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Moving cleaner fish from the wild into fish farms: A zero-sum game?

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ABSTRACT

Fish that engage in mutualistic cleaning behaviour ('cleaner fishes') have recently been popularized as a nature-based method of controlling ectoparasite outbreaks in fish farms. Outbreaks impact animal welfare and threaten wild fish populations; due to this, millions of cleaner fish (especially wrasses from the family *Labridae*) are wild-caught each year and transferred into Atlantic salmon (*Salmo salar*) farms to remove ectoparasitic sea lice (predominantly *Lepeophtheirus salmonis*) from farmed salmon and reduce spillover (i.e. parasites transferring from farmed to wild fish) onto vulnerable wild salmonid populations. However, we hypothesize that this practice may result in no net benefit to the infestation pressure on wild fish if gains in farm-based control trade off against the removal of lice from wild fish by wrasse moved from the wild into net pens. Such a scenario would entail a zero-sum game. We test our hypothesis using an ecological simulation of wrasse as cleaners of farmed Atlantic salmon and wild sea trout (*Salmo trutta*). We parameterized our simulation based on published models of sea lice epidemics from farms to calculate the relative impact of lice when wrasse are removed from the ecosystem to serve as cleaners. Our simulations revealed that a zero-sum game can emerge from this system at unexpectedly infrequent rates of cleaning by wrasse in the wild. Scandinavian wrasses are relatively data poor and parameterizing our simulation revealed a need for better data on the ecological role of these fishes in coastal ecosystems. For the first time, we suggest that wrasse fisheries may be a zero-sum game and that under a plausible set of conditions, fishing wrasse out of coastal ecosystems may do more harm than good for modulating sea lice epidemics. However, we emphasize that these results do not suggest that wrasse alone will play a role in resolving high infestation pressure of lice emanating from fish farms.

1. Introduction

Pathogens play a key role in ecosystems; by feeding on their hosts, parasites contribute to natural mortality in a population, thereby regulating abundance and driving selection (Lafferty et al., 2006, 2008). However, the establishment, spread, and outbreak of pathogenic species is a critical challenge confronted by domestic farming that threatens sustainability (Blaylock and Bullard, 2014). To reduce the spread of pathogens from reservoirs of farmed fish to wild populations, aquaculture management aims to limit the density of sea lice in cages and thereby the reproductive rate of lice, reducing export of infective stages into the environment (Parsons et al., 2020).

Confronting sustainability challenges from parasite outbreaks on farms, open net pen fish farm aquaculture is now increasingly relying on the use of cleaner fish that are stocked into net pens to eat parasitic lice and reduce infestation pressure in the area within and adjacent to the farm (Labridae and Cyclopteridae; Kristoffersen et al., 2014). These 'cleaner fishes' are stocked into the net pens and expected to feed on the lice to reduce density and epidemic potential (original research by Bjordal 1991 based on observations in Potts (1973), Samuelsen (1981), Hilldén (1981, 1983)). There is a thriving wild capture fishery that transports wild wrasse from fjords to fish farms for lice management; these wild wrasse fisheries move millions of wild wrasse from the fjords into net pens (Skiftesvik et al., 1996; Gonzalez and de Boer, 2017). In Norway, the Fisheries Directorate reported 54 million wrasse captured in wild fisheries for aquaculture cleaner fish from 2018-2020. Concerns about recruiting wild wrasse are manifold, including the condition of the fish in cages (Geitung et al., 2020), overfishing of wild wrasses (D'Arcy

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et al., 2013), phenotypic changes to wrasse populations (Halvorsen et al., 2017), and genetic introgression of alien wrasse that escape cages and interbreed with wild populations (Faust et al., 2018). Also troubling is recent evidence questioning whether cleaner fish currently manage sea lice epidemics in cages sufficiently to justify their use (Barrett et al., 2020). However, ecosystem impacts of wrasse fisheries have not been adequately explored (Philis et al., 2021))

Wild wrasses are important to coastal ecosystems and are known to engage in cleaning behaviour in the wild (Hillden et al., 1983; Breen, 1996). We hypothesize that the role of wrasse in the wild as cleaners is a potentially valuable ecosystem service that is not adequately accounted for and may therefore represent an ecosystem impact of wrasse fisheries. In game theory, zero-sum games emerge when benefits in one realm are enjoyed at the costs of another (a sum netting zero). To test our hypothesis, we conceptualized wrasse fishing as a game that transfers the benefits of direct lice cleaning behaviour on wild fish to indirect effects of reducing infestation pressure from fish farms by picking lice in sea cages. The outcome of the simulated game would resolve how active wrasse must be at directly picking lice in the wild to offset the benefits of moving them into sea cages where they have a known effect on infestation pressure calculable from published data. Simulations were parameterized with empirical data from the literature and realistic values for unknown parameters based on our own research. The simulation aims to determine how suitable wild-capture fisheries are for establishing cleaner fish for use in aquaculture and inform efforts to enhance industry sustainability.

2. Methods

2.1. Model Parameterization

We developed a model to simulate the result of a game between moving wrasse and leaving wrasse in place to determine whether a zero-sum solution emerged using R programming software (R Core Team 2022). The simulation was parameterized based on the transport of cleaner fish from the wild into fish farms (Fig. 1; Table 1). The model of wrasse cleaning behaviour relies on several key assumptions about wrasse, sea trout, and their interaction. The model parameters included the wrasse population in a fjord, rate and functional response of lice predation in cages and in the wild, sea trout abundance, and infestation pressure of sea lice in fjords as a function of lice abundance in cages. We describe below the evidence underlying these model parameters and our strategy for parameterizing the model. The model has two components

(1) indirect contribution of cleaner wrasse to wild salmonids. First, we modeled the extent to which stocking wild wrasse into the cages reduced infestation pressure of lice on wild fish based on published data. Infestation pressure in this context is the number of adult lice available to parasitize salmonids in a defined area. Reduced infestation pressure is a function of how many lice originating from farms will attach and develop on wild fish in a situation without the cleaner fish present in cages, and how much stocking wrasse will reduce this number. The difference between these two scenarios is the

Table 1
Model parameters for estimating the viability of wild capture wrasse fisheries for modulating sea lice epidemics from Atlantic salmon farms in a hypothetical coastal area.

Variable	abbreviation	Range	Average
Number of wrasse stocked (N individuals)	N_{wrasse}	0-100,000	50,000
Distance from fish farm (km)	D	0-20	10
Infestation pressure	IP	15-22	18.6
Number of wild sea trout (N individuals)	$N_{seatrout}$	500-30,000	10,000

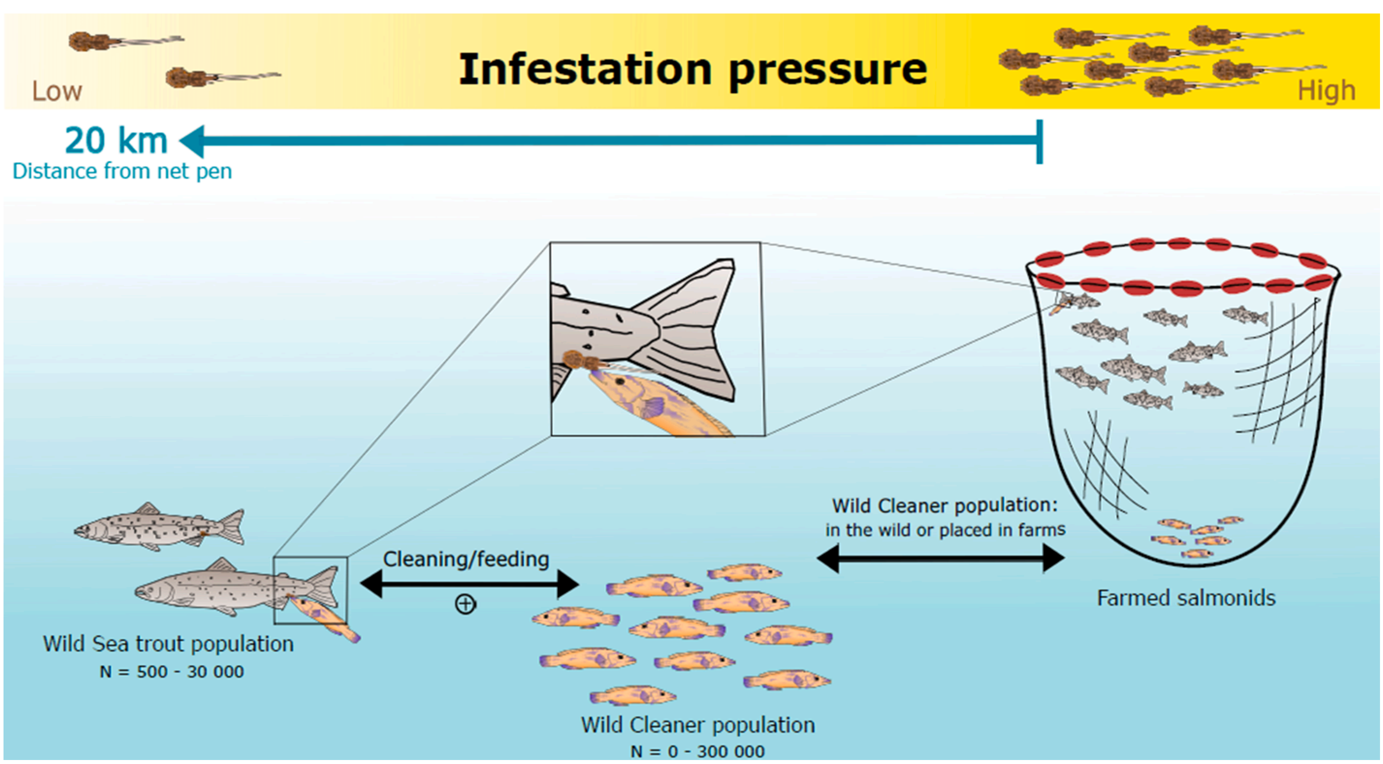

Fig. 1. Schematic illustration of the parameters of our simulation. We generated a fjord system with a single farm and infestation pressure around the farm radius according to lice infestation models (Kristoffersen et al., 2014). The wild sea trout population was allowed to vary in the model from 500 to 30,000 individuals. Three hundred thousand wild cleaners were allowed to vary between the wild where they cleaned wild sea trout or fish farms where they cleaned farmed salmon. The simulation was parameterized to optimize the rate of cleaning in the wild, which is not empirically known, to establish whether there is a zero-sum game in cleaner fish interactions in applications of cleaners in fish farms.

environmental effect of fishing and stocking wild wrasse in net pens.

(2) direct relief of sea lice by wild wrasse on wild salmonids. Second, we modeled how many lice are removed from the wild fish if the wrasse is allowed to remain and interact with the wild fish (cleaning them of lice at some variable rate). The aim of this model was to estimate in what parameter space the effect of wrasse picking sea lice in the wild generates a zero sum game, or whether there are net gains or losses with respect to lice burdens on wild fish from the lice management approach of moving wrasse into net pens (Table 2).

2.1.1. Indirect contribution of cleaner wrasse to wild salmonids

2.1.1.1. Effect of cleaner wrasse on louse populations in salmon farms. Barrett et al. (2020) constructed a statistical model of cleaner fish efficiency across 488 Norwegian salmon farms that completed a full grow-out cycle during 2016–2018. They compared the rate of change in adult female salmon louse density according to the number of cleaner fish stocked, finding that the detectable effect of cleaner fish in fish farms was highly variable, and that on average, cleaner fish slowed but did not stop louse population growth.

To parameterize the first component of the model, we required a similar function to Barrett et al. (2020), but one that predicted louse densities (rather than population growth rates) according to wrasse use. Starting with the same dataset of 488 grow-out cycles, we constrained the data to a defined season of wrasse use, spanning weeks 20–40 (about mid May to mid October) in each year from 2016 to 2018. For each week of this 'wrasse season' at each farm, we summed the number of wrasse stocked from week 20 up until the current week, and corrected for farm size using maximum allowable biomass as a proxy. To improve our ability to detect a wrasse effect on lice, we omitted weekly records where (i) the farm was thought to be less than 30 weeks into the grow-out cycle at the time (louse infestations vary with grow-out phase and season), (ii) delousing had been reported in the current or previous 2 weeks, or (iii) more than 20 wrasse per t had been used, as such high rates of cleaner fish use are not typical and are not expected to be efficient. The function was only fitted to data from weeks 31 to 40, when sea temperatures have typically warmed sufficiently for wrasse to be active feeders. Using the nls function in R, we fitted a negative exponential regression model in which the density of adult female sea lice at a farm was predicted by cumulative wrasse stocking effort. The fitted function was significant (df = 351, p = 0.01):

$$y = 0.5247 * exp(-0.1082 * W_{PT}) \quad (1)$$

where y is louse density, expressed as adult female sea lice per farmed salmon, and W_{PT} is the number of wrasse stocked over the season to date, expressed per t of allowable biomass. For context, an average salmon farm has a maximum allowable biomass of ~3500 t.

The wrasse effect was then further simplified into a reduction in the density of adult female sea lice, which it is assumed will lead to a corresponding reduction in the number of louse eggs released from salmon farms to infest wild fish. This reduction in infestation pressure is given as:

$$rel\_red = 1 - y/y_0 \quad (2)$$

Where *rel_red* is the relative reduction from a scenario with no wrasse stocked (y_0) to a scenario with a given number of wrasse stocked (y).

2.1.1.2. Lice attachment to adult salmonids. The population dynamics of lice are highly dependent on water temperature (Stien et al., 2005). External infestation pressure from fish farms are known to influence the lice dynamics in adjacent populations that infect wild fish (Kristoffersen et al., 2014; Vollset et al., 2019). Several models exist that use a number of gravid female lice in fish farms to calculate the infestation pressure on adjacent farms or wild fish (Sandvik et al., 2020). A simple model was developed by Aldrin et al. (2013) and further applied by Kristoffersen et al. (2014), which used a dataset on number of lice attached to fish in sentinel cages to develop a risk equation that predicted number of lice attaching to adjacent wild fish as a function of the distance from the farm (where the infestation pressure is a function of number of gravid female lice and the temperature). The decrease in infestation pressure by distance is as follows

$$RR_{ip} = \frac{e^{\left(-1.44-0.351\times\left(D^{-57}-1\right)/0.57\right)}}{e^{\left(-1.44-0.351\times\left(0^{-57}-1\right)/0.57\right)}} \quad (3)$$

where RR_{ip} is the risk reduction and D is the distance in kilometers from the fish farm

To estimate the number of lice on a sea trout at a given distance from the source (i.e. fish farm) we use the fitted equation between lice in cages and the log transformed external infestation pressure from Kristoffersen et al. (2014). The equation is a as follows:

$$lice = e^{(-14.603 + log(7\times days) + 0.843 \times log(IP\times RR_{IP}))} \times prop_{adult} \quad (4)$$

where weeks is the number of weeks (up to 10 weeks) the wild fish has been in the area, IP is the infestation pressure estimated from female lice as described in Kristoffersen et al. (2014), RR_{ip} is explained above, while $prop_{adult}$ is a correction for mortality of lice during development, where we argue that only 70% of the lice that is counted on fish in sentinel

Table 2
Summary of equations used and derived for the simulation, in which cleaning rate (∝) is optimized.

No.	Equation	Simple explanation	Contribution	Refs.
1	$y = 0.5247 * exp(-0.1082 * W_{PT})$	Effect of wrasse stocking on lice density (y) in farms	Indirect contribution to reducing infestation pressure	Barrett et al. (2020)
2	$rel\_red = 1 - y/y_0$	Benefit accrued from stocking wrasse in terms of reduction in lice infestation pressure that is attributable to wrasse	Indirect contribution to reducing infestation pressure	
3	$RR_{ip} = \frac{e^{(-1.44-0.351\times(D^{-57}-1)/0.57)}}{e^{(-1.44-0.351\times(0^{-57}-1)/0.57)}}$	Risk of infestation by lice on wild fish adjacent to fish farms	Indirect contribution to reducing infestation pressure	Kristoffersen et al. (2014)
4	$lice = e^{(-14.603 + log(7\times days) + 0.843 \times log(IP\times RR_{IP}))} \times prop_{adult}$	Infestation pressure of lice at a given distance from a fish farm	Indirect contribution to reducing infestation pressure	Kristoffersen et al. (2014)
5	$reduction = lice \times rel\_red$	Reduction in lice infestation pressure attributable to stocking of wrasse in fish farms	Indirect contribution to reducing infestation pressure	
6	$lice\,removal = ((cleaning\ rate \times Nwrasse) / Nseatrout) \times weeks$	Lice removed by wrasse depends on the number of wrasse cleaning, the number of trout available to be cleaned, the time at large, and the cleaning rate by wrasse	Direct contribution of wrasse to removing lice from wild trout	
7	$cleaningrate = \propto \times lice$	Cleaning rate by wild wrasse on wild trout depends on the amount of lice and ∝, the rate at which each wrasse consumes lice off of wrasse	Direct contribution of wrasse to removing lice from wild trout	
8	$reduction = liceremoval$	The direct effects of lice cleaning by wrasse constitutes the amount of lice removed	Direct contribution of wrasse to removing lice from wild trout	

cages will develop to adult stages (Grimnes and Jakobsen, 1996; Bjorn and Finstad, 1997, 1998). IP × RR_{ip} is equivalent to $IP_{c,t}$ in Kristoffer-esen et al. (2014), i.e. distance corrected external infestation pressure.

2.1.1.3. What is the reduction of lice on wild fish from stocking wrasse?. By combining the estimation of reduction in infestation pressure (1.1) and the effect of infestation pressure on number of lice on wild fish (1.2) we calculate the reduction in lice on wild fish due to stocking of cleaner fish as follows

$$reduction = lice \times rel\_red \quad (5)$$

where *reduction* is the number of lice alleviated from wild fish due to stocking of wrasse in the adjacent fish farms at some distance (km from farm).

2.1.2. Direct relief of sea lice by wild wrasse on wild salmonids

2.1.2.1. Spatiotemporal association of wrasse and trout. Kelts and smolts of both sea trout and Atlantic salmon (*Salmo salar*) exit freshwater and enter coastal seas in springtime when water temperatures in the ocean are approximately 8°C (Hvidsten et al., 1998; Jensen et al., 2012; Klemetsen et al., 2003). At approximately the same time, sea lice begin to proliferate (Tully and Nolan, 2002) and wrasse become active once again after a period of winter dormancy (Gonzalez and de Boer, 2017; Sayer and Davenport, 1996). Atlantic salmon mostly pass through coastal areas for the open ocean during spring whereas trout forage along coastal flats during spring and summer and return to freshwater for the spawning migration beginning in summer and until spawning in September-November (depending on latitude). The temporal overlap between these salmonids and wrasse depends on spatiotemporal dynamics, but in general is longer for sea trout than salmon (Armstrong et al., 2003; Skiftesvik et al., 2014). In some instances, we have observed that the trout use the fresher upper part of the water column as opposed to the wrasses often found in the more saline water underneath. This behaviour is probably a consequence of the infection and the resulting ionic disturbance caused by the lice feeding on the skin of trout. This causes the fish to become dehydrated and seek freshwater in order to restore its ionic balance (Birkeland and Jacobsen, 1997).

2.1.2.2. Sea lice predation by wrasse in the wild. Wrasse are generalist invertivores and have been confirmed to act as cleaner fish in the wild. Breen et al. (1996) observed ballan wrasse performing as cleaners and Hilldén et al. (1983) observed goldsinny wrasse cleaning fish in Sweden. Ballan and corkwing wrasse caught in Ireland and France were generalists that ate decapods, bivalves, and gastropods as well as a little bit of algae (Deady and Fives, 1995; Sayer et al., 1995). Goldsinny in Scotland ate a broad variety of invertebrates including hydrozoans, polychaetes, echinoderms, gastropods, bivalves, insects, amphipods, isopods, decapods, and a small amount of copepods, specifically *Metis ignea* (i.e. not sea lice; Sayer et al., 1995). Captive wrasse can consume a large number of lice (up to 58 in an individual recorded by Deady et al. 1995), 1.2–2.7% of the body weight (Treasurer, 1994). However, wrasse in cages seem to prefer to forage on alternative food sources rather than on lice (Deady et al., 1995). Insufficient work has been published on nutritional needs of wrasse or the energy content of lice, making it challenging to determine how efficient a food source they are for wrasse.

In captivity, wrasse display a linear feeding response to the abundance of lice. Leclercq et al. (2014) showed a density-dependent response of wrasse to lice infestations on Atlantic salmon smolts in experimental trials, but the functional response was linear (Type I). The Type I functional response of wrasse in cages suggested that there was no prey switching at low lice densities in captivity, and no satiation at high densities. There is also an important effect of temperature because wrasse have higher metabolic demands in warmer water (swimming performance maximized at 25°C; Yuen et al., 2019). Indeed, wild goldsinny had fuller stomachs later in the year (June-November) than earlier in the year (December-May; Sayer et al., 1995). Availability of alternative prey (opened blue mussels *Mytilus edulis*) did not affect lice consumption by wrasse (Leclercq et al., 2014). Given the available data on wrasse feeding responses to lice density, we have used a constant rate of cleaning where each wrasse removes a constant number of lice per week per trout, which we call "cleaning rate".

2.1.2.3. How many sea trout are in a typical Norwegian fjord?. Our simulation is not parameterized for all of Norway but one discrete marine unit, perhaps best conceptualized as a fjord that is homogeneous with respect to habitat and with a fish farm at the centre (Fig. 1). With approximately 1000 sea trout rivers catalogued in Norway yielding about 700 sea trout per home river by simple division, we assumed a sea trout population in our simulated fjord to be approximately 10 000 individuals, representing the populations of about 14 rivers.

2.1.2.4. Rate of sea lice predation by wrasse in the wild. We have only anecdotal observations of wrasse removing sea lice from salmonids in the wild, none of which have been captured on video. It is unrealistic to think that this behaviour never occurs in the wild given that wrasse will readily engage in cleaning in cages and tanks and have been observed cleaning other species in the wild (Hilldén et al., 1983; Breen, 1996). The pivotal question in this context is not whether or not the behaviour occurs, but rather, how effective it is in removing lice from wild trout. In this study, we estimated how many sea lice could be removed from each sea trout in an area by wrasse that potentially would be extracted from an area during fishing:

$$liceremoval = ((cleaning\ rate \times Nwrasse) / Nseatrout) \times weeks \quad (6)$$

Where N_{wrasse} is the number of wrasse within the impacted area, $N_{seatrout}$ is the number of sea trout in the area and weeks is the number of weeks this cleaning event takes place. Based on the indications from tank and cage studies in 1.1 we suggest that cleaning rate should either be estimated as a constant (i.e. that each wrasse removes a constant number of lice per week, or a type I functional response where:

$$cleaningrate = \propto \times lice \quad (7)$$

Lice taken per wrasse per week is the cleaning rate, in which lice is the average number of lice on each sea trout and ∝ is the slope where the intercept is 0. The rate ∝ is the lice cleaned per lice on a sea trout by an individual wrasse.

2.1.3. Estimating the result of a game when stocking wild wrasse into salmon cages

With these two estimates, *indirect effects* of wrasse on sea lice on wild fish due to stocking of wrasse in fish farms, and *direct lice removal* from the same wrasse in the wild, it is possible to estimate when fishing wrasse becomes a zero sum game. This is simply parameter space where:

$$reduction = liceremoval \quad (8)$$

To investigate the parameter space in which the effect of fishing and stocking wrasse in fish farms equals the effect of allowing the same wrasse to remove lice on wild fish we used the *optimize* function in R to minimize value *abs(reduction - lice removal)*. We focused on the unknown parameter cleaning rate (either as constant removal per week or the slope in the functional I response) and plot the value of where the mean lice reduction on wild fish due to stocking of cleaner fish is equal to lice removed from sea trout in the wild according to distance from the fish farm (D, in Eq. (3)), number of cleaner fish (N_{wrasse}, in Eq. (1)), number of sea trout in the area of impact ($N_{seatrout}$ in Eq. (6)), and infestation pressure calculated at the fish farm (log(IP) in Eq. (4); see Kristoffersen et al. 2014).

3. Results

3.1. What cleaning rates must wrasse have in the wild for wrasse fisheries to be zero sum game?

According to our simulations, cleaning by wrasse on sea trout in the wild does not have to occur frequently for the effect of moving wrasse to farms to have a zero-sum result on the wild sea trout lice infestation. For most parametrizations of the model, each wrasse would only have to engage in cleaning activity once per week for these two activities (i.e. stocking or cleaning behavior in the wild) to be equally beneficial to the wild trout based on known benefits of the wrasse in sea cages (Fig. 2). When parameterizing the cleaning behaviour of wrasse in the wild with a Type I functional response, in general, each wrasse would have to remove 5% of the lice on sea trout each week to achieve the zero-sum result in the game (Fig. 3).

3.2. Does the distance between the farm and the wild sea trout matter?

The simulation yields a zero sum at a lower cleaning rate the farther away the trout is from the fish farm. At a cleaning rate of 5% lice per week per wrasse, the game suggests moving wrasse to fish farms if sea trout are restricted within 10 km of the farm. In contrast, if cleaning behaviour occurs according to a Type I functional response, the effect would not depend on distance from the fish farm, because the cleaning behaviour of wrasse in the wild would be scaled according to the number of lice released from the farm.

3.3. Would it be better to stock more or less cleaner fish from the wild into fish farms?

Our simulation does not appear to be sensitive to how many wrasse are fished and stocked. The more wrasse that are stocked, the more important the wild wrasse seem to become, suggesting that stocking should be limited in order to preserve cleaning in wild wrasse.

3.4. Does it matter whether there are few or many wild sea trout?

The more trout that there are in the vicinity of the fish farms the more effective stocking becomes. In the net pen, the wrasse remove a constant number of lice independent of the trout in the wild. Therefore, decreasing the infestation pressure from fish farms by having cleaner wrasse in the net pens will be increasingly positive the more sea trout are around the fish farm.

3.5. Is the zero sum game equal across different lice numbers on the farm?

Along the same logic as the distance from a fish farm - if infestation pressure increases due to higher outbreaks levels in the net pen it is more effective to stock wrasse because the effect of wrasse in the net pen is a constant relative effect. However, if there is a Type I functional response such that wrasse scale the number of lice that they eat to increase their foraging on lice at high infestation pressure, the effect of cleaning behaviour of wrasse in the wild is constant, and the effect of infestation pressure disappears (Fig. 3).

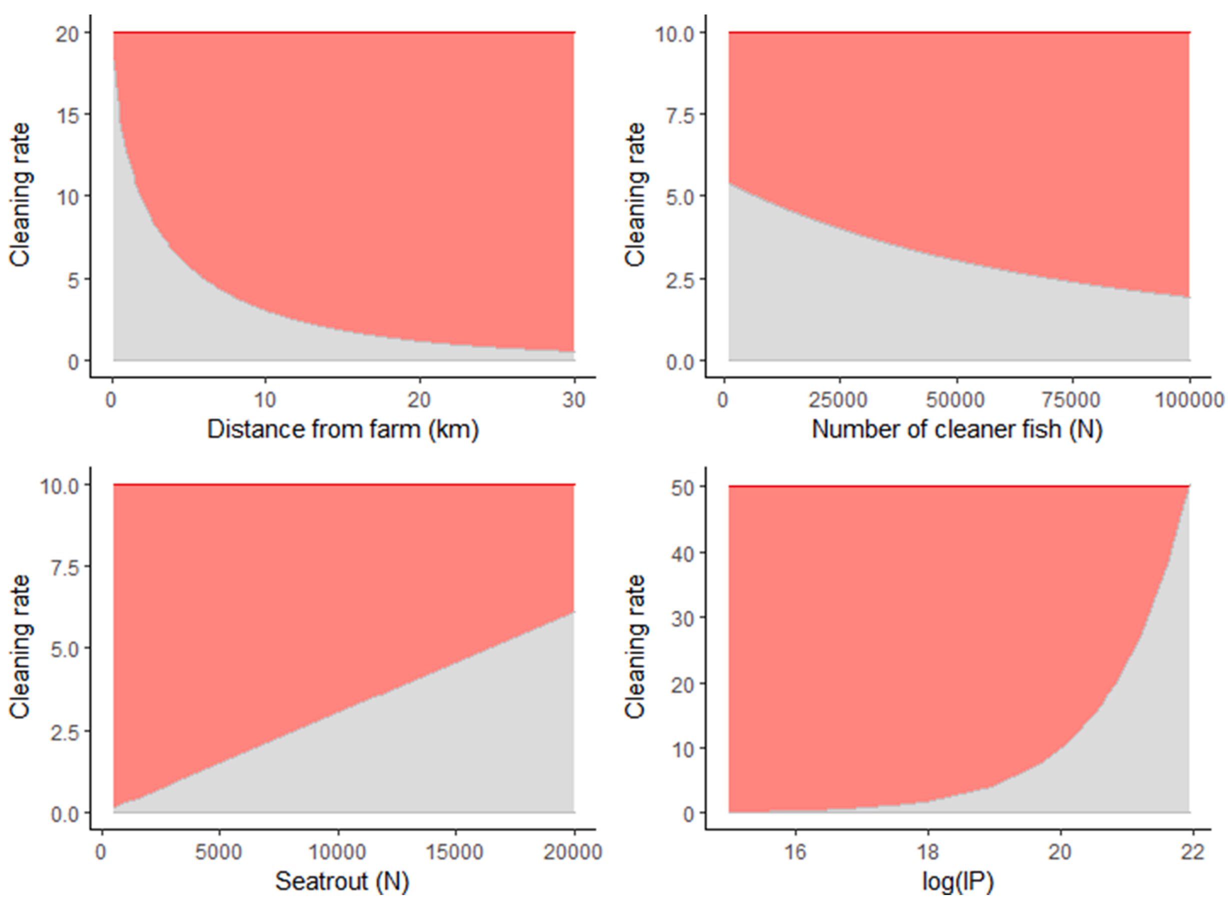

Fig. 2. Ratio between the effect of wrasse removing sea lice from sea trout in nature versus the effect of reducing infestation pressure from fish farm by placing the wrasse in the net pen, where red region indicates a net negative impact on wild sea trout, and grey regions indicate a net positive effect on wild sea trout. Cleaning rate is the number of cleaner events per wrasse on sea trout per week. Sea trout and cleaner fish are presented as number of individuals (N) and infestation pressure is the number of adult sea lice available to parasitize sea trout in the immediate area.

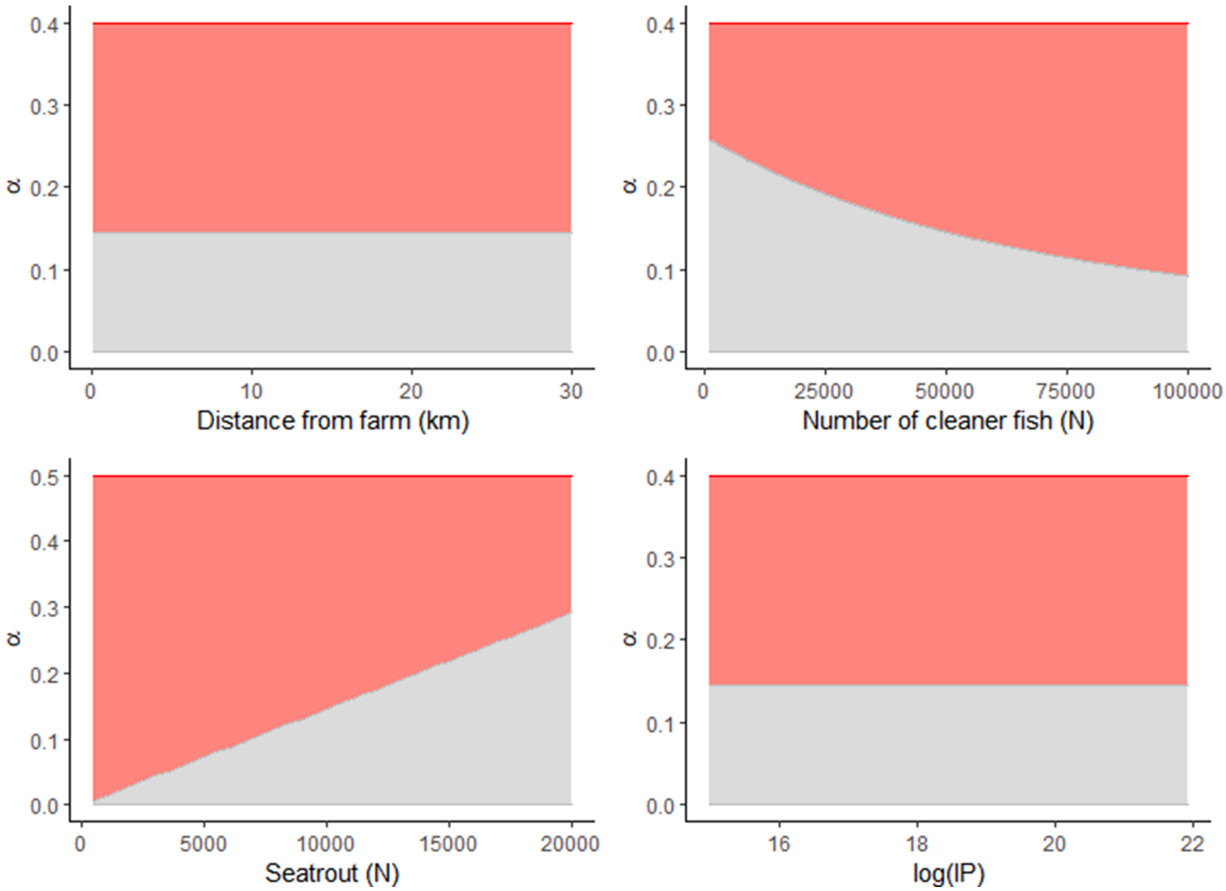

Fig. 3. Ratio between the effect of wrasse removing sea lice from sea trout in nature versus the effect of reducing infestation pressure from fish farm by placing the wrasse in the net pen, where red region indicates a net negative impact on wild sea trout, and grey regions indicate a net positive effect on wild sea trout such that the line is the zero-sum result of the game. Cleaning rate is a function of the average lice per sea trout such that there is a Type I functional response where events per wrasse on sea trout per week = cleaning rate × average lice per sea trout.

4. Discussion

Game theory is often applied to study wild wrasse systems and the power dynamic between cleaners and clients (e.g. Bshary 2002, Gingins et al. 2013, Bshary and Oliveira 2015). The dynamic between direct and indirect effects of cleaner wrasse on lice infestations was parameterized as a game in the simulation to determine whether lice picking behaviour in the wild could be an important ecosystem interaction and indeed, we illustrate how moving wild wrasse into net pens can have zero or even negative outcomes for the ecosystem when considering the broader impact of wrasse. The direct benefits of wrasse cleaning lice have not been considered when evaluating the costs and benefits of using cleaner fish for open net pen aquaculture parasite management and merit further study as a potential ecosystem impact of wrasse fisheries (Philis et al., 2021).

Our model suggests that average cleaning rates of wrasse on wild fish (direct effects) can be low but still comparably efficient in lowering infestation pressure on wild fish when wrasse are moved to farms (indirect effects). Despite great interest in the behaviour of cleaner fish such as wrasse in tropical systems, little data have been collected on the cleaning behaviour of temperate wrasses and there were no values available for cleaning rates with which we could parameterize our model. Instead, we opted to have the model optimize the cleaning rate in the wild, which settled at around 0.5 lice per wrasse per week (Type-0 FR) or 5% of lice per sea trout per wrasse per week (i.e. the slope in the Type-I FR). Both models suggested that infrequent cleaning behaviour by wrasse can still provide a key ecosystem service in the wild with respect to reducing lice loads on trout. Perhaps paradoxically, the model suggests that if there are more sea trout in the fjord, then it is better to place a wrasse in a farm than leave it to do the work directly upon wild trout. This result can be explained by the model parameterization, which increases the number of lice proportionally with the increase in abundance of trout. The underlying mechanism is the assumption that sea lice infestations are host-limited, such that more hosts will facilitate greater attachment and lice reproduction. It further assumes that cleaning behaviour of wrasse is density-dependent with respect to parasite abundance. We have very little data to support or refute this assumption, but if our model is correct, areas where trout populations are struggling may benefit from having a thriving wild wrasse population to help as cleaners. Nevertheless, our model does not suggest that wild wrasse can save sea trout from lice infestations caused by fish farming.

The zero-sum outcome occurred faster (i.e. at a slower cleaning rate) when the wild sea trout were distributed further away from the farm. If wrasse were removed from a location where they were functioning as cleaner fish on wild trout without farms and placed in a net pen to clean salmon in a sea cage in an area without sea trout, the effect of removing wrasse from the wild would be -∞. This occurs because the wrasse has a beneficial effect on the infestation pressure on the wild sea trout in nature by removing lice, while it has no effect on the wild sea trout in the net pen because the net pen is too far away. When the model was parameterized with a simple Type-I FR, this effect was eliminated because the wrasse would remove the same proportion of lice independent of the lice numbers on the wild sea trout.

The effect of infestation pressure at the farm had a strong influence on the outcome of the game if wrasse in the wild always removed a constant number of sea lice, but was eliminated when a Type-I FR was applied. We have no empirical knowledge about the functional response of temperate wrasse in the wild. Cleaning rates in tanks and cages appear to be positively correlated with lice densities, and in tanks with very high lice densities, ballan wrasse ate upwards of 200 lice per day without evidence of satiation (i.e. a Type I functional response: Leclercq et al. 2014). In small sea cages, Deady et al. (1995) estimated between 6 and 41 lice were eaten per goldsinny wrasse per day, at starting lice levels of 2.5–4.6 per salmon, whereas Skiftesvik et al. (2013) estimated at least 23 lice eaten per ballan wrasse per day at infestation levels that resulted in nine lice per salmon attached in control cages. Despite little experimental evidence at commercial scale (Overton et al., 2020), slower feeding rates may be expected in commercial farms than in experimental settings (Barrett et al., 2020). In 120 m circumference cages, Gentry et al. (2020) found only 0.3-1.8 lice per corkwing wrasse gut at infestation levels between 0.5 and 1.3 mobile lice per salmon, corresponding to a daily feeding rate of approximately 0.6–3.6 mobile lice, assuming lice are detectable in the gut for 12 h (Le et al., 2019). Lice feeding rates by wrasse can be expected to differ in laboratory experiments compared to in real world applications for five reasons: (1) low encounter rates modulated by requirements that farms maintain low lice densities (<0.2–0.5 adult females per salmon; Leclercq et al. 2014); (2) larger spatial scale of sea cages promoting segregation of wrasse into deeper layers of farms thereby limiting encounter rates between wrasse and affected farmed salmon (discussed in Tully et al. 1996); (3) cool temperatures in farms that reduce wrasse feeding activity and increase wrasse mortality (Bjelland et al., 1996; Geitung et al., 2020; Yuen et al., 2019); (4) poor acclimation to the sea environment or commercial cleaning duties (Brooker et al., 2020); (5) death or disappearance of wrasse from sea cages (19-32% lost after 3 months: Stien et al., 2020).

Our model has several limitations that warn against over-interpreting the effects to make decisions about lice management strategies at farms. Importantly, this model does not account for effects of lice infestation pressure on wild Atlantic salmon, and the optimal settings for reduction of parasite loads on wild sea trout revealed by the simulation may not be beneficial for wild salmon. Wild wrasse are unlikely to do any significant cleaning of migrating post-smolt salmon that are in coastal zones and have limited overlap with wrasse. Our model also does not consider alternative scenarios in which wrasse are not used as cleaner fish. Alternative lice management tactics include chemical, mechanical, and thermal treatments of farmed fish to kill lice and limit reproduction and infestation pressure from farms (Overton et al., 2019). Alternative methods have welfare implications on farmed fish and chemical treatments can spillover to wild animals (e.g. Parsons et al. 2020). Cleaner fish are still viewed as an important component of an integrated lice management strategy on fish farms. Ballan wrasse are the only wrasse species being commercially reared, and while production is slowly increasing (681 000 sold in 2019), they were only a fraction of the wrasse stocked into farms in Norway in 2019 (Fisheries Directorate, 2020). Philis et al. (2021) suggested that wild captured wrasse have a lower environmental impact than farmed wrasse or lumpfish based on a life cycle analysis but noted that the environmental impacts of removing wrasse from the wild were unaccounted for and required research. Our results amplify this need for knowledge considering fishing and moving wild wrasse to net pens is supported by such bioeconomic perspectives. It will be challenging to compare the effects of wrasse fishing on ecosystems compared to alternatives such as chemical and physical treatments because our results do not suggest that simply leaving wrasse in the wild is sufficient to alleviate infestation pressure from fish farms.

5. Conclusions

Simulations and game theory are effective tools in ecology for studying challenging processes that are difficult to observe; indeed, models and simulations are very important tools for modelling salmon migrations and lice dynamics for aquaculture management in Norway (e.g. Kristoferssen et al. 2014). We optimized lice cleaning rates in the model rather than using empirical values and we acknowledge that our thesis and conclusions depend to the assumption that wild wrasse perform non-negligible cleaning services to wild sea trout. Our efforts will hopefully stimulate increased interest into the potential ecosystem effects of wrasse fisheries and support additional studies on the behaviour of putative cleaner fish in coastal areas and fjords of Norway, Scotland, Sweden, Canada, and other countries where sea lice impact wild salmonids. With millions of wrasse being fished each year, ecosystem impacts of this exploitation should be additionally scrutinized alongside the phenotypic and genotypic effects and life cycle considerations of moving wrasse from the wild into net pens. Finally, we reiterate that this model does not suggest that wild wrasse can save sea trout from lice infestations caused by fish farming but that there may be a heretofore unrecognized interaction that merits further investigation given the urgency of impacts caused by lice outbreaks from farms on wild salmonids.

Data accessibility

Code for the simulation will be available at GitHub.com

CRediT authorship contribution statement

Robert J. Lennox: Conceptualization, Methodology. **Luke T. Barrett:** Methodology, Writing – review & editing. **Cecilie I. Nilsen:** Methodology, Writing – review & editing, Visualization. **Saron Berhe:** Methodology, Writing – review & editing. **Bjørn T. Barlaup:** Conceptualization, Writing – review & editing. **Knut Wiik Vollset:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors wish to declare no interests that could be perceived as in conflict with the content of this manuscript.

Data Availability

No data was used for the research described in the article.

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