



Use of agent-based modelling to predict benefits of cleaner fish in controlling sea lice, *Lepeophtheirus salmonis*, infestations on farmed Atlantic salmon, *Salmo salar* L.

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Abstract

Sea lice, *Lepeophtheirus salmonis*, are ectoparasites of farmed and wild salmonids. Infestations can result in significant morbidity and mortality of hosts in addition to being costly to control. Integrated pest management programmes have been developed to manage infestations, and in some salmon farming areas, these programmes include the use of wrasse. Wrasse prey upon the parasitic life stages of *L. salmonis* and can be stocked on farms at varying densities. Despite considerable variation in the usage of wrasse, there are few quantitative estimates of how well they can control sea lice and how best to optimize their use. To explore at what densities wrasse should be stocked in order to meet specific control targets, we built an individual-based model that simulates sea lice infestation patterns on a representative salmonid host. Sea lice can be controlled through the use of chemical treatments as well as by wrasse predators. We found that the wrasse can effectively control sea lice, and the densities of wrasse needed for effective control depend upon the source of the infestation and the targeted level of control. Effective usage of wrasse can result in decreased use of chemical treatments and improved control of sea lice.

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Introduction

Sea lice, *Lepeophtheirus salmonis* (Krøyer), are a well-documented parasite of farmed salmonids [Atlantic salmon, *Salmo salar* L., *Onchorhynchus mykiss* (Walbaum), *O. tshawytscha* (Walbaum), *O. kisutch* (Walbaum)], and infestations can be costly as a result of chemical treatments to salmonids as well as losses of fish due to mortality and morbidity (Costello 2009a). In addition to economic losses, high sea lice densities on farms may inflict substantial ecological costs when they infest wild salmonids (e.g. Krkosek, Lewis & Volpe 2005; reviewed in Costello 2009b), and this has led to damaging public perceptions of salmon aquaculture (e.g. Leiss & Nicol 2006). A number of methods have been pursued within the salmon industry to control sea lice infestations on farms. These include adoption of integrated pest management approaches in which management areas, defined by hydrological boundaries, are fallowed periodically to break the sea lice reinfection cycle, and all salmon in the management area are restricted to a single age cohort to avoid infection between age classes (Rae 2002). In addition to these practices, medicinal treatments are often necessary to control sea lice. While often very effective at reducing densities of attached sea lice (chalimus and mobiles) (Roth *et al.* 1996; Tully

& McFadden 2000; Stone *et al.* 2002), these treatments can be expensive (reviewed in Costello 2009b), are stressful to salmon (Burka *et al.* 1997), have potentially detrimental environmental impacts (Burridge *et al.* 2010), can be hazardous to the workers that dispense them and are proving to be less effective over time because sea lice are able to evolve resistance (reviewed in Denholm *et al.* 2002; Lees *et al.* 2008). While there are efforts to develop new treatments for sea lice to avoid the problem of resistance, no new chemotherapeutants have been licensed for use in aquaculture in the past decade.

Adding cleaner fish (i.e. fish that remove ectoparasites and dead skin from other fish) to salmon pens is an additional method that can be incorporated in integrated pest management plans for controlling sea lice populations. Cleaner fish prey upon sea lice with a preference for mobile pre-adult and adult lice. In contrast to medicinal treatments, cleaner fish are less expensive, can remain within cages until salmon are harvested, can be managed so that they cause no appreciable stress to salmon and are not known to be hazardous to workers or the environment where they are used (reviewed in Treasurer 2002). Species of cleaner fish used in aquaculture include five species of wrasse (family Labridae). Two additional species, cunner fish, *Tautogolabrus adspersus* (Walbaum), and lumpfish (family Cyclopteridae) are being trialled for future use. Recently, ballan wrasse, *Labrus bergylta* Ascanius, aquaculture programmes have been implemented in Norway and Scotland. This approach alleviates many concerns about overharvesting of wild wrasse and the risk of wrasse to salmon disease transmission (Costello 1996; Sayer, Gibson & Atkinson 1996; Varian, Deady & Fives 1996). Additionally, this development reflects a strong degree of confidence that wrasse are an effective control agent.

Despite substantial use over the past 20 years, there are few quantitative estimates of the effects of cleaner fish on sea lice populations. Several trials were conducted in the 1990s, with a variety of results. Some found very good control by wrasse (Bjordal 1991; Treasurer 1996), while others showed mixed (Kvenseth 1996; Tully *et al.* 1996; Young 1996) or negative effects of wrasse (MacKinnon 1995). Several factors likely contribute to this variation. Effectiveness of cleaner fish can be quite context-dependent, being reliant on factors such as the application regimens for chemical

controls, dispersal patterns of sea lice among farms and water temperature (reviewed in Costello 1996). Additionally, local factors such as amount of biofoul on nets (often a preferred food source for wrasse), net shape and size and the presence and location of refuges within the net may influence cleaner fish behaviour (e.g. Deady, Varian & Fives 1995; Costello 1996; Treasurer 1996). Not surprisingly, recommendations for how wrasse should be used on salmon farms vary widely. Reported densities of cleaner fish relative to densities of salmon range over an order of magnitude from 1:250 to 1:10 (e.g. Deady *et al.* 1995; Kvenseth 1996; Treasurer 1996), and we are not aware of any recommendations about how wrasse densities should be used relative to the calculated risk of sea lice infestations, which can also vary over an order of magnitude among farm sites (e.g. Revie *et al.* 2003).

The complex context dependency of wrasse behaviour and sea lice life history and migration create many logistical hurdles for experimental trials of wrasse; however, computer models present a more feasible approach. Modelling techniques have successfully been used to examine many facets of sea lice epidemiology, including effects of farmed salmon on sea lice abundances in wild salmon (Krkosek *et al.* 2005), effects of the timing and frequency of medicinal treatments on sea lice populations (Revie *et al.* 2005; Robbins *et al.* 2010) and transport of planktonic stages of sea lice based on hydrography, temperature and salinity (Amundrud & Murray 2009). To our knowledge, no models have explored effects of wrasse on sea lice populations. While they have not been used in models of sea lice, agent-based models in particular provide a flexible format for exploring context-dependent integrated pest management scenarios (reviewed in Grimm *et al.* 2005). They can readily accommodate age-based transitions and can incorporate static and dynamic events, thereby overcoming the challenges of system dynamic models.

In this study, we use an agent-based model to simulate the effects of cleaner fish on sea lice loads of farmed salmonids. The model addresses how best to identify effective wrasse densities in response to varying sea lice infestation risks, how the use of wrasse can impact on the number of medicinal treatments used in a production cycle and how the use of wrasse alters the demographics of sea lice.

The model

To explore how cleaner fish affect sea lice infestations on salmonids, we created a stochastic agent-based model of a single representative Atlantic salmon host, which can be parasitized by *L. salmonis*. The model consists of two hierarchical levels: on the lower level there are individual lice and wrasse predators. The salmon host provides the upper level where lice and wrasse interact.

Each individual louse has a unique identity state variable and progresses through developmental states (Fig. 1). *Lepeophtheirus salmonis* develop through multiple stages including an egg stage and three unattached stages (nauplii I and II and an infective copepodid). After attachment to a salmonid host, copepodids enter four chalimus stages (I, II, III and IV), followed by two mobile pre-adult stages and a single adult stage. Developmental states in our model include, egg, nauplii, copepodid, chalimus, preadult and adult (Fig. 1).

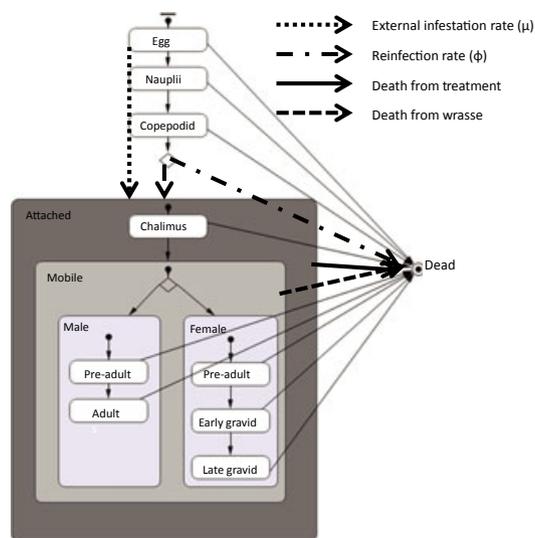


Figure 1 State charts used to model sea lice life history and survival. Arrows between states represent developmental transitions, while arrows towards the death circle indicate mortalities. Arrows in bold indicate transitions or causes of mortality that were altered for different model runs. Treatments removed attached sea lice with a set treatment efficacy. Wrasse predation events affected mobile sea lice at random at a rate determined by the wrasse density and feeding rate. External infestations became attached chalimus upon entering the model, and their entry occurred at a rate determined by the external infestation parameter (μ). The reinfestation rate (ϕ) is determined by the proportion of copepodids that attach to a host. Those that do not find a host will die.

We separated preadult and adult states according to males and females (determined probabilistically) and further divided female adult stages into first clutch females (referred to here as ‘early gravid’) that typically have low fecundity and subsequent clutch females (referred to here as ‘late gravid’) that typically have higher fecundity. This reflects patterns of fecundity observed in laboratory tests (reviewed in Stien *et al.* 2005). Females in both of these states contribute eggs to the next generation. Associated with each of these life stages are mortality rates based on an assigned probability.

Wrasse dynamics consisted only of predation events upon mobile lice because the timescale of the model does not incorporate the lifespan of these fish, and they do not reproduce inside salmon cages.

The level of the salmon host consists of a representative salmon host surface where sea lice attach and can be preyed upon by wrasse. The density of wrasse is scaled to be proportional to the surface area of the salmon host (equivalent to one salmon), and the infestations can be considered to represent average parasite loads on a population of salmon.

The model includes stochasticity at several levels. Developmental transitions are determined from a temperature-dependent equation, where each parameter value is randomly chosen from a normal distribution. Wrasse predation events occur at a constant rate, and feeding events are distributed exponentially across time so that the average number of feeding events per day is equal to the constant rate. Louse survival, sex determination, egg viability and success in attaching to a salmon host are also probabilistic with events distributed exponentially across time.

The model is designed to simulate typical events during the first year of the salt water production cycle. We did not include the second year of the production cycle because interactions between wrasse and salmon change as the salmon reach their market size (Costello 1996), and we do not have data to parameterize these changes. The salmon host was not infested initially, and infestations began when the host was parasitized by lice from an external source. Wrasse are typically assigned to pens at the same time that smolts are introduced. Thus, wrasse were able to feed on sea lice as soon as they began infesting salmon.

All modelling was carried out using the programming environment of Anylogic (v. 6.8 XJ

Technologies). The model uses a day as the time step with events and transitions occurring at each step and simulates the first year of the salmonid production cycle. State transitions occur in the following order in zero time: state exit actions (in the order from simplest state to composite state), transition actions, state entry actions (in the order from composite state to simplest state). The algorithm is repeated until all actions for a given time period have been completed.

Parameterization

Seasonal water temperature

Temperature (T) was modelled as a function of time (in days) by fitting 4 years of water temperature data from Scotland with a three parameter oscillatory sinusoidal curve

$$T(\text{time}) = a + b \times \sin^2\left(\pi \times \frac{(\text{time} + c)}{365}\right) \quad (1)$$

where a is the minimum temperature, b is a magnitude parameter, and c is a phase shift parameter ($a = 7.07$, $b = 6.19$, $c = 120$). These values allowed us to simulate the transfer of salmon smolts to salt water pens in the spring. These temperatures are characteristic of many places where salmonids are farmed and where temperatures are warm enough to use wrasse on farms (Bjelland *et al.* 1996).

Developmental transitions

With the exception of copepodids, developmental transitions of sea lice were temperature-dependent. We used developmental rates estimated in a meta-analysis by Stien *et al.* (2005, Table 1). These estimates used existing data on developmental times of *L. salmonis* across a temperature range to parameterize a modified Belahradek equation

Table 1 Estimates of temperature-dependent parameters for development rates of sea lice, *Lepeophtheirus salmonis*, based on Stien *et al.* (2005)

Life stage	B_1 (SE)	B_2 (SE)	v
Eggs	41.98 (2.85)	0.338 (0.012)	2
Nauplii	24.79 (1.43)	0.525 (0.017)	0
Chalimus	74.7 (33.64)	0.2355 (0.0070)	0.85
Preadult Male	67.47 (20.36)	0.197 (0.006)	0.80
Preadult Female	67.47 (20.36)	0.177 (0.006)	0.34

(1935). This equation is commonly used to model copepod development (Aksnes *et al.* 1997):

$$\tau_{ij}(T) = \left(\frac{\beta_{1ij}}{(T - 10 + \beta_{1ij}\beta_{2ij})}\right)^2 \quad (2)$$

where τ_{ij} is the minimum required development time for individual i in stage j at temperature T . β_1 is a shape parameter, and β_2^{-2} is the average τ at 10 °C. Means and standard deviations for β_1 and β_2 were estimated from data that were collected at temperatures ranging from ~7 °C to ~15 °C around 40 Scottish fish farms over the period 1996–2000 (Revie *et al.* 2002a,b). Variation in developmental rates was incorporated by selecting values for β_{1ij} and β_{2ij} from a normal distribution (also estimated by Stien *et al.* 2005). A stage-specific constant, v_j , was added to this temperature-dependent estimate, to represent additional time beyond the minimum development time (τ) needed to make developmental transitions. Total development time (δ) of individual i at stage j is

$$\delta_{ij} = \tau_{ij} + v_j \quad (3)$$

Values of v were from Stien *et al.* (2005). There is no evidence that copepodid developmental rates are temperature-dependent (reviewed in Stien *et al.* 2005), so all copepodids developed at a constant rate.

For female lice transitioning from the early gravid stage (with low fecundity) to the later gravid stage (with higher fecundity), development times of early gravid females were dependent upon egg development time, because eggs are attached to the female until they hatch. The length of time that a clutch takes to develop is determined by the temperature-dependent egg development rate. After a clutch of eggs hatch, it takes ~24 h to produce a second clutch, so gravid females transitioned from the early gravid stage to the later gravid stage did so at

$$\delta_{i,\text{early gravid}} = 1 + \tau_{i,\text{egg}} + v_{\text{egg}} \quad (4)$$

Parameters in the model yield mean generation times of 60 and 59 days for females and males, respectively, at 12 °C, and 123 and 115 days for females and males, respectively, at 7 °C. In comparison, Tully (1992) predicted generations times of 50 days at 12 °C and 114 days at 7 °C.

Natural mortality

Daily mortality probabilities based on life stage and sex also came from Stien *et al.* (2005, Table 2). We could not find an estimate for survival of copepodids, so we used the survival probabilities estimated for the chalimus stage. For all stages, mortality increased with decreasing temperature because development was slower at colder temperatures.

Development from copepodid to chalimus is a critical transition for sea lice, because it requires the copepodid to attach to a host, a process that is sensitive to local host densities and currents. Because attachment rates vary widely depending upon local conditions, we used several values for this rate in our simulations (see *internal sources of infestation*).

While there is some evidence that the viability of eggs increases with temperature (Ritchie *et al.* 1993), we did not have enough data to parameterize this pattern. Therefore, we used a constant value for egg viability (Table 1).

Sea lice fecundity

Fecundity of sea lice depended upon temperature (Table 2). Clutch size (γ_{clutch}) of females is estimated to be temperature-independent (Stien *et al.*

2005), but the time for eggs to develop is temperature-dependent. Therefore, sea lice produced eggs (α) at a daily rate of

$$\alpha = \frac{\gamma_{\text{clutch}}}{\delta_{\text{clutch}}} \quad (5)$$

where the clutch size is 150 eggs for the first clutch and 400 eggs for all subsequent clutches. In nature, sea lice eggs develop synchronously and complete development within ~65 h of each other (Johnson & Albright 1991). However, because we wanted to simulate an average louse on the average salmon host, we had female sea lice hatch eggs daily.

Wrasse predation

Wrasse can prey upon mobile sea lice at a constant rate, which is multiplied by the density of wrasse relative to a single salmon (Table 2). However, there were many instances when there were no mobile sea lice to be consumed. When this happened, that meal was recorded as predation on 'other food' and feeding continued as normal.

There are limited data available to quantify feeding behaviour of wrasse on sea lice. Treasurer

Table 2 Parameters estimates for constants used in the model

Parameter	Value used	Range reported in literature	Source
Egg viability	85%	70–92.5%	Heuch, Nordhagen & Schram (2000), Ritchie <i>et al.</i> (1993)
Nauplii mortality	0.17 individuals per day	No range available	Johnson & Albright (1991)
Copepodid mortality	0.17 individuals per day	No data available	No data available
Chalimus mortality	0.005 individuals per day	0.0008–0.005	Bjørn & Finstad (1998), Finstad, Bjørn, Grimnes & Hvidsten, (2000), Grimnes & Jakobsen (1996), Tucker <i>et al.</i> (2000)
Preadult male mortality	0.05 individuals per day	0.02–0.18	Bjørn & Finstad (1998), Finstad <i>et al.</i> (2000), Grimnes & Jakobsen (1996), Tucker <i>et al.</i> (2000)
Preadult female mortality	0.05 individuals per day	0.03–0.06	Bjørn & Finstad (1998), Finstad <i>et al.</i> (2000), Grimnes & Jakobsen (1996), Tucker <i>et al.</i> (2000)
Adult male mortality	0.05 individuals per day	0.03–0.06	Bjørn & Finstad (1998), Finstad <i>et al.</i> (2000), Grimnes & Jakobsen (1996), Tucker <i>et al.</i> (2000)
Adult female mortality	0.03 individuals per day	0.02–0.04	Bjørn & Finstad (1998), Finstad <i>et al.</i> (2000), Tucker <i>et al.</i> (2000)
Eggs in first egg string	150	70–152	Ritchie <i>et al.</i> (1993), Heuch <i>et al.</i> (2000)
Eggs in subsequent egg strings	400	152–583 (for farmed Atlantic)	Johnson & Albright (1991), Ritchie <i>et al.</i> (1993), Tully & Whelan (1993), Heuch <i>et al.</i> (2000), Orr (2007)
Time as copepodid	4.6 days	No other data	Johnson & Albright (1991)
Wrasse feeding rate	15, 30, 45	5.6–46 lice per day, not enough data to estimate temperature dependency	Bjordal (1991), Deady <i>et al.</i> (1995), Treasurer (1994)

(1994) conducted several trials in small net pens to estimate feeding rates of goldsinny wrasse, *Ctenolabrus rupestris* (L.), and estimated that wrasse ate between 26 and 46 lice per day (1.18–2.72% of their body weight) at 10–12 °C. These rates are supported by evidence from laboratory trials indicating rates of 28.3 and 45 lice per day in two separate trials (Bjordal 1991). These studies did not find predation of chalimus by wrasse. It should be noted, however, that Tully *et al.* (1996) found that goldsinny wrasse will prey on chalimus, though at a lower rate than mobile stages. No evidence was found for selectivity of wrasse among mobile stages (Tully *et al.* 1996). We are unaware of estimates of feeding rates of other species of wrasse on sea lice or effects of biofoul on sea lice feeding rates, although evidence suggests substantial biofoul of nets can cause predation rates of wrasse on sea lice to decline dramatically (Treasurer 1996).

Treatments

Chemical treatments were delivered dynamically as a function of the number of mobiles in the population. Each week, the number of mobile sea lice on the host was counted. If the mobile sea lice exceeded the 'treatment threshold', a treatment occurred, and attached sea lice were randomly selected for removal according to the treatment efficacy.

In our model, treatments intended to simulate the application of chemical bath treatments. The efficacy of bath treatments depends on the type of chemical used, the success of the application and the degree of resistance of sea lice to chemical treatments. For example, in laboratory trials, hydrogen peroxide kills an estimated 99% of mobile lice in naive sea lice populations and 25% of mobile lice in resistant populations (Treasurer, Wadsworth & Grant 2000). The synthetic pyrethroid, cypermethrin (commercially used as Excis[®] and Betamax[®]), kills an estimated 95% of attached sea lice (Revie *et al.* 2005). To approximate these scenarios, we used treatment efficacies of both 50% and 95%.

There is considerable variation among salmon aquaculture regions as to when salmon should be treated to reduce sea lice infestations. Recommended treatment scenarios are often dependent upon the time of year as well as the average number of mobile or adult female sea lice on a

salmonid. For example, in Norway, treatment is recommended for infestations ranging from an average of 0.5 mobiles per salmon during months that coincide with wild salmon migrations to 10 mobiles per salmon during the rest of the year (Dill *et al.* 2009). To test how different treatment scenarios altered the number and timing of chemical treatments and the role of wrasse, we ran simulations with treatment triggers of four mobiles per salmon and 15 mobiles per salmon.

Stocking densities of wrasse

To explore the effect of different stocking densities on sea lice loads and the number of treatments required, we used wrasse:salmon ratios of 0 (control), 1:200, 1:100, 1:50, 1:25 and 1:10. Salmon densities in the model were constrained to 1; therefore, to achieve these ratios, we reduced the feeding rate of the wrasse by its stocking density relative to a single salmon.

External and internal sources of infestation

Salmon farms vary considerably in their exposure to infective copepodids. This depends upon processes that affect rates of sea lice entering the farm from external sources as well as processes affecting the probability that offspring produced from louse on a salmon farm will attach to a local fish. Hydrodynamic conditions in and around salmon farms, local and regional sea lice management programmes, distances between farms, densities of fish within pens, number of fish and number of pens and amount of biofoul on pen nets (which increases recirculation of lice within pens) have all been shown to influence these rates (Costello 1996; Jansen *et al.* 2012). In areas where wild salmon also occur, this can be an additional source of copepodids (Saksida *et al.* 2011). To simulate several relevant scenarios, we altered the number of chalimus that attach from externally sourced copepodids (μ) as well as the proportion of copepodids from local parents that are able to find a new host (ϕ). We simulated farms with low, medium and high external sea lice pressure ($\mu = 0.3, 1, 2$) in combination with three values of internal sea lice pressure ($\phi = 5\%, 50\%$ or 95%).

External infection rate parameters are based on estimates made from other models (e.g. Revie *et al.* 2005). Attachment rates for local copepodids have been estimated at 0.25, 0.81 and 0.98 lice

per fish per day (Tully *et al.* 1996) in a cage study. While data suggest that temperature affects attachment rates of copepodids (Tucker, Somerville & Wootten 2000), we did not have enough information to parameterize this in the model.

Results

Simulations

We varied parameters in the model to simulate a number of relevant scenarios on fish farms. Table 3 illustrates the full extent of the simulations undertaken. For every scenario, the model was used to simulate the first year of a production cycle and repeated 100 times. We collected results on the number of treatments necessary over the year and the proportion of wrasse meals that were successful in removing a louse. The average number of chalimus and mobiles found on a host over the course of a year was recorded. These findings provided an insight to the sea lice infestation level, the impact of treatment and wrasse feeding behaviour. Access to an online version of the model is available at <http://tinyurl.com/wrassemmodel>.

Sea lice demographics

Adding wrasse to farms always decreased mobile lice, but had varying effects on chalimus depending upon the treatment scenario, treatment efficacy and the external infestation pressure. Because there were only slight effects of altering the internal infestation rate on sea lice demographics in the absence of chemical treatments, we only explored situations where the proportion of 'internal' copepodids attaching was 5%. In the absence of treatments, wrasse reduced both chalimus and mobile sea lice infestations (Fig. 2). When the external lice rate was 0.3 lice per day, a ratio of one wrasse per 200 salmon reduced chalimus from 33 to 14 and mobiles from 20 to 6 compared to the no wrasse treatments. Further increases in

wrasse density resulted in as few as eight chalimus and one mobile (Fig. 2a). The same trend occurred when the external lice infestations rates were increased to one and two lice per day; however, the overall lice loads were higher (Fig. 2e,i). For example, when the external lice rate was one louse per day, the average infestation was 65 mobiles and 110 chalimus, but dropped to 31 chalimus and eight mobiles when wrasse were stocked at 1:50.

When chemical treatments were used, the effects of wrasse on sea lice demographics were quite different. In most cases, wrasse caused chalimus to increase because fewer chemical treatments (which are lethal to chalimus) were necessary, but caused decreases or had no effect on mobile sea lice. For scenarios with a treatment trigger of 4, a treatment efficacy of 95% and low external infestation rates, there were two mobiles and five chalimus in the absence of wrasse. As wrasse stocking densities increased to 1:50, the average chalimus infestations increased to eight individuals per salmon and remained constant (Fig. 2c). This same trend was true when the external infestation pressure was higher (Fig. 2g,k). For example, when the external infestation pressure was one louse per day, the average infestation was two mobiles and nine chalimus without wrasse; however, if wrasse were used at densities of 1:10, chalimus increased to 25 individuals, while mobiles decreased to 1. When the treatment effectiveness was reduced to 50%, infestation levels of both chalimus and mobiles were slightly higher, but the effect of wrasse was the same. For example, in the absence of wrasse, lice loads were 11 chalimus and three mobiles at external infestation rates of one louse per day (Fig. 2b,f,j). When wrasse were added, thereby decreasing the need for chemical treatments, sea lice loads of chalimus and mobiles more closely resembled those seen when the treatment effectiveness was 95%.

Increasing the treatment trigger caused sea lice infestations to be greater. When the external

Table 3 Simulations investigated in this study. For each line, all factorial combinations were simulated 100 times

Wrasse densities	Treatment threshold	Treatment efficacy	External infestation rates (μ) (lice attaching per day)	Reinfection rates (ϕ) (% copepodids that find a host)
0, 1:200, 1:100, 1:50, 1:25, 1:10	4 mobiles	95%	0.3, 1, 2	5, 50, 95
0, 1:200, 1:100, 1:50, 1:25, 1:10	15 mobiles	95%	0.3, 1, 2	5, 50, 95
0, 1:200, 1:100, 1:50, 1:25, 1:10	4 mobiles	50%	0.3, 1, 2	5, 50, 95
0, 1:200, 1:100, 1:50, 1:25, 1:10	No treatments		0.3, 1, 2	5

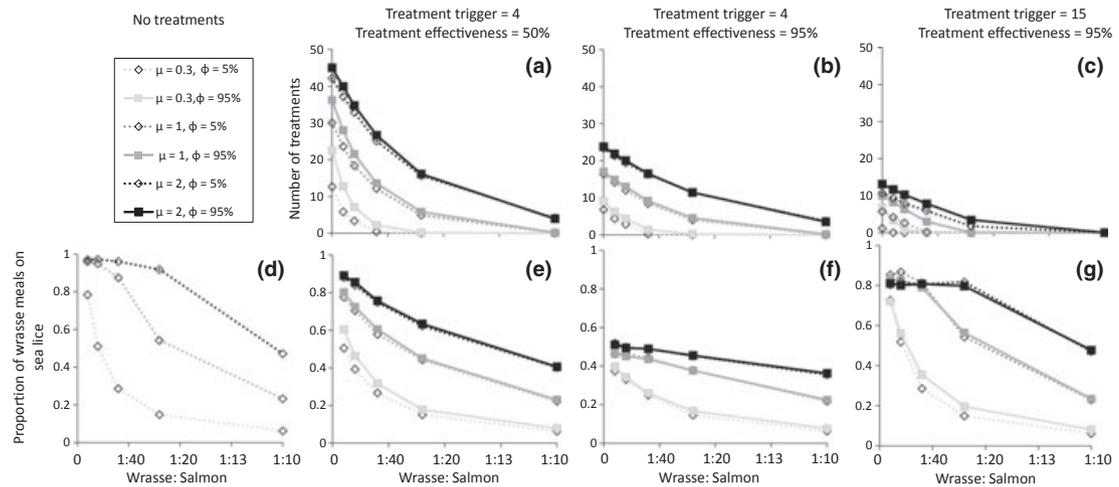


Figure 2 Effects of wrasse stocking densities on the average daily chalimus and mobile sea lice infestations for a number of infestation scenarios with different external infestation pressures (μ) and treatment conditions. Averages were calculated by averaging daily infestations for each day of a simulated year. The number of treatments given over that year is also shown. The reinfection rate (proportion of copepodids finding a host) is 5% for all of the scenarios shown.

infestation rate was low, the demographics of sea lice were more similar to those seen in the absence of treatments; adding wrasse caused decreases in both chalimus and mobiles; however, when the external infestation rate was 1 or greater, sea lice demographics followed the same trends as the other treatment scenarios (Fig. 2h,i). For example, for external infestation rates of 0.3 lice per day, the average infestation was 11 chalimus and six mobiles when wrasse were not used, but it dropped and remained close to eight chalimus and one mobile sea louse at wrasse densities equal to or greater than 1:50 (Fig. 2d). When the external infestation rate was one louse per day, the average infestation was 18 chalimus and seven mobiles in the absence of wrasse. As the ratio of wrasse increased, mobiles decreased to less than two individuals, while chalimus increased to 28 individuals (at 1:10, Fig. 2h).

Treatments

The number of treatments required in a year depended upon the treatment threshold and treatment efficacy as well as the wrasse stocking density and the internal and external infestation pressures. In the absence of wrasse, the number of treatments required to keep infestations below four lice per fish ranged from 12 to 45 when the treatment efficacy was 50% (Fig. 3a) and seven to 24 when efficacy was 95% (Fig. 3b). Between one and 13

treatments were required to keep infestations below 15 lice per fish when the efficacy was 95% (Fig. 3c). The lower values for these ranges occurred when the external infestation pressure was low, and the higher values when the external infestation pressure was high. Increases in the internal infestation pressure caused more treatments to be necessary when the treatment efficacy was 50% or the treatment threshold was 15.

In all treatment scenarios, adding wrasse reduced the number of treatments necessary to control sea lice, and in nearly all scenarios, if wrasse densities were high enough, chemical treatments were not necessary at all. When the treatment trigger was 4 and the treatment efficacy was 95%, less than one treatment per year was necessary if wrasse were stocked at 1:50 and the external infestation pressure was 0.3 lice per day or if wrasse were stocked at 1:10 and the external infestation pressure was one louse per day. At higher external infestation pressure (two lice per day), three to four chemical treatments per year were still required even when the density of wrasse was 1:10. These same trends occurred when the treatment efficacy was 15%. When the treatment trigger was 15, lower densities of wrasse were needed to reduce the number of treatments required to less than one per year. Wrasse-to-salmon ratios had to be between 1:200 and 1:50 when the external lice infestation rate was 0.3 lice per day, between 1:50 and 1:25 when the external lice

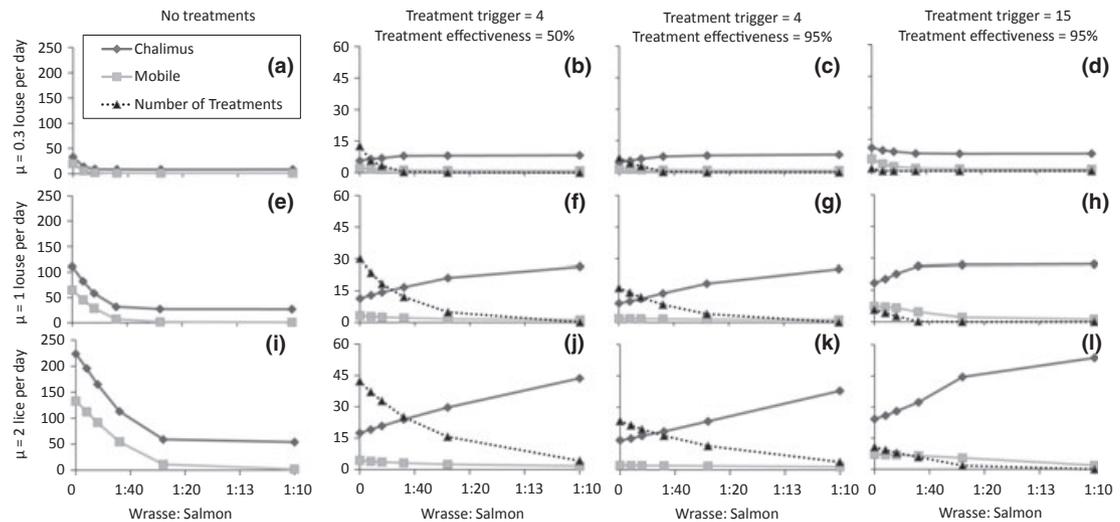


Figure 3 Effect of wrasse densities on the number of treatments given over the course of a year (a–c) and the proportion of wrasse meals where sea lice were consumed (d–g). The external infestation rate is indicated by μ , and the reinfection rate (proportion of copepodids finding a host) is indicated by ϕ .

infestation rate was one louse per day and 1:10 when the external lice infestation rate was two lice per day. For scenarios with a treatment threshold of 15, low internal infestation pressure reduced the number of treatments required when wrasse densities were high.

Wrasse feeding behaviour

Wrasse feeding efficiency as measured by proportion of sea lice meals depended critically on the density of wrasse and the external infestation pressure (Fig. 3d–g). The feeding efficiency of wrasse was higher when wrasse were stocked at lower densities and the external infestation pressure was high. All of these scenarios increased the amount of lice available for each wrasse. For example, in the absence of chemical treatments, between 80% and 100% of wrasse meals consisted of sea lice when wrasse were stocked at a ratio of 1:200, while between 5% and 50% of wrasse meals consisted of sea lice when they were stocked at 1:10 (Fig. 3d). For both of these cases, the higher feeding efficacy was associated with increased external infestation pressure.

The use of treatments also influenced the feeding behaviour of wrasse. In general, a low treatment trigger and a high treatment efficacy resulted in fewer wrasse meals containing lice. When the treatment trigger was four and the treatment efficacy was 50%, wrasse stocked at densities of

1:200 ate sea lice in 55%, 77% and 88% of their meals for external infestation rates of 0.3, 1 and 2 external lice per day, respectively. The proportion of meals that consisted of sea lice dropped to 6%, 23% and 40%, respectively, when wrasse were stocked at a density of 1:10 (Fig. 3e). When the treatment trigger was four and the treatment efficacy was 95%, wrasse stocked at densities of 1:200 ate sea lice in 37%, 46% and 52% of their meals for external infestation rates of 0.3, 1 and 2 external lice per day, respectively. Feeding efficacy fell to 6%, 22% and 35% when wrasse were stocked at densities of 1:10 (Fig. 3f). When the treatment trigger was 15 and the treatment efficacy was 95%, wrasse ate many more sea lice. Between 72% and 84% of their meals consisted of sea lice when wrasse were at 1:200 and fell to between 7% and 47% when wrasse were stocked at 1:10.

Discussion

The goal of this study was to investigate the effects of different concentrations of wrasse on sea lice infestations of farmed salmon in a variety of treatment and infestation scenarios. We found that wrasse can effectively control sea lice, and the densities of wrasse needed for effective control depend upon the source of the infestation and the targeted level of control. As the stocking densities of wrasse increased, fewer chemical treatments

were necessary, and in many scenarios, no treatments were necessary if wrasse were stocked at high enough densities. These results suggest that wrasse stocking densities should be adjusted to reflect local sea lice infestation concerns.

This is the first model we are aware of to use an agent-based approach to understanding sea lice infestations and integrated pest management. Traditionally, models exploring life history variation use either differential equations or delay differential equations (e.g. Revie *et al.* 2005; Frazer 2008; Frazer, Morton & Krkosek 2012). In the former, developmental transitions are rate-based and may not depend on the time spent in a particular life stage. This can result in accelerated dynamics, especially when there are rapid changes in population size as is the case when sea lice are treated. The latter approach avoids this problem by tracking cohorts so that life history transitions are a function of both time and age. This approach has the disadvantage, however, that there is no easy way to incorporate static events. In contrast, agent-based models can accommodate age-based transitions and can readily incorporate static and dynamic events, thereby overcoming the constraints of both system dynamic models (DeAngelis & Mooij 2005). This seems particularly useful when trying to understand integrated pest management systems, where dynamic control methods (e.g. predator–prey, pathogen–host, parasitoid–host) are often combined with static control methods such as chemical treatments. In these cases, field studies may not be financially, logistically or ethically feasible due to the scale of proper experimental designs and the necessity of an unmanaged control treatment.

Currently, there is limited information available about how local conditions and sea lice management goals can be used to inform farm managers about the number of wrasse to stock. Industry partners currently recommend that one wrasse should be stocked for every 25 salmon (Treasurer 2002); however, results from the individual-based model created in this study suggest that if the infestation source is local, the number of wrasse necessary to control an infestation may be up to an order of magnitude less than this. In this scenario, wrasse are able to prey upon mobile lice before they reproduce thereby reducing the reinfection cycle. In rare cases, such as when there is a high influx of sea lice from external sources, wrasse densities may need to be higher.

The treatment goals of a farm also influence which stocking densities of wrasse are appropriate. Not surprisingly, more wrasse are required to control infestations when the treatment threshold is low; however, in these same scenarios, wrasse have much less efficient feeding behaviour, and a lower proportion of their meals are used on sea lice. This occurs because there are fewer mobile lice available to eat. The role of wrasse is also gaining importance as resistance of sea lice to chemotherapeutics continues to increase (Denholm *et al.* 2002). When chemical treatments have low efficacy, wrasse are very inefficient at controlling sea lice at low densities, but they have a higher feeding efficiency because the treatments are not effective at reducing their food source. When wrasse are controlling sea lice to the level that chemical treatments are rarely or never necessary, their feeding behaviour is quite inefficient. This suggests that supplemental food sources should be available to wrasse when they are stocked at high densities, used in combination with very effective treatments or used in areas where treatment thresholds are low, or lowered during wild salmon migration.

In general, wrasse have a large influence on the population demographics of sea lice. As wrasse densities increase, mobile lice are controlled more effectively than chalmus. This occurs because wrasse do not prey on chalmus, so newly attached sea lice survive until they are controlled at a later stage. In contrast, chemical treatments are lethal to all attached stages, so when more treatments are being used (e.g. when there are no wrasse or very low densities of wrasse), average chalmus infestations are only slightly above that of mobiles. One important consequence of these altered demographics is that, while higher chalmus loads are unlikely to be especially stressful to salmon, should there be a lapse in the removal of mobiles (e.g. if wrasse are removed or there is a lapse in their feeding behaviour), there is more potential for an outbreak to occur.

Several assumptions were made in the model. While considerable detail was included in the models of sea lice survival and mortality, both the wrasse predators and salmonid hosts were very simplified. Wrasse in this model consumed sea lice at a constant rate regardless of environmental conditions or sea lice density. A major influence in this decision was the lack of data on context-dependent behaviour of wrasse. For example, sea lice densities, the amount of biofoul on net pens, cold temperatures and the availability of

supplemental food sources also influence wrasse feeding behaviour (Costello 1996; Kvenseth 1996); however, there are little quantitative data documenting these effects. Parameterization of these contingencies is also difficult because wrasse behaviour depends upon local factors such as the method and timing of wrasse stocking as well as the species of wrasse used. In addition, commercially raised wrasse are likely to exhibit different behaviours and feeding preferences than wild-caught wrasse (Cowx *et al.* 1998); however, the industry is so young that data on these differences do not exist. The assumption of constant wrasse population size is somewhat optimistic. Losses of wrasse due to mortality and escape can be common (e.g. Treasurer 1996), so wrasse may need to be stocked at densities higher than the recommended values in order to achieve the densities recommended in this article. As more data become available, we hope to improve the model so that wrasse can dynamically respond to local environmental changes. It is likely that increased complexity in wrasse behaviour would reduce the predictive effectiveness of wrasse slightly as most of the context dependencies mentioned here decrease wrasse feeding rates or densities.

Salmon are also not dynamic and were simplified in the model to a single representative individual. Even though salmon are always farmed in large numbers, we chose to model a single salmon because we were interested in understanding effects of wrasse on the mean infestation load of a salmonid more than the variation among hosts. One of the risks of this simplification, however, is that stochastic processes may influence overall outcomes more when they are modelled with a single representative host than if they are modelled with many hosts. By replicating scenarios 100 times and evaluating mean responses, we hope that this concern was avoided. It is interesting to note that in the situation where the treatment trigger level was set to 15 mobiles, with a presumed efficacy of 95% and no wrasse present, the estimated number of treatments was around 12. While this would appear a little high based on recent history, this scenario reflects the situation more commonly seen in Scotland and Norway in the late 1990s. In an article summarizing treatment interventions during that period, Scottish farms administered an average of 6.5 treatments in the second year of production with some sites using at least nine interventions (Revie *et al.* 2002b).

The article provides the first quantitative estimates of environmental influences on the effects of wrasse on sea lice population dynamics. Collectively, the results suggest that wrasse can be very effective in controlling sea lice on farmed salmonids. Optimal stocking densities and feeding efficiency of wrasse will depend upon local infestation scenarios and treatment goals. In many areas where wrasse are used, treatments may not be necessary if they are stocked at sufficiently high densities.

Several future research directions are suggested by this model. First, as more data become available, it would be useful to incorporate factors that may influence management outcomes. These include local effects on wrasse behaviour such as the effects of temperature and net biofouling on sea lice feeding rates, and species- and sex-specific differences in feeding behaviour. Behaviour and efficacy of wrasse may change in the second year of the salmon production cycle as a result of size differences between salmon and wrasse and losses of wrasse during the winter (Costello 1996; Treasurer 2002). Second, while the model described in this article is useful in its ability to incorporate stochastic differences between lice, and model sea lice life history, it would be useful to incorporate stochastic differences between salmon. In particular, sea lice tend to be over-dispersed among their hosts, especially when infestation levels are low (Heuch Peter, Gettinby & Revie 2011). As sea lice control improves, this may be a more common scenario, and it will be useful to investigate how over-dispersal of sea lice influences the effectiveness of wrasse as a biocontrol. In addition, salmonid biomass is negatively correlated with sea lice density (Jansen *et al.* 2012). The current model cannot evaluate this relationship. Development of a multi-host model would be useful for incorporating both of these factors. Finally, longitudinal data sets including wrasse: salmon densities, sea lice counts, biofoul on nets, water temperature and the use of other treatments need to be collected in order to quantify effects of wrasse in the field and validate this model.

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