortality between $F_{f,t+1}$ and $F_{f,t}$. We assume that if 10% of fish are killed, 10% of adult lice will also be killed. If all fish are harvested, then all lice will be killed in the process. The last component, $f_l(u_{t-2}, u_{t-1}, u_t)$, is the lice kill function due to chemical treatment.

The efficacy of chemical treatment varies depending on sea location, lice genetics, and water temperature (Stone et al., 1999). Here we assume that chemical treatment is effective for a three-month period, during which it kills both lice and copepodites (Gustafson et al., 2006). Since the efficacy of treatment decreases over time, the chemical-induced mortality functions are assumed to take the form $f_l(u_{t-2}, u_{t-1}, u_t) = (1-ku_t)(1-0.8ku_{t-1})(1-0.6ku_{t-2})$ and $f_c(u_{t-2}, u_{t-1}, u_t) = (1-zu_t)(1-0.8zu_{t-1})(1-0.6zu_{t-2})$, respectively.

As a first approximation, we assume that fish killed by lice do not have any economic value, but that infested live fish fetch the same price as un-infested fish. That is, the effect of sea lice is only evident through mortality, not other sub-lethal effects. In reality, sea lice can also reduce fish growth and feed conversion rates (Costello, 2006; Mustafa et al., 2001)—though the literature provides little information on these effects.

The impact of sea lice on farmed salmon is modeled as

$$F_{f,t+1} = F_{f,t} \exp\left(-d_f L_{f,t}/F_{f,t}\right) \quad (4)$$

where $F_{f,t}$ denotes Atlantic salmon abundance in the farm at the end of month t. After harvest, farms are fallowed for a short time to kill existing lice. Farmers then release the same amount of juveniles $F_{f,0}$ into their farms. The grow-out rotation is not therefore affected by lice and is assumed to be constant. d_f is the sea lice-induced mortality rate for farmed Atlantic salmon,[1] and $L_{f,t}$ is adult sea lice abundance at the farm at time t.

Wild salmon juveniles ($F_{w,t}$) are free of lice infestation in the river environment but are subject to re-infestation from the fish farm when migrating into marine environment from May to July. The number of lice at month t is the sum of new adults developed from copepodites attached to hosts, and the remaining lice from last period. The lice ($L_{w,t+1}$) dynamics in a well-mixed system is modeled as,

$$L_{w,t+1} = \rho\psi F_{w,t} X_t + L_{w,t}{}^*(1-v)^*\left(F_{w,t+1}/F_{w,t}\right) \quad (5)$$

Offshore lice dynamics are not modeled here. Instead, the effect of lice on adult wild fish stocks offshore is incorporated in a constant natural mortality rate.

2.3. A Distance-dispersal Environment

We also consider a distance-dispersal environment where transmission is captured by modifying the model described previously. Three features of the resulting compartmental model are: 1) constant transmission rates (d_1,d_2) between farmed and wild fisheries, with d_1 indicating copepodite transmission from wild spawning stocks to farmed salmon stocks and d_2 indicating copepodite transmission from farm stocks to wild juveniles; 2) unidirectional drift—copepodites that leave the salmon farm do not return; and 3) limited cross infection—lice produced by wild salmon mostly infect other wild salmon, and lice produced by farmed salmon mostly affect other farmed salmon. Copepodite dynamics in farm are given by:

$$X_{f,t+1} = \lambda\left(L_{f,t} + d_1 L_{w,t} I_{t=Aug,Sep}\right) + (1-d_2)X_{f,t}(1-\rho F_{f,t}) \times (1-\xi) f_c(u_{t-2}, u_{t-1}, u_t) \quad (6)$$

where $I_{t=Aug,Sep}$ is indicator function with a value of 1 during home-river migrating period, August and September, and 0 at other months. Adult lice dynamics for the farm and wild fishery dynamics are the same as those described by Eqs. (3) and (5). By contrast, copepodite dynamics in the wild are given by:

$$X_{w,t+1} = \lambda L_{w,t} + (1-\rho F_{w,t})(1-\xi)\left(x_{w,t} + d_2 x_{f,t}\right) \quad (7)$$

[1] As one reviewer points out, mortality in farmed fish is frequently an effect of treatment failure. Bath treatments, in particular, can stress fish.

2.4. Wild Pink Salmon Dynamics

To model wild salmon dynamics we consider one of the most commonly infected wild salmon—Pink salmon (*O. gorbuscha*). Pink salmon are the smallest salmon found in North America. They are also the least valued of commercially exploited salmon species. Wild spawning salmon home-migrate from August to September. The wild juveniles remain in the river environment from October until the following April. They then move into in-shore waters from May to July, before migrating to the ocean and remain there from August until the next July. Pink salmon have a two-year life cycle, including an even and odd-numbered year run. These two runs are reproductively isolated. The spatial separation between adult and juvenile salmon due to migration prevents louse transfer between odd- and even-numbered year runs (Krkošek et al., 2007).

We assume that the odd-numbered run dominates, with an initial escapement level of S_0, as compared to $0.5S_0$ for even-numbered year runs. Let S_n denote the escapement level of wild stocks in year n. This escapement level becomes spawning stock, which has a concave-down fry production function following a Ricker relationship $F_{1,n+1} = S_n \exp(\gamma - S_n/b)$, where $F_{1,n+1}$ is the number of fry in the next generation ($n + 1$), γ is the population growth rate. b determines the density dependent mortality rate, and is related to the carrying capacity of the system. The breeding stock dies after spawning. A natural mortality rate m applies to juvenile wild salmon in fresh water, therefore the population of surviving wild juveniles before migrating into the inshore area is $(1-m)F_{1,n+1}$.

When wild pink juveniles migrate into the inshore area from May to July, they are subjected to lice infestation from fish farms. For every farmed salmon grow-out cycle, 24 months, there are 2 copepodite infestations from wild stocks, i.e., in even and odd-numbered runs, and 2 lice infestations from farmed to wild stocks. The wild juvenile mortality rate induced by sea lice infestation is modeled using the Ricker equation (Krkošek et al., 2007; Marty et al., 2010) on a monthly time scale in accordance with time scale of the farmed fishery and lice dynamics. The damage function takes the form $F_{t+1,n} = F_{t,n}{}^* \exp(-d_w L_{wt}/F_{t,n})$, where $F_{t,n}$ is t-month old juveniles abundance of generation n, and d_w is the mortality rate induced by sea lice population L_{wt} attached to wild juveniles ($F_{t,n}$). It follows that the wild juvenile population prior to migrating into the open ocean from the inshore area would be

$$F_{n+1} = (1-m)F_{1,n+1} \prod_{t}^{May,June,July} \exp\left(-d_w L_{w,t}/F_{t,n+1}\right) \quad (8)$$

Note that $L_{w,t}$ is the total lice infestation of wild juveniles migrating into the ocean environment from May to July each year. Before returning to their natal river, wild stocks in the marine environment experience a fixed natural mortality rate φ. The wild adult abundance of generation $n + 1$, $F_{w,n+1}$, is thus given by:

$$F_{w,n+1} = (1-m)^*(1-\varphi)^* F_{1,n+1}{}^* \prod_{t}^{May,June,July} \exp\left(-d_w L_{w,t}/F_{t,n+1}\right) \quad (9)$$

Wild salmon fisheries differ from salmon aquaculture in terms of management objectives, institutional structure and regulations. Whereas the management objective for salmon aquaculture is to maximize private profit, the goal of wild salmon management typically focuses on a broader set of social objectives. Wild fishery managers limit (cap) harvest in the wild capture fishery so as to ensure escapement spawning targets that protect future harvest (Liu et al., 2011). We assume that the regulatory authority chooses fishing effort level by license limitation, and that each year a constant harvest proportion α is applied. Therefore, the total allowable catch (TAC_{n+1}) for each run is,

$$TAC_{n+1} = \alpha(1-m)^*(1-\varphi)^* F_{1,n+1}{}^* \prod_{t}^{May,June,July} \exp(-d_w L_{w,t}/F_{t,n+1}) \quad (10)$$

Eq. (8) suggests that TAC_{n+1}, equal to $\alpha F_{w,n+1}$, is subject to fluctuation due to sea lice infestation during the juvenile stage. The survival $(1-\alpha)F_{w,n+1}$ will then be the escapement level of wild spawning stock for the next generation, i.e., S_{n+2}.

3. A Bioeconomic Model of Farmed and Wild Fisheries

In each 24-month grow-out season, the salmon farmer feeds Atlantic salmon to weight W_f then instantaneously harvests all fish at the beginning of the last period, at a cost C_f per unit of weight. The farmer is assumed to target a specific market, and sells the fish at a fixed price P_f per kilogram. An adult Atlantic salmon weighs about 7 kg, fetches a price of \$6.5/kg (marineharvest.com). By comparison, an adult wild pink salmon weighs about 1.4 kg, and fetches a price of \$0.36/kg (adfg.alaska.gov).

Due to the proximity of wild migratory routes to the fish farms, sea lice infestation between wild and farmed fish cannot be prevented. Each period the producer has to decide whether or not to apply chemical treatment (u_t) to his farm. Note that Revie et al. (2005) predicts the impact of varying treatment interventions with sea lice compartments model. Our object here is to investigate optimal control strategies on salmon farms given the infection risk from wild salmon. We assume that farmers manage fish farms optimally with respect to other inputs than chemical treatment, and their disease control decision is separable from other productive inputs.[2]

Farmed Atlantic salmon weight growth is modeled as a polynomial function of time $w_{f,t} = a_1 t^2 - a_2 t^3$, where $t_1 = 1, \ldots, 24$, $a_1 = 0.0397, a_2 = 0.00112$ calibrated from Asche and Bjorndal (2012). Weight growth requires a certain quantity of food. For a given conversion ratio (f_{con}) between food and fish weight gain, the quantity of feed for each time step is $g(t) = f_{con}{}^*(w_t - w_{t-1})$.

3.1. The Private Producer's Problem

We first solve the disease control problem from the private producer's perspective, assuming a single farm and separating disease control from all other management actions. Given a discount rate δ, feeding cost C_{feed} per kilo, and louse treatment cost of $c_{treatment}$, the problem for the aquaculture producer is to maximize the present value of the stream of aquaculture revenue, net of control and feeding cost, V^p, by choosing a treatment policy:

$$\begin{aligned} V^p = & \max_{u_t} \sum_{j=1}^{40} \left(\frac{1}{1+\delta}\right)^{24j-1} \left(p_f - c_f\right) w_f F_{f,24n} \\ & - \sum_{t=1}^{960} \left\{ \left(\frac{1}{1+\delta}\right)^{t-1} \left((w_{f,t+1} - w_{f,t}) f_{con} c_{feed} F_{f,t} + u_t c_{treatment}\right) \right\} + S^p(F_{f,40}) \end{aligned} \quad (11)$$

subject to the lice and fish dynamics Eqs. (2)–(4) and the initial conditions $F_{f,0}$ and S_0.

The control u_t is a binary choice variable, $u_t \in [0,1]$. We model it long enough (40 grow-out seasons, or 80 years, or 960 months) for the steady-state equilibrium to be reached. We model fish production on a rotational scale (j) due to the batch nature of harvest, but a Monthly scale (t) for chemical treatment—since the farmer has to make disease control decisions every month. Given the weight difference term, $w_{f,2} - w_{f,1} = w_{f,j^*24+2} - w_{f,j^*24+1}$, j = 1, …40, is determined exogenously. Lice have no impact on weight gain.

As with all finite time horizon problems, we expect to see a departure from the steady state toward the end of the horizon (Epanchin-Niell and Wilen, 2012). To deal with this problem, we follow the logic of Epanchin-Niell and Wilen (2012), and set a terminal value to lock in the steady state equilibrium once it is reached after 40 rotations (80 years). This terminal value, the last term in Eq. (9), is the present value of the steady state harvest net of control costs from year 81 to infinity. Since the system reaches a steady state at rotation year 40, we are able to use the value at the 40th rotation to calculate terminal value. Let $TVP^p = (P_f - C_f) W_f F_{f,40}$ represent the profit from harvesting at the end of the 40th rotation, and $TVC^p = \sum_{936}^{960} ((w_{f,t+1} - w_{f,t}) f_{con} c_{feed} F_{f,t} + u_t c_{treatment})$ represent the cost of feeding and treatment during the 40th rotation (from month 936 to month 960) under privately optimal control. The terminal value is then,

$$S^p(F_{f,40}) = \sum_{j=41}^{\infty} \left(\frac{1}{1+\delta}\right)^{24j-1} (TVP^p - TVC^p)$$

3.2. The Joint Fisheries Manager's Problem

In contrast to the private fishery manager, the joint fisheries manager has to consider the effect that aquaculture has on the commercial wild salmon fishery. The harvest function for the wild capture fishery is assumed to take the form $h_n = F_{w,n}(1 - e^{-qE_n})$, which represents the discrete-time version of the Schaefer-Gordon harvest function in year n, where $F_{w,n}$ is the total number (not biomass weight) of wild adult fish in year n, q is the catchability coefficient and E_n is fishing effort in year n. Substituting $h_n = TAC_n$, and assuming that the unit cost per fishing effort is c_w, total annual cost (TC) in year n thus is $TC_n = \frac{c_w}{q} \ln \frac{F_{w,n}}{F_{w,n} - TAC_n} = \frac{c_w}{q} \ln \frac{1}{1-\alpha}$.

Assuming an adult pink salmon weight of w_w at harvest and price of p_w, the joint fisheries problem is to maximize the net present value V^J from farmed and wild fisheries, net of feeding, control and harvesting cost over time,

$$\begin{aligned} V^J = & \max_{u_t} \sum_{j=1}^{40} \left(\frac{1}{1+\delta}\right)^{24j-1} \left(p_f - c_f\right) w_f F_{f,24j} \\ & - \sum_{t=1}^{960} \left\{ \left(\frac{1}{1+\delta}\right)^{t-1} \left((w_{f,t+1} - w_{f,t}) f_{con} c_{feed} F_{f,t} + u_t c_{treatment}\right) \right\} \\ & + \sum_{n=1}^{80} \left(\frac{1}{1+\delta}\right)^{12n-1} \left(TAC_n w_w p_w - \frac{c_w}{q} \ln \frac{1}{1-\alpha}\right) + S^J(F_{f,40}, F_{w,40}) \end{aligned} \quad (12)$$

subject to the lice and fish dynamics, Eqs. (2), (3), (5), (8), and the initial conditions $F_{f,0}$ and S_0.

The last term of Eq. (10), $S^J(F_{f,40}, F_{w,40})$, is the scrap value of the state variables after 40 rotations (80 years), $S^J(F_{f,80}, F_{w,80}) = \sum_{j=41}^{\infty} \left(\frac{1}{1+\delta}\right)^{24j-1} (TVP^J - TVC^J + TVW^J)$. We also let $TVP^J = (P_f - C_f) W_f F_{f,40}$ represent harvesting profit for the 40th rotation, and let $TVC^J = \sum_{t=936}^{960} ((w_{f,t+1} - w_{f,t}) f_{con} c_{feed} F_{f,t} + u_t c_{treatment})$ represent feed and control costs during the 40th rotation under joint control (note that the time interval in TVC^J is one month). $TVW^J = (TAC_{79} + TAC_{80}) w_w p_w - \frac{2c_w}{1-q} \ln \frac{1}{1-\alpha}$, represents profit from harvesting wild fishery in years 79 (odd-numbered year run) and 80 (even-numbered year run). Together, these two years correspond to the 40th rotation for fish farming operations. n denotes a yearly time scale (as before) as wild salmon are harvested every year.

[2] Theoretically, a farmer could choose to operate near to wild stocks and to treat farmed salmon, or away from wild stocks and not treat farmed salmon. This perspective could be addressed by adding a percentage of wild stocks "close to" the farm, leading to contact transmission, and "far from" the farm, leading to no transmission.

Since it takes into consideration both sea lice externality that the fish farms impose on the wild fishery, and the externality imposed on fish farms by the migrating copepodites produced by gravid lice from wild spawning stock, the solution to the joint fisheries manager's problem will differ from the private producer's problem. Theoretically, the private producer controls lice up to the point where the marginal value of the damage inflicted on the farm is equal to the marginal cost of applying chemical treatment to control lice. In the rest of this study, we will refer "jointly optimal control" to the case where the lice externality on wild fishery is taken into consideration by the joint fisheries manager. However, we should bear in mind that the only control variable is the chemical treatment to control sea lice on the salmon farm, and the wild fishery is regulated through a fixed proportional harvest policy. "Quasi-optimized" might be a more accurate term to describe our model.

4. Results

4.1. Numerical Results

Given the complex nature of this integer non-linear, non-convex optimal control problem, closed form solutions for the value function and optimal control policy do not exist. Furthermore, multiple locally optimal solutions may occur. Therefore, we rely upon numerical methods to solve the problem. We run simulations first under the well-mixed environment and then distance-dispersal environment. The commercial Premium Solver Platform (multi-starting point) was used to approximate the solution with Branch and Bound method. The values for all parameters are provided in Table 1. Some of the parameters are taken directly from the literature, and some are calibrated for this study. None of the parameters adopted are empirically estimated.

4.2. The Well-mixed Coastal Environment

The frequency and timing of chemical treatment determines the effect of the chemical control on species and disease alike. The binary control policies applied by the private producer and the joint fisheries manager in the first four fish farm grow-out seasons (the first 8 years) are different. After 8 years, the treatment strategy for odd and even-numbered year runs are the same as in year 7 and 8. Therefore, we are able to use the first four grow-out seasons to summarize and characterize the differences in control policy between the private producer and the joint fisheries manager (Fig. 1).

Fig. 1 is a schedule for the private producer and joint fisheries manager to apply chemical treatment to salmon farm, gray indicating chemical treatment and white indicating no treatment in a particular month. We define a biological year as the period from the beginning of spawning stock migration (August) to the last month the wild juvenile is in the fresh water environment (July). Therefore, the odd-numbered biological year corresponds to odd-numbered year run, and the even-numbered biological year corresponds to even-numbered year run. We assume that the odd-numbered year run is the first to be subject to lice infection. In the first biological year, the private producer applies chemical treatment from August to October, then from May to July. From the third biological year on, the chemical control for the odd-numbered biological year will be repeated, applying chemical control from August to November, then from June to July. The treatment policy for even-numbered year run is the same for all periods. Chemicals are applied only from August to December. The joint fisheries manager's problem, on the other hand, requires that chemical controls be applied from August to December, and then from June to July for odd-numbered year run in the first year. From years 3 on for the odd-number year run, chemical control will be applied from August to November, and then from June to July. The treatment policy under jointly optimal control for even-numbered year run lasts from August to December—the same as that from privately optimal control.

In summary, the private producer applies less effort to control lice than the joint fisheries manager because private producer focuses only on farm profits, while joint fisheries manager has to consider the disease externality on the wild fishery as well. Feedback from the chemical treatment under jointly optimal control leads to a more abundant spawning wild stock than that under privately optimal control, hence more lice will disperse into a farm, leading to more control by the

Table 1
Parameter definition and value used for numerical simulation.

Parameter	Value	Note	Reference
$F_{f,0}$	1e6	Number of fish released into farm for each grow-out season	
S_0	1e6	Initial wild fish abundance	
ρ	1.5e-7	The probability that a copepodite attached to host	Frazer et al. (2012)
ε_1	0.25	Base settlement success for copepodite survival to adult stage	Frazer et al. (2012)
ε_2	0.15	Seasonal force impact coefficient	Bricknell et al. (2006)
ν	0.15	Louse natural mortality	Frazer et al. (2012)
k	0.85	Chemical treatment efficiency for sea lice	Gustafson et al. (2006)
z	0.85	Chemical treatment efficiency for copepodite	Gustafson et al. (2006)
λ	50	Natality	Frazer et al. (2012)
ξ	0.5	Copepodite natural mortality	Frazer et al. (2012)
s	5	Number of gravid lice attached on individual wild spawning stock	Frazer et al. (2012)
p_f	6.5	Farmed salmon price ($/kg)	Asche and Bjorndal (2012)
p_w	0.32	Wild salmon price ($/kg)	Liu et al. (2011)
δ	0.996	Monthly discount rate	Laukkanen (2001)
m	0.94	Wild juvenile natural mortality rate in fresh water	Liu et al. (2011)
φ	0.5	Wild juvenile natural mortality rate in marine environment	Liu et al. (2011)
γ	5.2	Wild stock growth rate	Liu et al. (2011)
b	4.5e6	Density dependent mortality	Liu et al. (2011)
d_1	0.7	Adult lice dispersal from wild spawning stock to farmed stocks	
d_2	0.3	Copepodite dispersal from farmed stocked to wild juvenile	
d_w	0.4	Sea lice-induced mortality rate for wild juvenile	Krkošek et al. (2007)
d_f	0.05	Sea lice-induced mortality rate for farmed stock	Krkošek et al. (2007)
c_f	1.5	Harvest cost per kilogram of farmed fish ($)	Asche and Bjorndal (2012)
c_{feed}	1	Feeding cost per kilogram of feeding ($)	Asche and Bjorndal (2012)
$c_{treatment}$	5e4	Treatment cost per chemical treatment	Mustafa et al. (2001)
f_{con}	1.1	Feed conversion ratio	Asche and Bjorndal (2012)
c_w	30	Unit cost per fishing effort for wild fishery	Laukkanen (2001)
q	1.6e-3	Catchability coefficient	Laukkanen (2001)
α	0.76	Harvesting proportion for wild fishery	Liu et al. (2011)
w_w	1.43	Adult pink salmon weight (kg)	Liu et al. (2011)

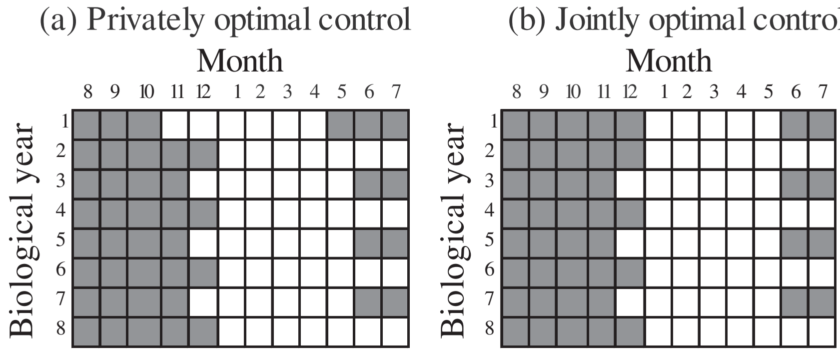

Fig. 1. Privately and jointly optimal control policies during the first eight biological years in a well-mixed coastal environment. A biological year is consisted of odd and even-numbered years, starting from August when wild spawning stock home-river migrate until the last month the freshwater environment (July). Gray indicates a chemical application and white indicates no treatment in that particular month.

joint fisheries manager. Since the joint fisheries manager's control policy decreases louse numbers, more wild fish survive the period they spend in coastal areas, more wild stocks are available for harvest, resulting greater net benefits in the wild fishery. The treatment policy by the fish farmer deviates from that of the joint fisheries manager only in the early years. One reason for the deviation is that sea lice control in the early stages has a greater impact on the total net present value than control at later stages, partly due to the effect of discounting. Since the control exercised by the fish farmer happens during the spawning stock migration period, it does reduce at least part of the external cost of aquaculture. The binary nature of control also helps the alignment of the fish farmer's and joint fisheries manager's objectives.

The consequences of the private producer's control policy are illustrated in Fig. 2. The peak level for adult sea lice abundance occurs when wild spawning stocks migrate back to the natal river. The peak level corresponding to odd-year runs falls to a very low level then climbs back up, while the peak level corresponding to even-year runs decreases until it levels off as the wild population approaches a steady state. The difference in treatment policy between odd and even-numbered years generates an oscillating pattern of sea lice infestation. Intuitively, all else equal, a reduction in wild spawning stocks implies less infection risk to farmed salmon stocks, and hence less infection risk to wild juvenile stocks in the next year. Since wild juvenile salmon mortality falls, this increases the abundance of wild adults in the ocean, resulting in a high spawning stock, high infestation risk to farm, and high infection rates of wild juvenile stocks, and therefore fewer adults and a smaller wild spawning stock in the following year. This oscillation pattern between the peak level of adult sea lice abundance associated with odd and even-numbered year runs also manifests itself for wild pink salmon harvesting levels, illustrated in Fig. 2c.

The oscillating pattern is also present in the joint fisheries management problem. The trajectory, on the other hand, is quite different. The adult sea lice abundance levels corresponding to odd and even-numbered year runs both decrease smoothly (Fig. 2b). This corresponds to a relatively smooth path for wild fishery harvesting level (Fig. 2d), which is in stark contrast to wild salmon harvesting level under privately optimal lice control.

Table 2 shows the net present value (NPV) and the steady state wild fishery harvesting and wild spawning stock levels under jointly and privately optimal disease controls. The difference between total NPV under

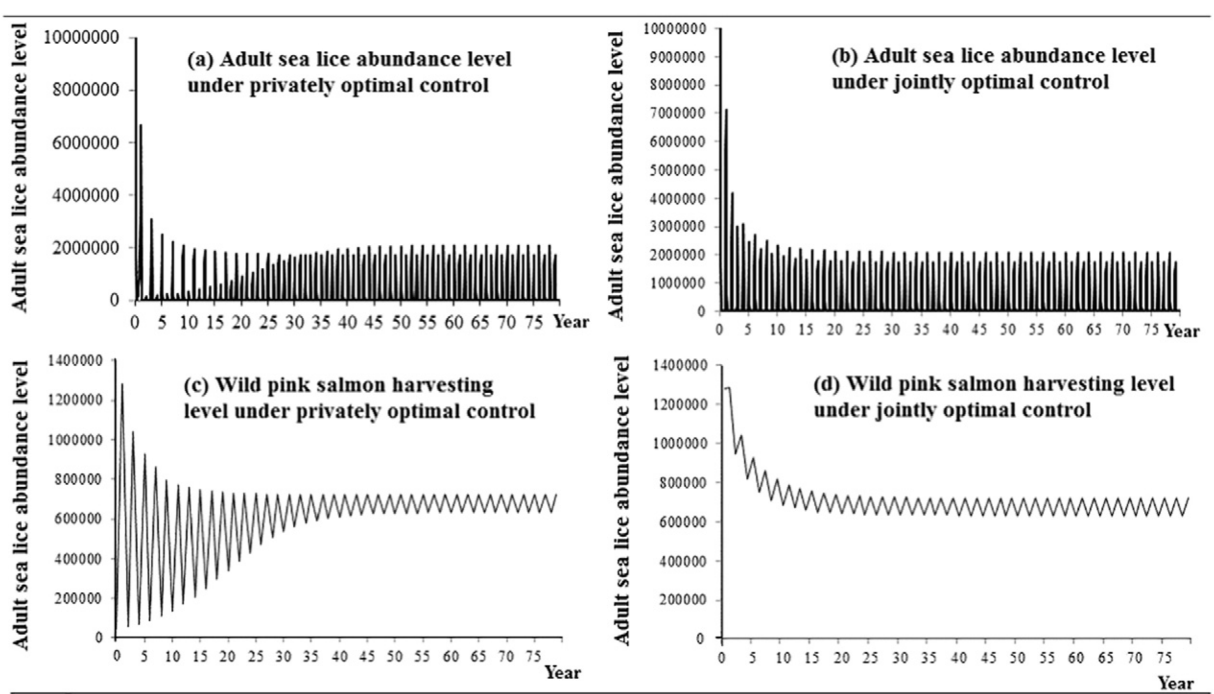

Fig. 2. Trajectories for adult sea lice abundance (*Ex-Ante* treatment) and wild salmon harvesting under private and joint optimum controls in a well-mixed coastal environment. The privately optimal control policy results in an oscillation pattern in the peak levels of steady state adult sea lice abundances and wild pink salmon harvest level. The increasing trend corresponds to odd-year numbered wild salmon run, and the declining one corresponds to even-numbered year wild salmon run.

Table 2
A comparison of results between the private producer and joint fisheries manager in a well-mixed coastal environment.

	Private producer	Joint fisheries manager
Total net present value	267,020,461	268,622,090
Aquaculture	261,630,726	260,708,939
Wild fishery	5,389,735	7,913,151
Wild fishery harvesting in the steady state		
Odd-numbered year run	632,100	632,100
Even-numbered year run	721,550	721,550
Wild spawning stock in the steady state		
Odd-numbered year run	199,610	199,610
Even-numbered year run	227,858	227,858

these two control strategies is not large (approximately 0.6% of total NPV under joint fisheries management). In other words, the externality generated by fish farms is quite small. This is because of the low price and small size of Pink salmon ($0.36/kg and 1.43 kg) relative to farmed Atlantic salmon ($6.5/kg and 7.3 kg). The steady state harvesting and spawning stock levels are approximately the same under both approaches because of the fixed proportional harvest regulation on the part of wild fishery.

4.3. The Distance-dispersal Environment

In a distance-dispersal environment, privately optimal disease control is applied from August to November, then from June to July for the odd-numbered year run, and from August to November for even-numbered year run (Fig. 3). The control strategy for odd- and even-numbered year runs is repeated. Jointly optimal control requires more disease control than privately optimal control. In the first year it extends from August to December, then from the next June to July for the odd-numbered year run. Once again, the control strategy for odd- and even-numbered year runs is repeated from the third year on, with odd- and even-numbered year runs seeing chemical treatment starting from August to November, then from June to July.

Sea lice levels and harvests are very similar under privately and jointly optimal control for both farmed and wild fisheries (Fig. 4). Both produce a slow decrease in the peak level of adult sea lice in the farm and in the number of wild pink salmon harvested. This is in sharp contrast to the well-mixed coastal environment. Table 3 shows the net present value (NPV) and the steady state wild fishery harvesting and wild spawning stock levels under jointly and privately optimal disease controls. The difference between total NPV under these two control strategies is not significant (0.012% of total NPV under joint fisheries management), and the externality is $0.03 million versus $1.6 million in the well-mixed coastal environment. This is expected due to the encounter-dilution effect imbedded in our model for the well-mixed coastal environment. In the distance-dispersal environment, there are higher wild harvesting and stock levels in the odd-numbered year run, but lower in the even-numbered year run. Due to the very low value of the distance-dispersal externality, we report only results for the well-mixed coastal environment in the following.

5. Sensitivity Analysis

5.1. The Effect of Sea Lice-induced Mortality Rate on Wild Fishery

The previous results are based on the assumption that wild fishery is subject to an intermediate level of sea lice-induced mortality rate. The effect of sea lice on the decreasing wild salmonid has triggered intense debate (Marty et al., 2010; Krkošek et al., 2007). Therefore we tested the impact of optimal disease control policies of variation in the sea lice –induced mortality rate (d_w) on wild salmon stocks.

Fig. 5a shows the effect of lice control in farm on the wild fishery harvesting level when we introduce different levels of sea lice-induced mortality rate on wild stock, while keeping other parameters at their base value. The greater the effect of lice on wild fishery, the greater the variation between odd- and even-numbered year harvests of wild fish induced by the joint control policy. On a separate note, we also found similar oscillation pattern but less variation in a distance-dispersal environment when investigated the effect of different sea lice-induced mortality rates on wild fishery.

5.2. The Effect of Wild Salmon Prices

We also conducted sensitivity analysis to investigate the effect of wild salmon price on optimal disease control in fish farms. Ideally a variable price should be applied to reflect the fact that commodity prices may be sensitive to total supply. Farmed and wild caught salmon compete in the same market, and estimation of demand requires data for all marketed salmon species (Asche et al., 1999). The price of wild salmon would be expected to vary both with the species involved. In 2015 the ex-vessel price of pink salmon was around one half the price of chum salmon, one third the price of coho salmon, and one tenth the price of Chinook salmon (Alaska Department of Fish and Game, 2016). A second potential reason for variation in the price of wild salmon is willingness-to-pay for non-marketed ecosystem services associated with wild salmon. Therefore, we conducted sensitivity analysis based on different fixed price levels. Fig. 5b also shows the effect of optimal control of sea lice in farms on the harvesting level in wild fishery when the unit price of wild stock is $0.36/kg, $3.6/kg and $5.4/kg while keeping other parameters at their base values. The greater the value of the disease externality the stronger the control program required in the salmon farms, and the lower the difference between odd- and even-numbered year harvests of wild fish.

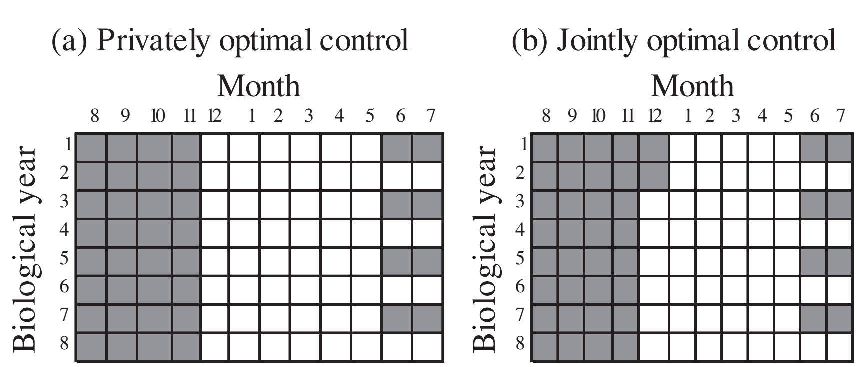

Fig. 3. Privately and jointly optimal control policies during the first eight biological years in a distance-dispersal environment.

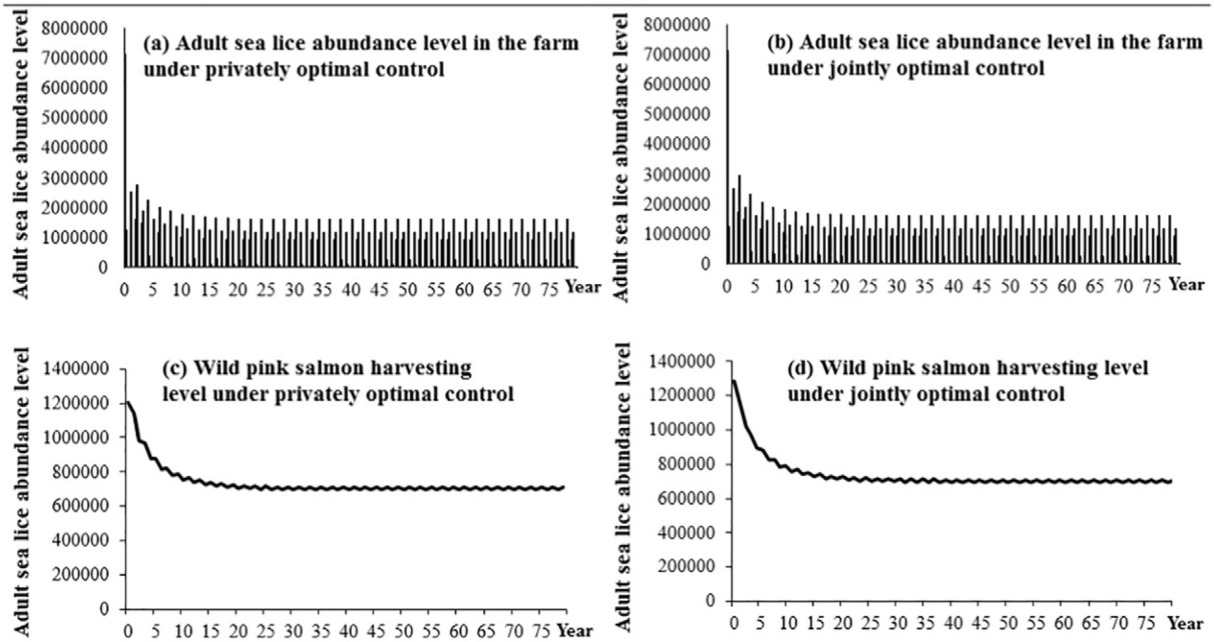

Fig. 4. Trajectories for adult sea lice abundance (*Ex-Ante* treatment) and wild salmon harvesting level under private joint optimum controls in a distance-dispersal environment. Oscillation pattern is also seen in the steady state, with the lower level corresponding to odd-numbered year wild salmon run and higher level corresponding to even-numbered year wild salmon run.

6. Discussion

Salmon aquaculture is one of the fastest growing industries worldwide (FAO, 2014). Salmon farming production surpassed wild caught salmon production in late 1990s, and has now become an economic driver for many regional economies. It has also become a major source of environmental impacts. At the top of the list of environmental impacts are sea lice transmission between salmon farms and the nearby wild fisheries where sea lice can be predictable and controllable in farms, but farms have no incentive to eradicate sea lice and still provide an externality. This is similar to the problem created by California Abalone farmers who keep a more tolerant stock by managing water temperature on farms but provide a potent reservoir with greater chance of externality (Lafferty and Ben-Horin, 2013). Current regulations are often not adequate to mitigate externality such as this (Lafferty and Ben-Horin, 2013). We show that two types of environments (a well-mixed environment versus a distance-dispersal environment) would determine the underling sea lice transmission dynamics, hence providing different insights into the economic management of sea lice. Indeed, the interaction between pathogens and stocks and impact of pathogens on aquatic animals depends on the nature of transmission (Murray, 2009), reflected by surrounding hydrodynamic environment (Adams et al., 2012). We find that the externality generated by the marine aquaculture is not significant, but the externality value investigated in a well-mixed coastal environment is greater than that in a distance-dispersal environment. We also show that in a well-mixed environment the steady state trajectories for wild salmon stocks are different under privately and jointly optimal management strategies, but similar in a distance-dispersal environment.

Table 3
A comparison of results between the private producer and joint fisheries manager in a distance-dispersal environment.

	Private producer	Joint fisheries manager
Total net present value	270,890,914	270,922,592
Aquaculture	262,778,434	262,724,995
Wild fishery	8,112,480	8,197,597
Wild fishery harvesting in the steady state		
Odd-numbered year run	695,515	695,515
Even-numbered year run	710,791	710,791
Wild spawning stock in the steady state		
Odd-numbered year run	219,636	219,636
Even-numbered year run	224,460	224,460

Both privately and jointly control regimes approach the same steady state harvesting and spawning stock levels due to the sole control variable of chemical application and the fixed proportional harvest regulation. However, we find that the variability in wild salmon stocks between odd- and even-numbered year runs is highly sensitive to the effect of lice on the wild fishery, and the price of wild pink salmon. When the mortality rate of wild stocks induced by the sea lice is high, the optimal disease control policy forces considerable year-to-year variation in wild stocks. As the mortality rate of wild stocks induced by the sea lice falls, the year-to-year variation in wild stocks also falls. We also find that where susceptible wild pink stocks are of low commercial value, control regimes result in significant fluctuations in wild stocks. By contrast, where susceptible wild stocks are of high commercial value, control regimes generate more stable wild populations.

An interesting implication of this result is that the main effect of a decrease in the effect of lice on wild fish stocks (or an increase in the value of wild fishery) is not an increase in the steady state level of wild populations but increase in the temporal stability of those stocks. This is due to a combination of the fixed proportion harvest regulation on wild capture fishery, the binary disease control policy. To the extent that variations in the abundance of wild fish stocks signals variation in the resilience of those stocks to environmental stresses, this implies that a decrease in the effect of lice on wild stocks or an increase in the value of wild fishery induces policies that enhance ecosystem resilience.

Of course the bioeconomic model used to explore the system does rest on a particular set of assumptions. The first is that copepodites and adult lice both have a one-month life cycle. This is based on the lumping of free-living stages and stages during which copepodites attach to fish hosts. In reality, the timing of different stages varies with temperature, and the copepodite's life span could be longer in lower temperatures. Environmental factors also impact louse survival, growth, and the lice natality. Secondly, lice are assumed not to evolve and develop any resistant strains in response to chemical treatment. The assumption here is that lice are either killed or not affected by the chemical

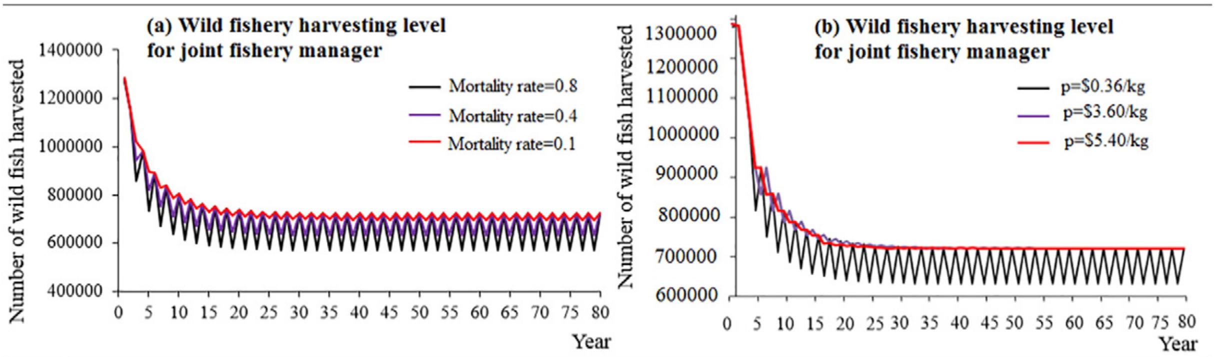

Fig. 5. The effect of mortality induced by sea lice and wild salmon price.

treatment, and lice surviving the chemical treatment still have the same growth and natality rates. The development of lice resistant to chemical treatment would come at a cost—it takes time for the surviving and exposed lice to develop the same growth and natality rate as lice in the absence of chemical treatment (McEwan et al., 2015). Finally, it is assumed that wild juveniles with a non-lethal infestation level may still maintain the same growth rate. Evidence suggests that parasite infestation would influence wild stock dynamics, that the physical impact is additive, and that the exposed wild stock during infestations would suffer significantly lower growth rates, leading to a smaller spawning sizes (Krkošek et al., 2007).

While there is no agreement on the impacts of lice on wild fish populations, concerns have been raised about the potential for negative effects. Hence, government regulations have been implemented to reduce sea lice infestation risk on wild fisheries. This study suggests the importance of strengthening lice treatment during wild salmon migration periods, through the coordination of strategies for managing fish farms and wild-salmon fisheries. Three cautions are in order. First, the value of the sea lice externality of fish farms is very sensitive to the value of the affected wild fish. Indeed, if we take the market price of the most commonly affected wild fish, Pink salmon, as a proxy for its social value, then the socially optimal level of lice control is little different from the privately optimal level of lice control. A second caution is that although we consider possible instruments (see supporting information) for implementing a socially optimal disease control policy, the binary nature of the control prevents implementation of a Pigovian approach —in which farmers are confronted by the marginal social cost of their control decisions. Nevertheless, we consider that the modeling approach adopted here has the potential to improve the efficiency of disease management in aquaculture. In addition, we consider a fixed harvesting rule in an effort to mimic a current fishery regulation. Modeling a variable control effort for wild capture fishery is required to fully understand the cost of salmon lice. This offers a potential avenue for future research.

Acknowledgments

This work on the disease control aspects of this problem benefits from support from grant number 1R01GM100471-01 from the National Institute of General Medical Sciences (NIGMS) at the National Institutes of Health.

Appendix A. Supplementary data

Limitations of current policies, potential mechanism for internalizing sea lice externality and sensitivity analysis for other key parameters are provided in Appendix S1. Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.ecolecon.2017.03.012.

References

Adams, T., Black, K., MacIntyre, C., MacIntyre, I., Dean, R., 2012. Connectivity modelling and network analysis of sea lice infection in Loch Fyne, west coast of Scotland. Aquac. Environ. Interact. 3, 51–63.

Alaska Department of Fish and Game, 2016. Commercial Salmon Fishery Exvessel Prices. Alaska Department of Fish and Game, Juneau, AK (http://www.adfg.alaska.gov/index.cfm?adfg=commercialbyfisherysalmon.salmoncatch_exvessel, Access October 2016).

Anderson, R.M., May, R.M., 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. J. Anim. Ecol. 47, 219–247.

Asche, Frank, Bjorndal, Rrond, 2012. The Economics of Salmon Aquaculture. second ed. Wiley-Blakcwell.

Asche, F., Bremnes, H., Wessells, C.R., 1999. Product aggregation, market integration and relationships between prices: an application to world salmon markets. Am. J. Agric. Econ. 81, 568–581.

Asche, F., Hansen, H., Tveterås, R., Tveterås, S., 2009. The salmon disease crisis in Chile. Mar. Resour. Econ. 24, 405–411.

Ashander, J., Krkosek, M., Lewis, M., 2012. Aquaculture-induced changes to dynamics of a migratory host and specialist parasite: a case study of pink salmon and sea lice. Theor. Ecol. 5, 231–252.

Bricknell, I.R., Dalesman, S.J., O'shea, B., Pert, C.C., Mordue Luntz, A.J., 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. Dis. Aquat. Org. 71, 201–212.

Burge, C.A., Eakin, C.M., Friedman, C.S., et al., 2014. Climate change influences on marine infectious diseases: implications for management and society. Annu. Rev. Mar. Sci. 6, 249–277.

Conrad, J.M., Rondeau, D., 2015. Bioeconomics of a marine disease. Mar. Resour. Econ. 3, 393–416.

Costello, M., 2006. Ecology of sea lice parasitic on farmed and wild fish. Trends Parasitol. 22, 475–483.

Costello, M.J., 2009. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. Proc. R. Soc. B 276, 3385–3394.

Epanchin-Niell, R.S., Wilen, J.E., 2012. Optimal spatial control of biological invasions. J. Environ. Econ. Manag. 63, 260–270.

Fischer, C., Guttormsen, Atle G., Smith, M.D., 2015. The effects of strategic firm behavior on aquatic ecosystems: disease risk and market power in salmon aquaculture. https://www.nhh.no/globalassets/departments/business-and-management-science/seminars/2015-fall/141015.pdf (Access October 2016).

Fischer, C., Guttormsen, Atle G., Smith, M.D., 2016. Disease risk and market structure in salmon aquaculture. Water Econ. Policy. http://dx.doi.org/10.1142/S2382624X16500156 (Access August 2016).

Food and Agriculture Organization, 2014. The State of World Fisheries and Aquaculture Opportunities and Challenges.

Frazer, L.N., 2009. Sea-cage aquaculture, sea lice and declines of wild fish. Conserv. Biol. 23, 599–607.

Frazer, L.N., Morton, A., Krkošek, M., 2012. Critical thresholds in sea lice epidemics: evidence, sensitivity and subcritical estimation. Proc. R. Soc. B 279, 1950–1958.

Gramig, B.M., Horan, R.D., Wolf, C., 2009. Livestock disease indemnity design when moral hazard is followed by adverse selection. Am. J. Agric. Econ. 91, 627–641.

Gustafson, L., Ellis, S., Robinson, T., Marenghi, F., Endris, R., 2006. Efficacy of emamectin benzoate against sea lice infestations of Atlantic salmon, *Salmo salar* L.: evaluation in the absence of an untreated contemporary control. J. Fish Dis. 29, 621–627.

Horan, R.D., Fenichel, E.P., Wolf, C.A., Gramig, B.M., 2010. Managing infectious animal disease systems. Ann. Rev. Resour. Econ. 2, 101–124.

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 (42), 15506–15510.

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.

Lafferty, Kevin, Ben-Horin, Tal, 2013. Abalone farm discharges the withering syndrome pathogen into the wild. Front. Microbiol. 4, 373.

Lafferty, K.D., Harvell, C.D., Conrad, J.M., Friedman, C.S., Kent, M.L., et al., 2015. Infectious diseases affect marine fisheries and aquaculture economics. Annu. Rev. Mar. Sci. 7, 471–496.

Laukkanen, M., 2001. A bioeconomic analysis of the northern Baltic salmon fishery: coexistence versus exclusion of competing sequential fisheries. Environ. Resour. Econ. 18, 293–315.
Liu, Y., Bjelland, H.V., 2014. Estimating costs of sea lice control strategy in Norway. Prev. Vet. Med. 117, 469–477.
Liu, Yajie, Sumaila, U.R., Volpe, J.P., 2011. Potential ecological and economic impacts of sea lice from farmed salmon in wild salmon fisheries. Ecol. Econ. 70 (10), 1746–1755.
Marty, G.D., Saksida, S.M., Quinn II, T.J., 2010. Relationship of farm salmon, sea lice, and wild salmon populations. Proc. Natl. Acad. Sci. 107 (52), 22599–22604.
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 (10), e0139128. http://dx.doi.org/10.1371/journal.pone.0139128.
Murray, A.G., 2009. Using simple models to review the application and implications of different approaches used to simulate transmission of pathogens among aquatic animals. Prev. Vet. Med. 88, 167–177.
Mustafa, A., Rankaduwa, W., Campbell, P., 2001. Estimating the cost of sea lice to salmon aquaculture in eastern Canada. Can. Vet. J. 42 (1), 54–56.
Naylor, R.L., Goldberg, R.J., Mooney, H., Beveridge, M., Clay, J., Folke, C., Kautsky, N., Lubchenco, J., Primavera, J., Williams, M., 1998. Nature's subsidies to shrimp and salmon farming. Science 282, 883–884.
Revie, C.W., Robbins, C., Gettinby, G., Kelly, L., Treasurer, J.W., 2005. A mathematical model of the growth of sea lice, *Lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo salar* L., in Scotland and its use in the assessment of treatment strategies. J. Fish Dis. 28, 603–613.
Stone, J., Sutherland, I.H., Sommerville, C.S., Richards, R.H., Varma, K.J., 1999. The efficacy of emamectin benzoate as an oral treatment of sea lice, *Lepeophtheirus salmonis* (Krøyer), infestations in Atlantic salmon, *Salmo salar* L. J. Fish Dis. 22, 261–270.
Stone, J., Sutherland, I.H., Sommerville, C.S., Richards, R.H., Varma, K.J., 2000. Field trials to evaluate the efficacy of emamectin benzoate in the control of sea lice, *Lepeophtheirus salmonis* (Krøyer) and *Caligus elongatus* (Nordmann) infestation in Atlantic salmon *Salmo salar* L. Aquaculture 186, 205–219.
Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, E., Kvamme, B.O., et al., 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES J. Mar. Sci. http://dx.doi.org/10.1093/icesjms/fsu132.
Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E., Jackson, D., 2013. Salmon lice-impact on wild salmonids and salmon aquaculture. J. Fish Dis. 36, 171–194.
Tucker, C.S., Sommerville, C., Wootten, R., 2000. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. J. Fish Dis. 23, 309–320.