



Delayed maturity does not offset negative impact afflicted by ectoparasitism in salmon

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Abstract

The negative effects of parasitism on host population dynamics may be mediated by plastic compensatory life-history changes in hosts. Theory predicts that hosts should shift their life-history towards early reproduction in response to virulent pathogens to maximize reproduction before death. However, for sublethal infections that affect growth, hosts whose fecundity is correlated with body size are predicted to shift towards delayed reproduction associated with larger body size and higher fecundity. This has been observed in Atlantic salmon and parasitic sea lice, via mark-recapture studies that recover mature fish from paired groups of control and parasiticide-treated smolts. We investigated whether such louse-induced changes to age at maturity can offset some of the negative effect of mortality on population growth rate in salmon using a structured population matrix model. Model results show that delayed maturity can partially compensate for reduced survival. However, this only occurs when marine survival is moderate to poor and growth conditions at sea are good. Also, the impact of delayed maturity on population growth when parameterizing the model with empirical data is negligible compared with effects of direct mortality. Our model thus suggests that management that works on minimizing the effect of sea lice from fish farms on wild salmon should focus mainly on correctly quantifying the effect of parasite-induced mortality during the smolt stage if the goal is to maximize population growth rate.

Keywords Population matrix model · Parasite · Salmonids · Salmon lice

Introduction

Plasticity in life-history traits allows animals, such as salmon, to respond to a fluctuating environment (Caswell 1983; Hutchings and Jones 1998), including parasitism. For example, parasitism is associated with life-history changes such as smaller broods in red grouse (Redpath et al. 2006), reduced survival and reproductive success of African buffalo (Gorsich et al. 2015), and trade-offs between immunocompetence and brood size and tail length in birds (Norris and Evans 2000). Theory predicts that hosts should shift towards early reproduction in response to virulent pathogens to maximize reproduction before death (Chadwick and Little 2005; Leventhal et al. 2014). However, for sublethal

infections, the host response may instead shift to delayed reproduction that results in larger body size and higher fecundity (Stearns and Koella 1986).

Anadromous salmon return to spawn in their river of origin after spending one or more winters at sea (termed sea-winters, SW). Age at maturity is population dependent and under strong selective pressure in Atlantic salmon (*Salmon salar*) (Barson et al. 2015). Reduction in marine growth is generally associated with delayed age at maturity in salmon (Hutchings and Jones 1998). Delayed age at maturity has also been observed in Atlantic salmon in relation to parasitism by sea lice (*Lepophtheirus salmonis* and *Caligus elongatus*) via experimental studies that release tagged smolts in paired groups, one a control and the other receiving a treatment against marine ectoparasitic copepods (randomized control trials, RCTs) (Vollset et al. 2014). Fish impacted by these parasites (i.e. untreated individuals) are fewer (Gargan et al. 2012; Jackson et al. 2013; Krkosek et al. 2013; Skilbrei et al. 2013; Vollset et al. 2015) but also older, and as a consequence larger, and more fecund, when they return to the river to spawn. Fecundity in salmon is

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increasing non-linearly with size, meaning that as salmon grow a larger proportion of their body mass is devoted to egg production (Fleming 1996). Consequently, delayed maturation could in theory compensate for the decrease population growth inflicted by elevated mortality by increasing the proportion of older and more fecund females returning to the river to spawn. By this mechanism, flexible maturation schedules could compensate for mortality inflicted by the parasite. Alternatively, the effect of shifting maturation may be undermined by mortality during the extra year at sea.

Susdorf et al. (2018) parameterized a population matrix model to evaluate the population effect of reduced host growth through on the overall population growth rate due to sea lice. However, Susdorf et al. (2018) did not explore a relationship between reduction in growth and delayed maturity in their model. Motivated by the earlier findings that groups impacted by sea lice mature older and larger (Vollset et al. 2014), we sought to investigate whether this life history change could offset the negative impact of the parasite on the population growth rate. We developed and analysed a population matrix model of the combined effects of sea lice on direct mortality and life-history plasticity (i.e. delayed reproduction) on the population dynamics of Atlantic salmon. First, we quantify the magnitude of change in maturation needed to fully offset direct mortality from the parasite. Secondly, we parameterize the model with data extracted from randomized control trials of from the river Vosso, Norway. Our model indicates that while partial compensation by shifting age at maturation is possible, the data lie in a region of parameter space where parasitism results in a net reduction of the Atlantic salmon population growth rate and therefore recruitment.

Material and methods

We developed a population matrix model for the abundance of (female) Atlantic salmon that was structured by age and reproductive status and parameterized for the Vosso salmon population in Norway (60.64783° N, 6.11266° E). The model assumes no mate limitation (i.e. there is an excess of males) and does not include reproductively mature parr. Repeat spawning was assumed to be negligible; e.g. Jonsson, Hansen, and Jonsson (1991) report that repeat spawners varied from 2 to 13% of the female population in large rivers. We begin with a model that ignores density-dependent survival arising from competition to focus on the population growth rate at small population sizes that is relevant for persistence and recovery. The Vosso population is currently below historical abundances and has been below the carrying capacity of the river for most years in recent decades. To also consider density dependence that is thought to occur during the freshwater juvenile phase, we analysed a second

model with density-dependent juvenile survival to focus on equilibrium abundances. Our analyses of this model focus on the potential compensatory effects of life-history plasticity on population growth or abundance, as well as the sensitivity of those results in relation to uncertainty in the parameter estimates.

The population-projection matrix

The model consisted of 10 stages, four in freshwater (0 + parr, 1 + parr, 2 + parr, 3 + parr, 4 + parr) and 6 in marine waters (immature 1SW, immature 2SW, mature 1SW, mature 2SW and mature 3SW) (Fig. 1). We follow the standard nomenclature of salmon ecology where the “+” denotes the fish is between the given age and the next, and “SW” indicates “sea winter”, which is the number of years a fish has been at sea. Atlantic salmon represent a classic birth pulse population that spawns in autumn. The census time for our model is May to focus on the marine stage when immature salmon smolts migrate from freshwaters into marine environments and begin to encounter sea lice. Because census time is in May, we must take into consideration the mortality from May to time of spawning in November for adults returning. To correct for this, we added 3 months of marine mortality for 1SW (May–July) fish 1.5 months marine mortality for 2SW fish (May–mid June), with the rationale that the 3SW enter into the river on average around May–June, 2SW in July and 1SW in August and that the mortality in freshwater is negligible (the main mortality would be sports fishing, but fishing has been very limited during the years when the population level has been low).

The life-cycle graph of the model is in Fig. 1 and the corresponding transition matrix \mathbf{A} is given in Table 1.

In Fig. 1, Φ indicates the transitional value from one stage to the next. This value includes both survival and the proportion of individuals transitioning to a given stage. The parameter values and their calculations are listed in Table 2. In the following text, we briefly explain how we estimated the transitions among life stages. Details, calculations and exact values are also given in Tables 3, 4, 5 and 6. We also extract data for minimum and maximum values for each parameter, which later will be used in sensitivity analysis as explained in ‘Analysis’ (1).

Survival rates in freshwater

We have little data on survival rates from eggs to smolts and base our calculations mostly on the study by Symons (1979). Survival from egg to 0 + parr (Segg0) was given to be 0.13 ranging from a minimum of 0.09 to a maximum 0.2. Survival from 0 + parr to 1 + parr was given to be 0.41 (min 0.28, max 0.44). Furthermore, from Symons (1979), we use the annual survival from 1 + parr and older as the survival from 1 + parr to 2 + parr ($S_{12}=0.57$)

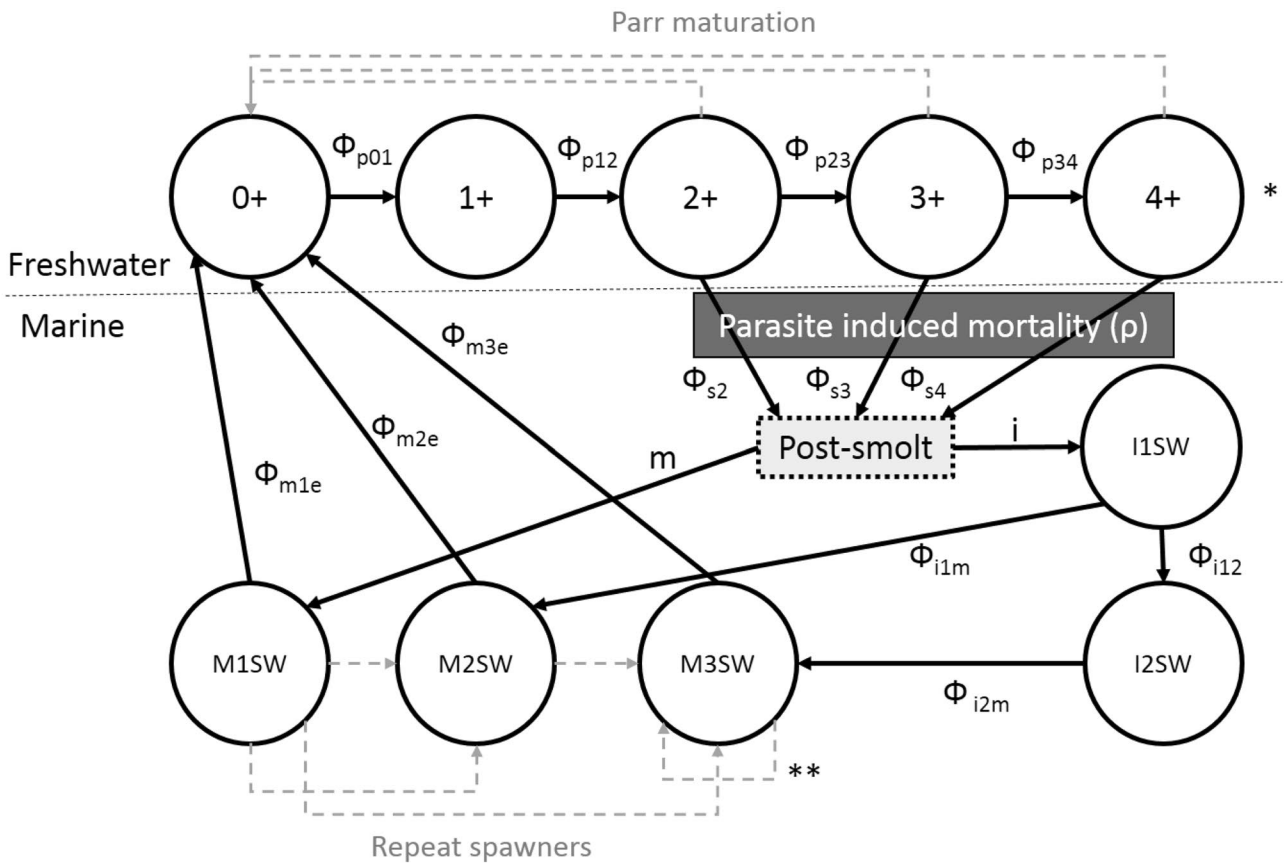


Fig. 1 Schematic figure of population matrix model. Circle denotes the age stages tracked in the model, while arrows indicate the yearly transitions. In freshwater, the different parr stages is indicated (0+ to 4+). In the marine waters, the different adult mature (M) and immature (I) stages are indicated for the ages 1 to 3. The grey lines indicate

part of the life cycle that is ignored for simplicity. Note that “post-smolt” is not an age stage but is in the transition between a parr and an adult stage. * There are potentially older parr stages than 4+. ** This loop is to illustrate that 3SW can in theory survive and return to spawn

and the juvenile to smolt survival as the survival from 2+parr to 3+parr and similarly 3+parr to smolt 4+parr ($S_{2+}=0.65$). In addition, we let the minimum and maximum survival estimates for the survival from 1+parr to 2+parr to vary from the minimum juvenile to smolt survival (0.35) to the estimated highest survival during a year (0.65) that were observed in the data.

Probability of smoltifying

The proportion of the surviving individuals staying in the river or leaving the river as smolts was based on the age distribution of smolts caught in either the rotary screw in the river outlet of the Vosso river or in trap nets in the estuary (60.64020° N, 5.95096° E) (Barlaup 2013). Data were collected in the

Table 1 Transition matrix. Φ symbolizes the transition values indicated in Fig. 1. See table for specific transition values. Stage labels are defined in the text. ρ is parasite-induced mortality

	0+	1+	2+	3+	4+	I1SW	I2SW	M1SW	M2SW	M3SW
0+								Φ_{m1e}	Φ_{m2e}	Φ_{m2e}
1+	Φ_{p01}									
2+		Φ_{p12}								
3+			Φ_{p23}							
4+				Φ_{p34}						
I1SW			$\Phi_{s2i} \times \rho$	$\Phi_{s3i} \times \rho$	$\Phi_{s3i} \times \rho$					
I2SW						Φ_{i12}				
M1SW			$\Phi_{s2m} \times \rho$	$\Phi_{s3m} \times \rho$	$\Phi_{s4m} \times \rho$					
M2SW						Φ_{i1m}				
M3SW							Φ_{i2m}			

Table 2 Calculations of link values as noted in Table 1. Calculations are based on symbols as explained in Table 4. Between indicates between which life stage the link values correspond to, where any number with an associated “+” indicates a parr life stage, “I” indicates immature adults, “M” indicates mature adults, “SW” with associated number (for example 2SW) indicates number of winters at sea

Link	Calculations	Between
Φ_{p01}	S01	0+ to 1+
Φ_{p12}	S12	1+ to 2+
Φ_{p23}	$S23 \times (1 - Ps2)$	2+ to 3+
Φ_{p34}	$S34 \times (1 - Ps3)$	3+ to 4+
Φ_{s2i}	$SS \times Ps2 \times (1 - P1SW)$	2+ to I1SW
Φ_{s3i}	$SS \times Ps3 \times (1 - P1SW)$	3+ to I1SW
Φ_{s4i}	$SS \times (1 - P1SW)$	4+ to I1SW
Φ_{s2m}	$SS \times Ps2 \times P1SW$	2+ to M1SW
Φ_{s3m}	$SS \times Ps3 \times P1SW$	3+ to M1SW
Φ_{s4m}	$SS \times P1SW$	4+ to M1SW
Φ_{i12}	$Ssea \times P3SW$	I1SW to I2SW
Φ_{i1m}	$Ssea \times (1 - P3SW)$	I1SW to M2SW
Φ_{i2m}	$Ssea^{(1/3)}$	I2SW to M3SW
Φ_{m1e}	$S1SW \times Segg0 \times F1 \times \varphi$	M1SW to 0+
Φ_{m2e}	$S2SW \times Segg0 \times F2 \times \varphi$	M2SW to 0+
Φ_{m3e}	$Segg0 \times F3 \times \varphi$	M3SW to 0+

years 2003–2012. The proportion of fish caught leaving the river as 2-year-olds ($Pe2$) divided by the proportion leaving the river as 3-year-old or older ($Pe3^+$) is equal to the proportion smoltifying as 2-year-olds divided by the proportion smoltifying as 3- or 4-year-olds, when taking account of the mortality. This can be summed up in the following equation:

$$\frac{Ps2}{[Ps3 \times S23 \times (1 - Ps2)] + [S23 \times S34 \times (1 - Ps2) \times (1 - Ps3)]} = \frac{Pe2}{Pe3^+} \tag{1}$$

Table 3 Calculations of other parameters than noted in Table 2. Symbols are given in the main text

Symbol	Description	Calculation
Ps2	Proportion 2+ smoltifying as 2-year-old	$\frac{Ps2}{[Ps3 \times S23 \times (1 - Ps2)] + [S23 \times S34 \times (1 - Ps2) \times (1 - Ps3)]} = \frac{Pe2}{Pe3^+}$
Ps3	Proportion 3+ smoltifying as 3-year-old	$\frac{Ps3}{S34(1 - Ps3)} = \frac{Pe3}{Pe4}$
P1SW	Proportion maturing as 1SW	$\frac{1}{1 + e^{4.5 \times P3SW + 1.87}}$
P2SWII	Proportion of immature 1SW maturing as 2SW	$1 - P3SW$
F1	Fecundity 1SW	$\frac{0.4467 \times cm^{2.208}}{2}$
F2	Fecundity 2SW	$\frac{0.4467 \times (cm + gsea12)^{2.208}}{2}$
F3	Fecundity 3SW	$\frac{0.4467 \times (cm + gsea23)^{2.208}}{2}$
φ	Density-dependent mortality	$\varphi = 1 - \frac{1}{1 + \frac{c \times gsn}{c}}$

where S23 is the yearly survival the second year in the river (given above as 0.57), S34 is the yearly survival the second year in the river (given above as 0.65), Ps3 is the proportion of fish leaving the river after three winters while $Pe2$ and $Pe3^+$ are the proportion of smolts leaving the river as 2-year-olds and 3-year-olds or older, respectively. This assumes a constant freshwater population structure. By solving this equation, it is possible to calculate Ps2 used in the matrix model.

To be able to calculate the Ps2, we need an estimate of the proportion of smolts leaving the river after three winters ($Ps3$). This was found by solving the following equation:

$$\frac{Ps3}{S34(1 - Ps3)} = \frac{Pe3}{Pe4^+} \tag{2}$$

while $Pe3$ and $Pe4^+$ are the proportion of smolts leaving the river as 3-year-olds and 4-year-olds or older. Note that all fish surviving more than 3 years in the river was assumed to smoltify the next season (i.e. Ps4 is set to 1 and not written explicitly in the equation). Minimum and maximum values of Ps2 and Ps3 were found by taking the minimum year of the data of proportion of fish leaving the rivers while keeping the yearly survival average.

Smolt and marine survival

We calculated the monthly marine smolt survival (mMS) by assuming a constant monthly survival rate for a period of 6 months (mSS) and assuming that on average the salmon stayed 25 months at sea (i.e. going to sea in mid-May and returning to the river in mid-June two years later), and portioning the survival from smolt to adults return (SR) into their respective months, so that:

$$SR = mSS^6 \times mMS^{21} \tag{3}$$

Table 4 Values extracted from literature. “Avg” signifies average, “Min” minimum values, “Max” maximum values

Symbol	Description	Avg	Min	Max	Reference
ρ	Parasite-induced mortality	0.18	0	0.5	See paragraph
Segg0	Survival from egg to 0+	0.13	0.09	0.2	Symons (1979)
S01	Survival from 0+ to 1+	0.41	0.28	0.44	Symons (1979)
S12	Survival from 1+ to 2+	0.57	0.35	0.65	Symons (1979)
S2+	Survival from 2+ to 3+	0.65	0.6*	0.7*	Symons (1979)
mSS	Monthly smolt survival	0.68	NA	NA	See text
mMS	Monthly marine survival	0.97	0.98	0.96	ICES
SR	Smolt to adult survival	0.03	0.01	0.01	Barlaup (2013)
Pe2	Proportion of smolt exiting as 2-year-old	0.37	0.03	0.61	Barlaup (2013)
Pe3+	Proportion of smolt exiting as 3-year-old	0.63	0.39	0.97	Barlaup (2013)
Pe3l3+	Proportion of smolt exiting as 3-year-old given that they have not smoltified as 2-year-old	0.89	0.77	0.98	Barlaup (2013)
Pe4l3+	Proportion of smolt exiting as 4-year-old given that they have not smoltified as 2-year-old	0.11	0.02	0.23	Barlaup (2013)
P3SWII	Proportion of immature 2SW maturing as 3SW	0.36	0.17	0.66	Barlaup (2013)
Cm	Length at maturation for 1SW	60	55	64	Barlaup (2013)
gsea12	Growth at at sea from 1 to 2SW	15			Barlaup (2013)
gsea23	Growth at at sea from 2 to 3SW	15			Barlaup (2013)
Teggs	Total eggs deposited a given year	NA	NA	NA	
C	Carrying capacity (according to eggs deposited—calculated as 2 eggs per m ² with a total area of 1,530,110 m ²)	3,060,220	NA	NA	Hindar et al. (2007)

were mSS is monthly smolt survival, mMS is monthly adult survival, and SR is smolt-to-adult survival. SR was based on data from the Vosso release group experiments recaptured in the trap nets in the fjord and estuary of the Vosso (Barlaup 2013). To calculate SR, we divided the percent of fish recaptured as adults in the trap nets by the capture efficiency of the trap nets that was estimated at 15% (range 10–20%) based on mark-recapture studies (B. Barlaup unpublished data). The average smolt to adult survival (SR) was therefore estimated to be ~3% with a minimum of 0.1% to a maximum of 10%. According to the International Council of Exploration of the Seas (ICES), a rough estimate of monthly marine adult mortality of Atlantic salmon in the North Atlantic is approximately 0.03 and the monthly marine survival

(mMS) was therefore set to 0.97. As an example, solving equation [3] for mSS with an SR of 0.03 (i.e. 3%) would be $(0.03/0.97^{21})^{1/6} = 0.62$. Consequently, survival from parr to the adult through the smolt stage (SS) would be 6 months of smolt survival and 6 months of adult survival (i.e. $mSS^6 \times mMS^6 = 0.047$). The marine survival the second year at sea (Ssea) is $0.97^{12} = 0.69$. We also argue that survival is size dependent (Peterson and Wroblewski 1984) and that marine survival the following year at sea is higher because of size-dependent survival and therefore survival the third year was set to $Ssea^{1/3}$, which is equivalent to that survival increase from 0.69 to 0.88 during the third year at sea. In the above scenario therefore, survival would go from 0.047 the first year at sea, 0.69 the second year at sea and 0.88 the third year at sea.

Table 5 Stage durations of survival parameter, where symbols are abbreviations used in the model and throughout the manuscript, while description and calculation are self-explanatory, and duration indicates stage duration in months

Symbol	Description	Calculation	Duration (months)
Segg0	Survival egg to 0+	Segg0	6
S01	Survival from 0+ to 1+	S01	12
S12	Survival from 1+ to 2+	S12	12
S23	Survival from 2+ to 3+	S2+	12
S34	Survival from 3+ to 4+	S2+	12
SS	Survival from parr to adult through post-smolt stage	$mSS^6 \times mMS^6$	12
Ssea	Survival 1 year at sea	mMS^{12}	12
S1SW	Additional 3 months mortality in sea for 1 SW	mMS^3	3
S2SW	Additional 1.5 months mortality in sea for 2 SW	$mMS^{1.5}$	1.5

Table 6 Sensitivity analysis changing the values to minimum and maximum. Parameter are described in Table 2. “Min” signifies minimum values, while “Max” signifies maximum values. See text for description of λ , and equilibrium abundance. See Table 4 for a description of parameters

Parameter	Baseline value	Min	Max	λ		Equilibrium abundance	
				Density-independent model		Density-dependent model	
				Min	Max	Min	Max
Cm	60	55	64	1.18	1.23	1795	2017
gsea12	20	10	25	1.18	1.26	1800	2122
gsea23	20	10	25	1.20	1.23	1883	2014
Segg0	0.13	0.09	0.2	1.14	1.30	1067	3434
S01	0.41	0.28	0.44	1.13	1.22	1041	2133
S12	0.57	0.35	0.65	1.11	1.23	848	2321
S23	0.65	0.6	0.7	1.20	1.22	1785	2071
S34	0.65	0.6	0.7	1.21	1.21	1912	1944
Pe3I3+	0.89	0.77	0.98	1.20	1.17	1916	1594
P4I3+	0.11	0.02	0.23	1.21	1.20	2023	1879
mMS	0.97	0.99	0.95	1.20	1.21	1819	2057
SR	0.03	0.01	0.1	0.93	1.35	0	4726
P3SW	0.36	0	0.72	1.20	1.22	1977	1905
ρ	0.18	0	0.5	1.25	1.12	2627	879

Probability of maturing

The probability of maturing was calculated in a similar manner as the probability of smoltifying. Data on the proportion of salmon maturing as 1SW fish was based on age distributions from Vosso salmon from Vollset et al. (2014)

$$\frac{P1SW}{Ssea(1 - P1SW)(P2SW|I + P3SW|I \times Ssea^{1/3})} = \frac{PR1}{PR2^+} \quad (4)$$

where P1SW is probability of salmon maturing after 1 year at sea, P2SWII and P3SWII is probability of maturing after 2 year given that it has not matured after 1 year at sea (denoted by “II”), Ssea is the yearly survival at sea (explained above), while PR1 and PR2⁺ is the proportion of adults returning to the river as grilse (1 year old—1SW) and multiple sea winter (more than 2 years at sea—MSW). P2SWII was calculated following the same logic, while P3SWII = 1 – P2SWII. Since we are tracking the population of females, the data used to calculate proportion of 1SW, 2SW and 3SW had to be corrected for sex bias. We used the following sex bias estimates: 10% female 1SW, 70% female 2SW and 55% female 3SW (Forseth and Thorstad 2016). This implies that only 10% of the fish that return to mature as 1SW are female, while 70% of fish returning as 2SW are female.

In the model, we are interested in how the overall age distribution of spawners would affect the population growth rate (λ). In most multiple sea winter populations, the proportion of salmon maturing as 1SW and 3SW in a given year is negatively correlated because they are controlled by similar processes. We therefore chose to describe the probability of maturing as

1SW (P1SW) as a function of probability of fish P3SWII (i.e. probability of maturing after more than two winter given that you have not matured after 1SW. This allows us to alter the whole age distribution by changing one parameter (P3SWII), not only the relative proportion between two maturation ages. The proportion maturing as 1SW was fitted as logistic function of maturing to P3SWII using data from the Vosso release group studies (Barlaup 2013). The fitted logistic model was as follows

$$P1SW = \frac{1}{1 + e^{(4.5 \times P3SWII + 1.87)}} \quad (5)$$

where the proportion of immature 1SW maturing as 2SW (P2SWII) was 1 – P3SWII. The plot of the fitted line is given in the supplementary material Fig. A1.

Fecundity and egg survival

Fecundity was estimated using the body length-egg abundance relationship from Fleming (1996)

$$F = 0.4667 \times SL^{2.208} \quad (6)$$

where SL is the standard length of the spawning salmon. Length at maturation at 1SW was the ~60-cm standard length based on data of the Vosso (Barlaup 2013). Length as 2SW was calculated as the length of 1SW plus 1 year’s growth at sea (gsea12) whereas length as 3SW was calculated as length of 1SW plus the growth after 2 years at sea (gsea12 + gsea23). Growth at sea was set to 20 cm the second year at sea (gsea12) and 20 cm the third year at sea (gsea23), which is the approximate difference in length

between the age classes returning to the Vosso River caught in surveillance fishing with a trap net in the estuary during the period 2001–2012 (Barlaup 2013).

Parasite-induced mortality (ρ)

Parasite-induced mortality (ρ) was parameterized as an attributable fraction, i.e. a value that defines what proportion of the fish dies due to the parasite. ρ affects the survival of salmon during the first year at sea and was allowed to range from 0 to 0.5 (i.e. 0 to 50% reduced survival) based on the following reasoning. Because there is no compensatory mechanism for survival involved in our model, this value is equivalent a percent remaining of recruitment equal to $(1-\rho)*100$. In the study by Vollset et al. (2015), the estimated lost recruitment due to sea lice for salmon from Norway was calculated to be on average 11.1% with a confidence interval ranging from 4.4 to 17.9% and substantial variation among trials. Vollset et al. (2014) estimated the lost recruitment to be 31.9% for the Vosso salmon, while Krkosek et al. (2013) estimated it for salmon from Norway, Scotland and Ireland to be on average 39% (CI 18–55%). Other studies using correlative methods have estimated the lost recruitment as 50% in Ireland (Shephard and Gargan 2017). Consequently, in the model ρ ranging from 0.0 to 0.5 captures the range of estimates above.

Effect of parasites on growth

Sublethal effects of sea lice likely impair growth, which may affect subsequent body size, fecundity and the optimal age-at-maturity. The impacts of sea lice on growth and mortality are likely to be temporally correlated (i.e. years with high impact on survival will also be years with high impact on growth). The meta-analysis of Vollset et al. (2015) estimated a ρ of 0.114 and a reduction in body size of 123 g for 1SW salmon. To model this, we reduce the length at 1SW linearly up to 10% at $\rho=0.5$. The equation we use is

$$SL_{\text{lice}} = SL \times (1 + (\rho) \times -0.2) \quad (7)$$

where SL_{lice} and SL is the standard length of 1SW affected and unaffected by sea lice, respectively, while ρ is parasite-induced mortality. A 10% reduction in SL (given a ρ of 0.5) would correspond to a decrease of ~700 g of 3 kg 1SW fish. For a ρ with a value of 0.1–0.2 (which is more commonly estimated in release group studies), our equation would correspond to a reduction of ~120–250 g, which is within the range of what was observed in Vollset et al. (2015).

Density-dependent mortality

For the density-dependent model, it is understood that density-dependent mortality mainly occurs during the egg to parr

stage when juveniles compete for territories and food (Einum and Nislow 2005). According to Hindar et al. (2007), the spawning target of the Vosso river is 2 eggs per square metre. The area of the river is approximately 1,530,110 m². This was used to calculate the carrying capacity ($C=2 \times 1,530,110$) of the river, and the density-dependent mortality was calculated according to a Beverton-Holt equation as

$$\phi = 1 - \frac{1}{1 + \frac{T_{\text{eggs}}}{C}} \quad (8)$$

where T_{eggs} is the total eggs spawned in the river that year. This assumes that C eggs laid result in $C/2$ parr, and that at most C parr can survive from the egg stages.

Visualization of the Eqs. 6–9 is plotted in the supplementary.

Analysis

Elasticity and sensitivity analysis

We first used a standard elasticity analysis to explore how the population growth rate of Atlantic salmon responds to small changes in the parameters of the model. The population growth rate λ was numerically calculated as the dominant eigenvalue of the density-independent population projection matrix. The sensitivity and elasticity were calculated using the popbio library in R (Stubben and Milligan 2007), which is based on the methods described in (Caswell 2001), and is calculated as follows

$$e_{ij} = s_{ij} \times \left(\frac{\partial \lambda}{\partial a_{ij}} \right) \quad (9)$$

where e_{ij} and s_{ij} are the elasticity and sensitivity of the object and λ is the population growth. Sensitivity was calculated as

$$s_{ij} = \frac{a_{ij}}{\lambda} \quad (10)$$

The elasticity of the density dependent model was calculated as the relative change in equilibrium abundance defined as the abundance returning spawners of population after 100 years. Note that we are working with a non-zero equilibrium for the density dependent model. Finally, we explored of uncertainty in the parameter values by estimating λ and equilibrium abundance when changing relevant parameters from its minimum to maximum.

Can life history plasticity compensate for parasite-induced mortality?

We quantified how parasite-induced delayed maturity may compensate for the effects of parasite induced mortality (ρ) on the population growth. Delayed maturity of fish can result in older, larger and more fecund recruits, although there may be fewer of them, which may offset or cancel out the direct effects of parasite-induced mortality on population growth.

To explore this, we numerically solved for the maturation parameter (P3SWII) that balanced the parasite-induced effect on survival, that is

$$\text{Minimize}|\lambda(A) - \lambda(B\rho)| \quad (11)$$

where A is the matrix without parasite induced mortality (ρ) and B ρ is the matrix with a given parasite-induced mortality and likelihood of maturation at age 3SW (P3SWII). Our aim was to explore the parameter space in the model where a shift in age at maturity fully compensates for the parasite-induced mortality (ρ). This was explored and plotted for a range of marine growth (gsea12), parasite induced mortalities (ρ) and marine survival (SR) values.

Effects of sea lice on the Vosso salmon population including growth and maturation effects

Finally, we parameterized the model according to the RCT studies from the river Vosso presented in Vollset et al. (2015) for each release year, and compared how parasite-induced mortality alone and with impacts on growth and age at maturity would have affected the population growth rate. In the study by Vollset et al. (2015), data were only available from 2001 to 2011. We have updated the dataset until 2014. In addition, because in some release groups length and proportion of different age groups were scarce, we averaged the data across years. In some years, length data within each age category were missing, and needed to be imputed using average values from the remaining dataset. The data are listed in Table 7.

Results

Elasticity and sensitivity analysis

Population and transient dynamics of both models are illustrated in Fig. 2. There are clear cyclic transient patterns in the model with this parameterization because the recruitment from the adult initiation populations propagates through the model. These oscillations are to be expected, as the subdominant eigenvalues of the transition matrix were $0.54 + 8.93i$ and $-0.36 + 0.8i$ (Caswell 2001).

The elasticity of the equilibrium abundance in the density-dependent model was very similar to the elasticity

of the growth rate in the density-independent model. We therefore only present the elasticity analysis of the density independent model (Fig. 3). The population growth rate had the highest elasticity for transitions between the early life stages (p0 + to p1 + and p1 + to p2 +, both 0.17). The population growth rate also had high elasticity to changes in the transition values from parr to adult, which is the stage transition that sea lice affect in the model. Finally, the elasticity analysis shows that the growth rate changed more when transitions to and from the 2SW stage was altered relative to the other sea ages. This is because the standard model is parameterized with the highest proportion 2SW salmon. The stable stage distribution associated with the density independent model consists of 5% 1-SW 69% 2-SW and 27% 3-SW. The observed distribution in data from Vosso in the years 2001–2012 was 4%, 70% and 26%, based on averaged annual proportion in surveillance fishing.

To explore the effects of uncertainty in the parameter values, the effects of changing each parameter from its minimum to maximum value are presented in Table 6. Similar to the elasticity analysis, survival parameters during early life stages were important parameters both for the density-independent and density-dependent model. For example, equilibrium abundance varied from 1086 to over 3000 when changing the egg survival from minimum to maximum. Overall, model results varied significantly with changes in marine survival (SR) and parasite-induced mortality (ρ) (e.g. equilibrium abundance varied from 0 to over 4000 for SR and from 879 to over 2627 for ρ). In contrast, age at maturity (P3SW) was less important only varying the equilibrium abundance between 1905 and 1977.

The population growth rate decreased with parasite-induced mortality and increased with the proportion of fish maturing older than 2SW, and with the growth at sea (Fig. 4). The effect of maturing was less pronounced when lice affected the growth at sea (i.e. size at maturation was negatively correlated to parasite-induced mortality). This can be observed by comparing the slope of the contour lines in the two set of plots in Fig. 4. Although the outcomes of the density independent (Fig. 4a and b) and the density-dependent model (Fig. 4c and d) are slightly different (population growth λ versus equilibrium abundance), the general patterns in the two models were similar.

Can shifting age at maturity offset the negative effect of parasite-induced mortality on population growth?

The change in proportion of the female population that needs to mature as 3SW to offset the negative effect of parasite-induced mortality on population growth rate depends on

Table 7 Data extracted from release group studies in the Vosso project used for calculation of Fig. 6. “Year” is release year, “N” is total number of adulted recaptured “N released” is total number of smolt released, “Survival” is proportion of smolts recaptured as adults, Length is total length in cm, while whether it is untreated or treated is indicated with either “control” or “treated”. Parameter names are abbreviations corresponding to the ones explained in Table 2. Other text is self-explanatory

Year	N	N released	Survival (control)	Length ISW (control)	Growth 1st year at sea (control)	Growth 2nd year at sea (control)	Proportion matured as 3SW (control)	Proportion matured as 1SW (control)	Survival (treated)	Length ISW (treated)	Growth 1st year at sea (treated)	Growth 2nd year at sea (treated)	Proportion matured as 3SW (treated)	Proportion matured as 1SW (treated)
Parameter names			SR	CM	gsea12	gsea23	P3SW	P1SW	SR	CM	gsea12	gsea23	P3SW	P1SW
2001	8	5580	0.0073	61.5	24.5	6.5	0.59	0.134	0.0117	60	24.5	6.5	0.667	0.0798
2002	28	9400	0.017	62.6	19.4	17	0.72	0.201	0.0227	61.6	19.4	17	0.654	0.124
2003	72	8125	0.0211	62.2	21.5	11.8	0.654	0.0922	0.0977	62.7	21.5	11.8	0.614	0.106
2005	53	21,937	0.014	58.4	23	12.8	0.631	0.00323	0.0164	58.9	23	12.8	0.625	0.00456
2006	8	13,000	0.00308	59.6	17.5	16.4	0.86	0.0267	0.00513	60	17.5	16.4	0.795	0.0335
2007	104	29,530	0.0218	59	11.7	20.5	0.788	0.0218	0.0248	60.8	11.7	20.5	0.638	0.0495
2008	183	30,145	0.0363	58	13.9	16.7	0.744	0.0115	0.0448	60.5	13.9	16.7	0.767	0.0274
2009	739	25,850	0.203	59.4	20	15.6	0.671	0.00815	0.179	59.7	20	15.6	0.662	0.0106
2010	379	28,000	0.0843	60.5	19.8	12	0.635	0.0503	0.0962	61.1	19.8	12	0.669	0.098
2011	487	44,400	0.0703	62.7	18	15.6	0.637	0.065	0.0792	62.8	18	15.6	0.65	0.107
2012	559	44,000	0.0757	55.5	17.7	18	0.651	0.0441	0.0916	56.9	17.7	18	0.649	0.0683
2013	102	20,000	0.0347	58.7	17.4	15.5	0.648	0.0495	0.0333	58.6	17.4	15.5	0.637	0.0487
2014	1087	38,400	0.188	59.7	21.9	14	0.646	0.108	0.19	59.7	21.9	14	0.65	0.107
Total	3809	318,367	0.0598	59.8	18.9	14.8	0.683	0.0627	0.0686	60.2	18.9	14.8	0.667	0.0665

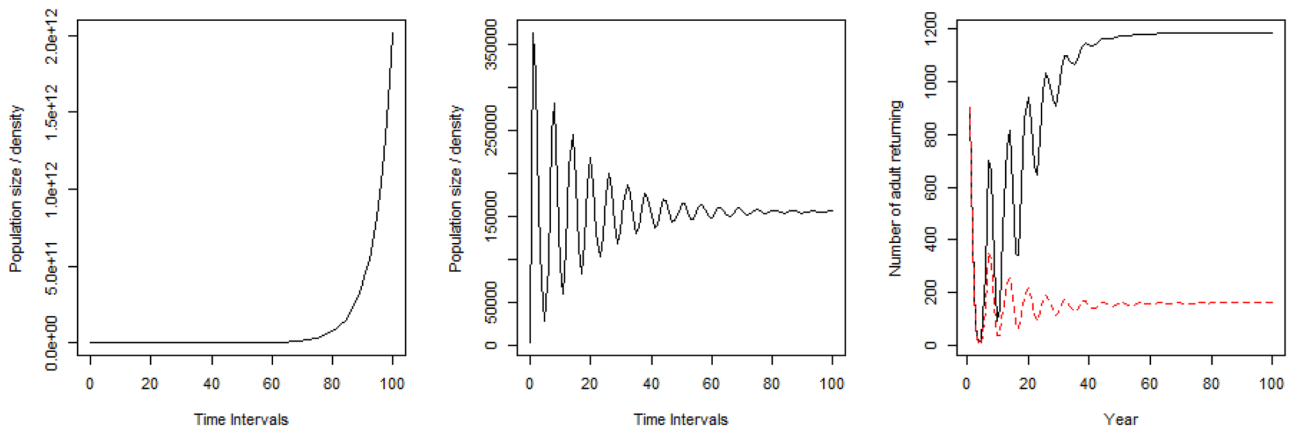


Fig. 2 Dynamics of population matrix model. Left figure plots total population size (including all life stages) in a density-independent model. Mid figure explores transient dynamics of the density-independent model by plotting the total population size divided by divid-

ing all elements by the dominant eigenvector. The right figure illustrates the dynamics of the number of adult returns in a population with (dashed line) and without 50% parasite-induced mortality. The starting population has 300 individuals in each life stage

marine survival and growth at sea. Figure 5 illustrates the proportion of 3SW that is needed to offset the reduction in population growth rate (λ) due to parasite-induced mortality by shifting the age distribution. For this example, the model is parameterized with four different marine survival conditions (SR=0.03, 0.05, 0.1 and 0.15, Fig. 5a-d). To explore how marine growth may impact the effect of maturation scheduling, the model is also plotted with conditions where salmon grow 5 to 30 cm extra each year (gsea12 and gsea23). A3-dimensional plot of the Fig. 5b is given in the appendix to aid interpretation (Fig. A3). The model functions so that it shifts age at

maturation to minimize the difference in growth rate between a theoretical population that *is not* affected by the parasite and a population that *is* affected by the parasite. Thus, if the model has a scope to shift the age at maturation, the affected population growth rate (λ) would be equal between the affected and unaffected population. The results indicate that when growth is high and marine survival is low (Fig. 5a), delaying maturation will compensate for the small reductions in population growth due to parasitism. This means that by increasing age at maturation salmon can in theory increase λ until all fish mature as 3SW (although this is not likely for a salmon population). On

Fig. 3 Elasticity matrix for the model with standard parameters in the density-independent model. P stands for parr stages, I immature, M mature and SW sea winter. A examples p0+ is parr stages between 0 and 1 year, I1SW is immature 1 sea winter salmon and M3SW is mature 3 sea winter salmon

	p0+	p1+	p2+	p3+	p4	I1SW	I2SW	M1SW	M2SW	M3SW
p0+								0.0033	0.0896	0.073
p1+	0.1658									
p2+		0.1658								
p3+			0.1099							
p4				0.012						
I1SW			0.0537	0.0939	0.0115					
I2SW						0.0558				
M1SW			0.0022	0.0039	5e-04					
M2SW						0.1034				
M3SW							0.0558			

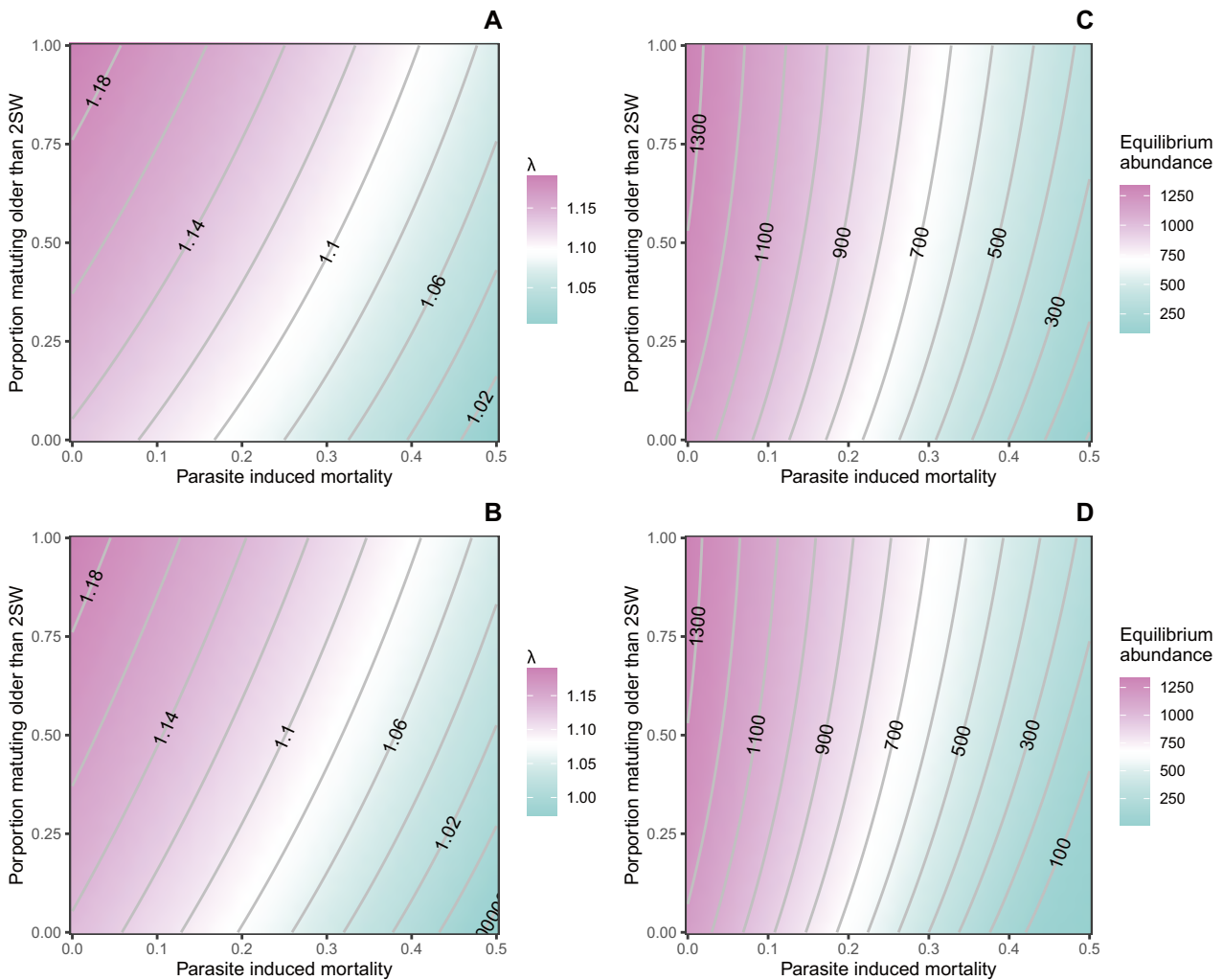


Fig. 4 Contour plots of effects of proportion maturing older than 2SW (P3SWII) versus parasite induced mortality on the population growth (λ) in a density-independent model (left panel) and the equilibrium abundance of the density-dependent model (right panel). The upper panel is a model without impacts of parasites on growth, while the lower panels includes a reduced effect of parasite on growth

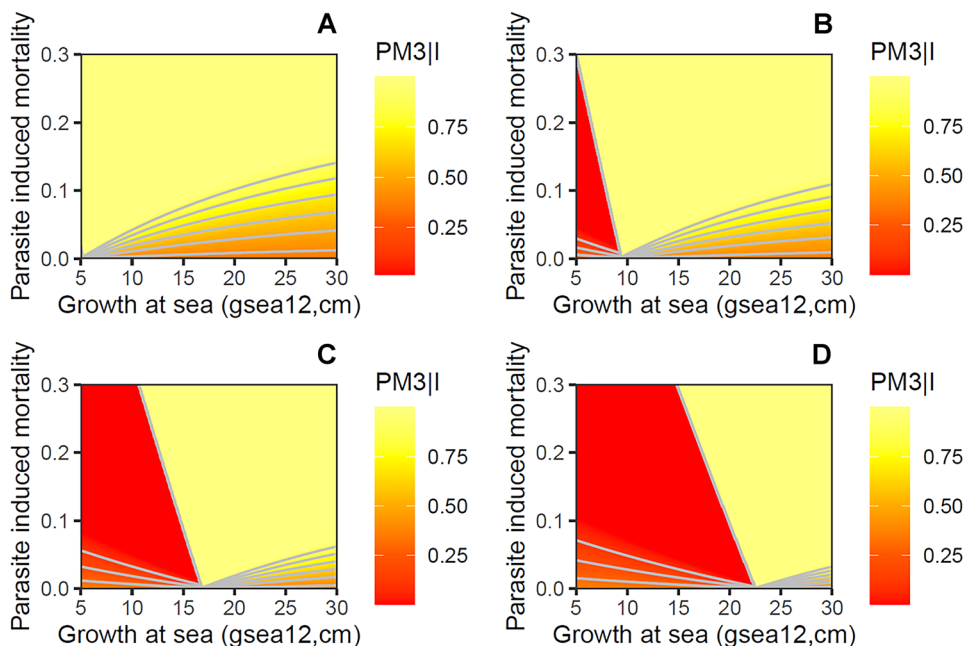
the other hand, if survival is high (Fig. 5d, 0.15) and growth is slow, the best strategy is to decrease age at maturation. The ability to increase λ by shifting age at maturation is, however, relatively small during periods of high marine survival (i.e. SR is high). The effect of shifting age at maturation during periods of low marine survival is larger. However, during periods of low marine survival and high parasite-induced mortality, the population growth rate would be so low that the population would not be able to persist ($\lambda < 1$). Figure 5 shows a striking feature where during high parasite-induced mortality there is a clear shift where the entire population either matures as 1SW or 3SW. This results from that along this feature population growth is higher when fish mature earlier or later depending on the marine growth, and that the model attempts to minimize

the large effect of the parasite-induced mortality by changing maturation as much as possible.

Effects of sea lice on the Vosso salmon population

In Table 7, we present the parameters which have been extracted from the Vosso RCT trials from Vollset et al. (2014). When parameterizing the model to the yearly data from the RCT studies in the Vosso River, the population growth rate in the louse-exposed groups was on average 1.29 compared with 1.33 in the treated group, but the difference varied with time (Fig. 6, right panel). Similarly, the average equilibrium abundance was 3086 compared with 3852 (solid versus open circles in Fig. 6, right

Fig. 5 Theoretical proportion of 3 SW in a population that minimize the difference in population growth rate (λ) between a population affected by parasites versus a population unaffected by the parasites. Solid line and colours indicate values of P3SWII. Dashed line is the resulting population growth rate (λ)

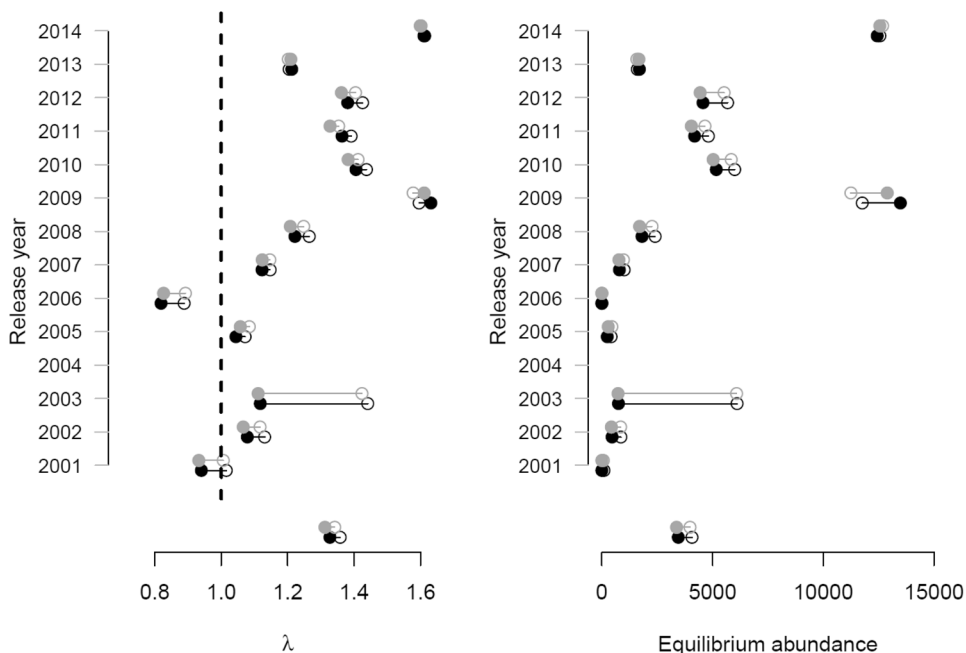


panel). The additional effect of both size and maturation was small compared with the effect of sea lice on marine survival, indicating that the effect of mortality is stronger on population persistence than the effect of changes in size and age at maturation. This can be observed in Fig. 6, by comparing the population growth rate and equilibrium abundance in the estimates parameterized with observed size and age at returns (grey) versus estimates with the baseline parameterization (black).

Discussion

Indirect impacts of parasites on host population dynamics are well studied in various host-parasite complexes (Albon et al. 2002; Anderson and May 1978; Tompkins and Begon 1999; Tompkins et al. 2015). These impacts may be more costly than direct mortality when they alter the potential of the host population to exploit resources, evade predators or reproduce (Miller et al. 2014; Tompkins et al. 2015).

Fig. 6 Estimated population growth rate (λ) and equilibrium abundance from models parameterized with data from randomized control trials from the river Vosso as explained in Vollset et al. (2015). Open circles are groups of fish given treatment against salmon lice while solid dots are groups not given treatment. Comparisons between grey and black symbols are the same groups either parameterized with size and age distributions (P3SWII) for the given release group (black) or parameterized with the baseline values (1SW = 60 cm, 2SW = 75 cm 3SW = 90 cm, P3SWII = 0.36, grey). The lower points are estimates based on averaged values



However, a shift in age at maturity could be a plastic compensatory demographic response to parasitism in instances where parasitism has relatively high effects on growth and but low acute mortality (Michalakis and Hochberg 1994). In this study, we analysed the relative effects of parasite-induced mortality versus parasite-induced delayed reproduction on the overall population growth and equilibrium abundance of Atlantic salmon. We found that delayed maturation can increase population growth rate and thereby offset some of the negative impact of parasite induced mortality under some conditions. In our model, this occurred during periods of low marine survival and simultaneously good growth conditions at sea. However, when survival at sea is high and growth rate is relatively poor, delaying maturation reduces overall population growth rate, and exacerbates the effect of the parasite.

When salmon grows fast at sea, it is preferable to remain longer at sea because time spent feeding will increase offspring yield. Less intuitive, perhaps, is that the strategy to mature later is better when salmon are less likely to survive at sea. When overall marine survival is poor, staying longer at sea is better because fish at sea have already passed the bottleneck of high smolt mortality. Higher survival in later stages of marine life will then yield a relatively better strategy than returning early. In general, results from empirical studies on the impact of parasites on age at maturation in salmon suggest that salmon always mature later when they are impacted by sea lice (Vollset et al. 2014). Our model agrees with these observations in the parameter space of intermediate marine survival. However, the effect of changing age at maturity according to the observed data from Vollset et al. (2014) on population growth rate is small compared with the overall effect of varying marine survival and varying parasite induced mortality.

The effect of increasing age at maturation to compensate for parasite-induced mortality was weaker if there was a negative correlation between parasite-induced mortality and growth at sea (models comparison in Fig. 4). This makes intuitive sense because increasing age at maturity increases population growth by increasing the total biomass returning to spawn. If these individuals are growing slower, returning older would offer much less benefit. Susdorf et al. (2018) built a similar matrix model for the North Esk River salmon to explore how varying body size in the range at which sea lice impacts salmon would impact the size of the population after 50 years, and to what degree it would impact resilience (defined as years required to approach stable stage). They found that sea lice effects on body condition could have a large effect on population growth and equilibrium abundance. Our results also indicate that negative effects on growth will have negative population-level consequences. However, in addition we argue that plasticity in age at maturation is a flexible life history trait which may offset the neg-

ative effects of parasitism on growth and survival, making it difficult to directly model impacts of reduced growth without taking this into account. In addition, our model results suggest that in the empirical data on returning salmon, mortality during post-smolt stages is a much more important parameter than size at maturation.

The density-dependent model yielded similar results as the density-independent model, with a relatively large effect of parasite-induced mortality compared with the impact of age-at-maturity. The average population would stabilize at around 3000–4000 individuals returning to the river. However, the estimated equilibrium abundance using the parameters from the different years from the RCT trials from the Vosso rivers varied from a maximum above 10 000, to a minimum of ~0 (Fig. 6). In addition, the effect of parasitism on equilibrium abundance varied from reducing the number of fish by a few hundred to several thousand in one year (2003, Fig. 6). This data point is an outlier in the dataset indicating a significant seven-fold increase in survival when salmon is treated against sea lice (Vollset et al. 2014). Historical data have suggested that catches from the Vosso population have been > 10 000 kg averaging over 10 kg per fish during its prime, demonstrating that the river has the potential to produce the numbers reproduced by the model given high survival conditions at sea. This model, however, ignores kelt survival (i.e. fish that survive to spawn another year), which should be an interesting topic to further explore related population stability as discussed in Halttunen (2011).

It is important to note that this model does not take into consideration the conditional association between the different parameters that could in theory affect the pattern and magnitude of the impact of parasites on the population. For example, sea lice can simultaneously impact survival, growth, condition and life history changes in Atlantic salmon (Wagner et al. 2008). To explore this, we parameterized the model according to the release group studies in Vosso. Our results indicated that in this dataset life history changes and size effects have relatively little effect compared with the effect of salmon lice-induced mortality (and perhaps more importantly) variation in marine survival. Our results therefore suggest that the effects of sea lice parasites on Atlantic salmon are mainly through the effect of mortality rather through secondary effects on size and maturation.

This model is clearly a simplification of the biological processes involved in maturation in salmon. For example, in reality individual salmon are met with temporally fluctuating environment which may offer confused cues to pathways which have evolved to drive patterns of life-history plasticity. Their individual behaviours are functions of their evolutionary past and their biological and physical constraints. For example, choices are made based on the evolutionarily shaped hormonal system with its physical limitations

(Jensen et al. 2020) and is a result of multiple trade-offs that are ignored in simple modelling frameworks like ours. For example, a simple trade-off between growth and maturation has been ignored in the model, although it is well known that decision to mature is a function of size (Hutchings and Jones 1998). Our overall goal of this model exercise was to explore if there are room for salmon to compensate for the loss inflicted by maturation within likely parameter space. This appears not to be the case.

Concluding remarks

We have explored how effects of parasite-induced shifts in age at maturation can potentially compensate for mortality from sea lice parasitizing wild Atlantic salmon. Our model suggests that the shifts in age at maturation can be positive or negative depending on population growth and survival at sea, but are in general in agreement with delayed maturity associated with slower growth in the intermediate range of survival observed for Atlantic salmon (Vollset et al. 2014). Consequently, the overall population effect of this shift in age at return may be positive during periods of moderate to high marine growth, but small or perhaps even counter-productive and negative during periods of low marine growth. However, the effect of such shifts associated with the RCT data suggests that such changes in life-history have only a small effect on population growth and equilibrium abundance. Our model thus suggests that management that works on minimizing the effect of sea lice from fish farms on wild fish should focus mainly on quantifying the effect of parasite-induced mortality during the smolt stage, if the goal is to minimize effects on population growth rate.

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Author contribution KWV led the modeling, analysis, and writing. MK assisted with the modeling and contributed to the writing and editing of the manuscript.

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Data availability All data used in the model and model configurations are available in the text and tables. Empirical data are summarized across years in the model. More detailed data are available upon request from the main author.

Declarations

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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