

A stage-structured model for the sea lice population at individual salmon farms

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Abstract

This paper introduces a stage-structured model for parasitic salmon lice populations on cage populations of farmed salmon hosts at individual salmon farms. The model is built in discrete time with daily time steps. The model divides the life cycle of salmon lice into different distinct stages where the lice can age within each stage to a given stage-age. The number of lice at a certain stage either develop into the consecutive stage during a day or stays in the same stage and ages by a one stage-age day. Not all lice develop into the next stage, only a proportion survives and only a proportion do not develop. Furthermore, of the lice that develop into the next stage, only a proportion survives and a proportion develop. Lice can develop into the next stage at all stage-ages. At one location there are several cages and each cage is modelled individually. The cages are connected through the first stage which is named the recruitment stage and is a group of different early life stages of the sea lice. The expected lice frequency at a each cage and each stage is modelled as a function of i) expected lice frequency the previous day, ii) mortality proportion, iii) development proportion and iv) reproduction factor dependent on stage. The mortality and development proportion are modelled as functions of explanatory variables such as sea temperature, weight and biomass of fish at each cage.

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1 Utvidet sammendrag på norsk

Dette arbeidet er utført som en del av prosjektet “Utvikling av demografisk lokalitetsmodell for lakselus”. Veterinærinstituttet, Norsk Regnesentral og Marine Harvest deltar i prosjektet. Prosjektet er finansiert av Regionalt forskningsfond Midt-Norge.

I det følgende presenterer vi en populasjonsmodell for lakselus knyttet til ett enkelt oppdrettsanlegg. Dette er en prototypmodell som bør forbedres og utvikles videre. På sikt tenker vi oss at modellen kan fungere som et verktøy til å holde rede på forekomst og demografisk profil på lusepopulasjoner i enkeltmerder, og på aggregert lokalitetsnivå, på bakgrunn av regelmessige lusetellinger og relevante bekjempelsesdata. Videre tenker vi oss at modellen skal kunne brukes til å lage prognoser for utvikling av lusepopulasjonen ved gitte lokalitet noe frem i tid, la oss si noen måneder, som igjen kan brukes til strategisk planlegging av lusebekjempelse. Herunder, tenker vi at modellen skal kunne brukes til testing av effekter av ulike tiltak og scenariosimulering (hva-hvis analyser) av ulike tiltaksstrategier.

Hoveddelen av rapporten, som er skrevet på engelsk, inneholder en detaljert beskrivelse og matematisk formulering av modellen. Fokuset er på den tekniske beskrivelsen, og ikke på fortolkning av resultatene, fordi rapporten er tenkt brukt som en basis for videreutvikling av modellen seinere.

Stien et al. (2005), fra nå av kalt S05, utviklet en stadiestrukturert populasjonsmodell for livssyklusen til lakselus, og estimerte modellparametrene fra laboratoriedata. Inspirert av denne modellen har vi konstruert en modifisert populasjonsmodell der modellparametrene estimeres på bakgrunn av data på lusetall og behandlingsepisoder fra Marine Harvests oppdrettsanlegg på Langskjæra utafor Frøya.

Lakselusa har flere distinkte utviklingsstadier i sin livssyklus. Vi slår her noen av disse stadiene sammen og opererer med i) lus i rekrutteringsstadiet (egg og nauplius-larver), ii) copepoditter (planktoniske larver som potensielt kan smitte vertsfisk), iii) chalimus (larver som er fastheftet til fisken), iv) pre-adulte lus og v) adulte lus (begge de siste stadiene lever på, og kan bevege seg rundt på, fiskens overflate). Adulte (kjønnsmodne) lus deles i hunner og hanner.

Modellen har en tidsoppløsning på ett døgn. Hvert døgn kan en lus enten i) dø, ii) forbli i samme stadium, eller iii) utvikle seg til neste stadium, med unntak av adulte lus som ikke kan utvikle seg videre. Rekruttering av nye lus foregår enten ved ekstern rekruttering fra naboanlegg eller ved intern rekruttering fra adulte hunnlus. Hvor fort denne utviklinga foregår avhenger blant annet av sjøtemperaturen. I tillegg kan dødelighet av lus økes ved hjelp kjemoterapeutisk lusebe-

handling. Beregninger gjøres per merd, men kan aggregeres til et gjennomsnitt over alle merder.

Modellen har omtrent 25 parametre. Disse er relatert til rater for dødelighet, utvikling til nye stadier og reproduksjon, og hvordan disse avhenger av blant annet sjøtemperatur og behandling mot lus. Vi bruker informasjon fra S05 til å fastsette intervaller for plausible verdier av en del av disse parameterne. Innafor de gitte intervallene estimeres parameterne ved hjelp av data fra oppdrettsanlegget på Langskjæra.

Vi har data fra Langskjæra fra mai 2009 og ut oktober 2010. I mai 2009 blei det satt ut fisk i fire merder. Etterhvert blei deler av disse ført over til ytterligere fire merder, slik at vi til sammen har data fra åtte merder. For hver merd har vi opplysninger om antall fisk og gjennomsnittsvekt av fisken, samt om når det har blitt gjennomført medikamentell behandling og med hvilket medikament. Videre har vi data fra lusetelling. For hver telling har vi oppgitt antall lus talt på omtrent 20 fisk per merd, fordelt på antall chalimus, antall adulte hunnlus og antall andre bevegelige lus (pre-adulte og adulte hannlus). Når det gjelder lus i chalimusstadiet veit vi at kun en mindre andel av antall lus blir oppdaget, særlig hvis fisken blir stor.

Figurene 1 to 8 viser data og modellberegninger for antall lus per fisk i hver merd, fordelt på stadiene chalimus, adulte hunnlus og andre bevegelige lus. Figur 9 viser tilsvarende i gjennomsnitt over alle merder.

Figur 10 viser hvordan ekstern og intern rekruttering (påslag av nye lus) varierer over tid. Fisken er fri for lus ved utsett, så i starten er det kun ekstern rekruttering, men ganske snart blir intern rekruttering viktigst.

Et av bruksområdene for en slik modell vil være prognoser for framtidig lusenivå, gjerne betinget på hvilke tiltak som blir gjort. For å illustrere dette har vi reestimert modellen basert på data til og med 31. august 2010, og predikert framtidig lusenivå. Resultatet er vist i figur 11.

Modellen vi har presentert er en prototyp modell og kan forbedres på flere måter. En bør da bruke data fra flere oppdrettsanlegg til å estimere og validere modellen. Vi mener at resultatene så langt er såpass lovende at modellen bør videreutvikles langs de linjer vi skisserer i "conclusions"-kapitlet.

2 Introduction

All industrialised farming facilities meet the challenging problem of infectious diseases. A disease outbreak tends to inflict large economic consequences as well as possible spread to wild life and therefore it is of upmost importance to understand the dynamic development of the disease. The introduction of mathematical models helps us to understand some of the underlying factors for the spread as well as evaluating different treatment strategies that can deal with the problem at hand. In this paper we will focus on the salmon louse, *Lepeophtheirus salmonis*, an ectoparasite that infects both farmed and wild salmonids. The louse causes skin damage to the salmon which in severe cases causes death.

Stien et al. (2005), from now on termed S05, developed a population model for the life cycle of a sea lice, and estimated the model parameters from the available laboratory data. Inspired by their population model, we will construct a modified population model for salmon lice infecting farmed salmon on a cage level, but that includes interactions with the neighbouring cages and recruitment of lice from external sources. The model can be built in a continuous time or in discrete time frame with small, e.g. daily, time steps, and in the presentation below we will only use a daily time step.

The salmon louse has several distinct developmental stages. S05 grouped the lice life cycle into six stages. In the first three stages, i) the egg stage, ii) nauplius larvae, and iii) copepodites, the salmon lice develop into being infectious to salmonid hosts while drifting as plankton in the water current. The next three stages; iv) chalimus larvae, v) pre-adults and vi) adult lice, are all parasitic and live on the surface of a fish host. The chalimus larvae are sessile, whereas the pre-adults and adults are mobile and may move about on the surface of the host.

The model is estimated from data from one cohort of farmed salmon from one salmon farm. The paper focuses on the technical aspects of the model, with little emphasis on interpretation of the results.

The model is deterministic, and can be improved further by including stochastic elements.

3 Data

The data presented here are from the Norwegian marine fish farm Langskjæra, located close to Frøya in the county Sør-Trøndelag. Atlantic salmon were stocked

from the 25th of May in 2009 to the 27th of October 2010. At different times and from different cages, lice counts covering different developmental stages on a sampled number of fish were registered. The time between each lice count at a specific cage varies, but in general the time span is around 7 days. The number of fish sampled to register the number of lice varies from 10 to 120. Three types of distinct lice stages are registered: i) chalimus larvae, ii) other mobiles and iii) adult females. The other mobiles category include pre-adult and adult male lice grouped together. In addition to lice counts, also chemotherapeutic treatments, temperature, biomass, weight, the number of fish and time of stocking were registered. The seawater temperature was missing for 6.0% of the days. The missing temperatures were imputed by linear interpolation. The mean seawater temperature in the time span considered here was 9.6°C. The cage numbers are named 2,3, 4, 6, 7, 8, 9 and 10. Cage numbers 2, 3, 8 and 9 were stocked first, while cage 4, 6, 7 and 10 were stocked later by transferring some of the fish from the cages already stocked. Cleaner fish were not used to control lice infections in the present cohort of salmon.

We have also data for external infection pressure. These are first calculated as monthly values as a weighted sum of the observed sea lice abundance at neighbouring farms. The weights are taken from Aldrin et al. (2012) and depend among others on the seaway distances from the neighbouring farms to Langskjæra and of the number of fish at the neighbouring farms. The monthly values are further linearly interpolated to daily values, and then normalised to have an average value of one. Finally, they are shifted 20 days backwards. (This gave the best fit, and here we will only present results for this specific shift.)

4 General introduction without cages

In the presentation below there are no restrictions on the stage categories: eggs, nauplius larvae, copepodites, chalimus larvae, pre-adults and adults, but in later chapters we will group the first three stages into a planktonic recruitment stage to simplify the model with fewer parameters.

We will now sketch how a model for the lice population at one farm might look like with daily time steps. Define first the following quantities:

- N_{ta}^s : the number of lice in stage s at the start of time (day) t and at stage-age a (in days) within that stage (also called stage-age below).
- m_{ta}^s : the mortality rate at time t , i.e. proportion of lice that die within one day,

for lice in stage s and stage-age a .

- d_{ta}^s : the development rate, i.e. the proportion of lice in stage s and stage-age a that develop into stage $s + 1$ at time t .

The general idea is that for $a = 0$, the lice are recruited into stage s from the stage below, and that for $a > 0$, the lice can develop into the next stage. We assume further that within a day,

- lice die,
- the surviving lice might develop to the next stage and
- fish can be moved to another cage or be slaughtered.

First, for $a = 0$, this can be written as:

Change of stage equation:

$$N_{t(a=0)}^s = \sum_{a'} N_{(t-1)a'}^{(s-1)} [1 - m_{(t-1)a'}^{(s-1)}] d_{(t-1)a'}^{(s-1)}. \quad (1)$$

The interpretation of this equation is: The new lice in stage s can be recruited from all ages a' in the stage below, therefore, the total number of new lice is found by summing over all a' . Furthermore, of the number of lice $N_{(t-1)a'}^{(s-1)}$ the time before, only a proportion $[1 - m_{(t-1)a'}^{(s-1)}]$ of the lice survives, and further a proportion $d_{(t-1)a'}^{(s-1)}$ develop into the next stage s .

Similarly, for $a > 0$, this can be written as:

Same stage equation:

$$N_{t(a>0)}^s = N_{(t-1)(a-1)}^s [1 - m_{(t-1)(a-1)}^s] [1 - d_{(t-1)(a-1)}^s]. \quad (2)$$

The interpretation of this equation is that a proportion of the fish survives, a proportion $[1 - m_{(t-1)(a-1)}^s]$ of lice survives at least one day, and a proportion $[1 - d_{(t-1)(a-1)}^s]$ of the survivors who does not develop into the next stage $s + 1$.

These basic equations above must be modified for some of the stages:

- For the last stage, the adult stage, the lice must be divided into a male and a female stage.
- For the egg stage, the recruitment is not related to the number of lice in the stage below (there aren't any), but to the number of female adults. Furthermore, the development rate d , which is less than one, must be replaced by a reproduction factor r that can be much higher than one.

- For at least some of the egg, nauplius and copepod stages, there may be an additional external recruitment e_{ta}^s from the neighbouring farms. We have chosen to model this as an external recruitment to a combined Recruitment stage, which consists of eggs and nauplius.
- For the adult stage, no lice will develop into the next stage.
- Because some of the fish are moved from one cage to another, a weight function $w_{t'c}$ dependent on movement of fish from cage c' to c will be present in all the stages except the recruitment stage of the lice.

The mortality rates of lice m_{ta}^s will depend on stage and the stage-age. S05 did not find enough evidence that mortality being dependent on sea temperature, but this will be reconsidered in this project. The mortality rates will certainly also depend on whether the fish has been treated against lice, unless the lice have become resistant towards the treatment.

The development rates d_{ta}^s will depend on stage, stage-age and sea temperature. S05 divided the time of development from one stage into a new stage into two parts: First a minimum development time which was highly dependent on sea temperature, and then an exponential distributed time with a constant, temperature-independent rate. If we transfer this to the development rate d_{ta}^s , it means that for a fixed temperature, the development rate is zero for stage-ages less than the minimum development time, and constant for higher stage-ages. The approach of S05 assumed constant sea temperatures throughout the development from one stage to another. This has to be modified, since the sea temperatures can change significantly over time at least in cold periods where the development rates are low and the development times are correspondingly large.

The weight function of fish $w_{t'c}$ will depend on cages c and c' as well as time point t . The sum of weights over all cages and an abstract absorbing cage 0 (e.g. died, slaughtered and moved to other farms) will add up to 1. The weight rate is known for each cage and at each time point.

The rates for mortality, development, reproduction and external transmission can be modelled as random, i.e. they can vary randomly from time to time and from cage to cage. However, their expectations will be modelled as functions of stage, stage-age, sea temperature and other factors.

5 Cage-wise population model

From now on, the index c is used for cage. Combine the egg and nauplius stages into a common recruitment stage symbolised by R . Use the symbols CO , CH , PA and A for the four resulting stages. Assume that the lice are not cage-specific in the recruitment stage because they are drifting in the water. We define the following quantities:

- N_{tac}^s : the number of lice in stage s , at the start of time t , at stage-age a and in cage c .
- N_{tac}^{sg} : the number of lice of gender g in stage s , at time t , at stage-age a and in cage c .
- m_{tac}^s : the mortality rate at time t , i.e. proportion of lice that die within one day, for lice in stage s and stage-age a and cage c .
- d_{tac}^s : the development rate, i.e. the proportion of lice in stage s , stage-age a and cage c that develop into stage $s + 1$ at time t .
- r_{ta} : the reproduction rate.
- A_{tc} : the number of fish at the start of time t in cage c .
- $C_{tc'c}$: the number of fish moved from cage c' to cage c at the end of time t if $c' \neq c$, and the number that stay in cage c' if $c' = c$.
- $w_{tc'c}$: the moving rate of fish, i.e. the proportion of fish that will be moved from cage c' to cage c at the end of time t , given by

$$w_{tc'c} = C_{tc'c}/A_{tc'}. \quad (3)$$

From any of the real cages fish can be moved to an abstract absorbing cage $c = 0$, which means that fish either die, become slaughtered or are moved to other fish farms. If we sum all the moved fish to cage c at the end of time t we will get the number of fish in cage c at time $t + 1$. Therefore, $\sum_{c'} w_{tc'c} A_{tc'} = \sum_{c'} C_{tc'c} = A_{(t+1)c}$. Now, the number of lice that survives and develops in cage c' is $N_{(t-1)(a-1)c'}^s (1 - m_{(t-1)(a-1)c'}^s) (1 - d_{(t-1)(a-1)c'}^s)$. Of this lice from cage c' only a proportion $w_{(t-1)c'c}$ is moved to cage c and therefore, $\sum_{c'} w_{(t-1)c'c} N_{(t-1)(a-1)c'}^s (1 - m_{(t-1)(a-1)c'}^s) (1 - d_{(t-1)(a-1)c'}^s) = N_{tac}^s$. Note that fish that has lice and are slaughtered will not be counted because they die with the fish. Note also that fish that die or become slaughtered will probably have more lice than other fish because fish that die might have a lot of lice which can cause death and fish that become slaughtered probably are taken

out because they look more infected than other fish. This issue will not be considered here.

Furthermore, define

$$N_{ta\bullet}^s = \sum_c N_{tac}^s \quad (4)$$

$$N_{tac}^s = N_{tac}^{sf} + N_{tac}^{sm} \quad (5)$$

$$N_{t\bullet c}^s = \sum_a N_{tac}^s. \quad (6)$$

Model for the Recruitment stage

$$N_{t(a=0)}^R = \sum_c \sum_{a'} [N_{(t-1)a'c}^{Af} (1 - m_{(t-1)a'c}^{Af}) r_{(t-1)a'}] + \phi N_{t-1}^{Ext} r_{(t-1)(a=0)}, \quad (7)$$

$$N_{t(a>0)}^R = N_{(t-1)(a-1)}^R [1 - m_{(t-1)(a-1)}^R] [1 - d_{(t-1)(a-1)}^R], \quad (8)$$

where m denotes the mortality rate of lice, d the development rate, r the reproduction factor, and f denotes the adult female lice.

Furthermore, the term $\phi N_{t-1}^{Ext} r_{(t-1)(a=0)}$ represents external infection pressure or recruitment from neighbouring farms. The proportionality factor ϕ adjust the whole term so even if the new eggs and larvae are produced at neighbouring farms, this term represents the proportion that will reach the current farm at the COpepodid stage. Second, N_{t-1}^{Ext} denotes the reservoir of adult females at neighbouring farms, computed outside the model as a weighted sum of adult female lice at neighbouring farms, where the contribution from each farm is weighted according to its distance to the current farm. And finally, $r_{(t-1)(a=0)}$ represents the recruitment rate. The distribution of stage-age a for females at neighbouring farms are unknown, and note that instead we fix a to be 0. We could have chosen another fixed value for a , but this is anyway compensated for by the proportionality factor ϕ . However, $r_{(t-1)(a=0)}$ does depend on sea temperature, see later.

We can ignore the movement of fish here since they are moved after lice development and lice mortality.

Model for the COpepodit stage

$$N_{t(a=0)}^{CO} = \sum_{a'} N_{(t-1)a'c}^R [1 - m_{(t-1)a'c}^R] d_{(t-1)a'c}^R, \quad (9)$$

$$N_{t(a>0)}^{CO} = N_{(t-1)(a-1)}^{CO} [1 - m_{(t-1)(a-1)}^{CO}] [1 - \sum_c d_{(t-1)(a-1)c}^{CO}], \quad (10)$$

where the development rate $d_{(t-1)(a-1)c}^{CO}$ represents the rate of which the copepods infect fish in cage c and thus enters the CHalimus stage. The sum over cages,

$d_{(t-1)(a-1)c}^{CO} = \sum_c d_{(t-1)(a-1)c}^{CO}$ is then the total development rate. This does in fact not depend on stage-age, but we have here kept the stage-age index for consistency.

Model for the CHalimus stage

$$N_{t(a=0)c}^{CH} = \sum_{a'} N_{(t-1)a'}^{CO} [1 - m_{(t-1)a'}^{CO}] d_{(t-1)a'c}^{CO}, \quad (11)$$

$$N_{t(a>0)c}^{CH} = \sum_{c'} w_{(t-1)c'c} N_{(t-1)(a-1)c'}^{CH} [1 - m_{(t-1)(a-1)c'}^{CH}] [1 - d_{(t-1)(a-1)}^{CH}]. \quad (12)$$

Model for the Pre-Adult stage

$$N_{t(a=0)c}^{PA} = \sum_{a'} \sum_{c'} w_{(t-1)c'c} N_{(t-1)a'c'}^{CH} [1 - m_{(t-1)a'c'}^{CH}] d_{(t-1)a'c'}^{CH}, \quad (13)$$

$$N_{t(a>0)c}^{PA} = \sum_{c'} w_{(t-1)c'c} N_{(t-1)(a-1)c'}^{PA} [1 - m_{(t-1)(a-1)c'}^{PA}] [1 - d_{(t-1)(a-1)}^{PA}]. \quad (14)$$

Model for the Adult female stage

$$N_{t(a=0)c}^{Af} = q \sum_{a'} \sum_{c'} w_{(t-1)c'c} N_{(t-1)a'c'}^{PA} [1 - m_{(t-1)a'c'}^{PA}] d_{(t-1)a'c'}^{PA}, \quad (15)$$

$$N_{t(a>0)c}^{Af} = \sum_{c'} w_{(t-1)c'c} N_{(t-1)(a-1)c'}^{Af} [1 - m_{(t-1)(a-1)c'}^{Af}], \quad (16)$$

where q is the proportion of recruited female adults.

Model for the Adult male stage

$$\begin{aligned} N_{t(a=0)c}^{Am} &= (1 - q) \sum_{a'} \sum_{c'} w_{(t-1)c'c} N_{(t-1)a'c'}^{PA} [1 - m_{(t-1)a'c'}^{PA}] d_{(t-1)a'c'}^{PA} \\ &= \frac{1 - q}{q} N_{t(a=0)c}^{Af}, \end{aligned} \quad (17)$$

$$N_{t(a>0)c}^{Am} = \sum_{c'} w_{(t-1)c'c} N_{(t-1)(a-1)c'}^{Am} [1 - m_{(t-1)(a-1)c'}^{Am}]. \quad (18)$$

6 Models for the mortality, development, reproduction and external recruitment rates

The various rates can in general depend on for instance stage, treatment, sex, sea temperature, stage-age, cage and random effects. However, only very simple models and no random effects will be used as well as incorporating as much information as possible from S05. All rates must be ≥ 0 and the mortality and the development rates are restricted to be ≤ 1 (per day) as well.

Mortality rates:

The mortality rate depends on stage and treatment, where information on mortality rate without treatment is partly taken from S05, and the additional mortality is estimated from data. The mortality rate for the recruitment stage include lice that just drift away from the farm when they are still alive.

Dropping the superscript s that indicate name of stage, we have

$$m_{tac} = \text{logit}^{-1}(\eta_{tac}^m) = \exp(\eta_{tac}^m)/(1 + \exp(\eta_{tac}^m)), \quad (19)$$

where

$$\eta_{tac}^m = \text{logit}(m_{tac}) = \beta_0^m + \beta^{ml} x_{tc}^l + \sum_b \beta_b^{mt} x_{tcb}^t, \quad (20)$$

where x_{tc}^l is the ratio of the number of cleaner fish to the number of salmon in cage c . Assume there has been a treatment b at time t_b^0 , then the treatment covariate $x_{tcb}^t = 1$ if

$$t_b^0 \in [t - \Delta_b^{del} - \Delta_b^{dur}, t - \Delta_b^{del}],$$

where Δ_b^{del} is a time delay between treatment and effect and Δ_b^{dur} is the duration of the effect. The window where the covariates is 1 is

$$t \in [t_b^0 + \Delta_b^{del}, t_b^0 + \Delta_b^{del} + \Delta_b^{dur}].$$

Note that treatment H_2O_2 can happen the same day as louse are counted. For this particular treatment, the treatment always happens before counting lice. Technically this causes problems because we only have daily time steps and it is difficult to differ even when we know which happened first. We solve this problem by subtracting Δ_b^{del} by one. The treatment H_2O_2 has an immediate effect and to see this immediate effect we will have to move the date of treatment one day before. Technically this is done by defining $\Delta_b^{del} = -1$.

In a meeting with Solveig Gaasø, Marine Harvest, at Hitra 25. September 2012, we got the following information:

- Alphamax and Slice increases the mortality on both CH, PA, Af and Am.
- Salmosan increases the mortality on PA, Af and Am, but not on CH. However, this information is not fully consistent with the data. Salmosan has been applied once to each of the eight cages. For six of these, the CH abundance before treatment were positive, and the CH abundance decreased after treatment all times. For the remaining two treatments, the CH abundance was zero both before and after treatment.

- H_2O_2 increases the mortality on on Af (and Am?), and has also effects on the egg string, but does not affect CH and PA. Neither this information is fully consistent with the data. H_2O_2 was applied once at each of two cages, and both times the abundance of mobile lice decreased considerably after treatment. The abundance of CH was zero both before and after treatment on both cases.
- Alphamax has effect from about two days after treatment, with a duration of about one week in the summer and two weeks in the winter.
- Slice has effect from about 5 days after treatment, with a duration of about four weeks in the summer and eight weeks in the winter.
- Salmosan has an immediate effect, and the duration of the effect is about one week.
- H_2O_2 has an immediate effect, with a short duration.

For the duration of the treatments we assume:

Treatment	Δ^{del}	Δ^{dur}	Comment
Alphamax	2	$84/T_t$	Duration two weeks at 6 degrees
Slice	5	$336/T_t$	Duration eight weeks at 6 degrees
Salmosan	1	7	
H_2O_2	-1	1	

Without any cleaner fish and treatment, and without lice that drift away from the farm, $\exp(\beta_0^m)/(1 + \exp(\beta_0^m))$ corresponds to the mortality rate μ in s05. Plausible ranges for β_0^m for the different stages are therefore (from Table 5 in S05):

Parameter	Stage	Lower limit	Upper limit	Comment
β_0^m	R	logit(0.170)		no upper limit because drifting away is possible in the nauplius stage
β_0^m	CO	logit(0.230)		no upper limit because drifting away is possible
β_0^m	CH	logit(0.002)	logit(0.01)	
β_0^m	PA	logit(0.020)	logit(0.18)	
β_0^m	Am and Af	logit(0.020)	logit(0.06)	

Here, we ignore that S05 use a model in continuous time whereas we use a time-discrete model with time unit one day. This is fine as far as the rates from S05 are sufficiently lower than 1.

For the time being, we assume that β_0^m for the R and the CO stages are equal.

There has not been used cleaner fish in the data period, and therefore $\beta^{ml} = 0$ for all stages. Based on the information above, including the preliminary study of the data, we assume that $\beta_b^{mt}, b = 1, \dots, 4$ are 0 for stages R and CO, and non-negative for the other stages, and that each of these coefficients are equal for the stages CH, PA, Am and Af. Thus, these are four non-negative parameters.

Treatment	Parameter	Stage	Lower limit	Upper limit	Fixed
Cleaner fish	β^{ml}	R, CO			0
Alphamax	β_1^{mt}	R, CO			0
Slice	β_2^{mt}	R, CO			0
Salmosan	β_3^{mt}	R, CO			0
H_2O_2	β_4^{mt}	R, CO			0
Cleaner fish	β^{ml}	CH, PA, Af, Am			0
Alphamax	β_1^{mt}	CH, PA, Af, Am	0		
Slice	β_2^{mt}	CH, PA, Af, Am	0		
Salmosan	β_3^{mt}	CH, PA, Af, Am	0		
H_2O_2	β_4^{mt}	CH, PA, Af, Am	0		

Development rates, but the CO stage is not included

The development rate depends on stage and a generalised accumulated temperature, or energetic variable as we define below. Furthermore, the development rates has an upper limit that corresponds to the constant and instantaneous development rate (ν in S05) after minimum development time (τ in S05). The development rate does not depend on cage c , except in the COpepodid model which is treated below.

Let x_{ta}^e be the value of the energetic variable. Dropping the s superscript, the model for the development rate is

$$d_{ta} = \exp(\eta_{ta}^d) / (1 + \exp(\eta_{ta}^d)) \cdot \nu, \quad (21)$$

where both the first factor and the second factor ν is between 0 and 1. Furthermore,

$$\eta_{ta}^d = \beta_0^d + \beta_1^d x_{ta}^e. \quad (22)$$

The energetic variable x_{ta}^e is defined as

$$x_{ta}^e = \sum_{t'=t-a}^{t'=t} (T_{t'} + \alpha_2)^2, \quad (23)$$

where T_t is the sea temperature at time t and α_2 is a parameters from Equation (7) in S05. In the cases where T_t is not observed we use the last observed values.

The motivation for the definition of x_{ta}^e is that Equation (7) in S05 models the (average) minimum time to development as $\alpha_1(T + \alpha_2)^{\alpha_3}$ for a fixed T , which means that the development happens when the stage-age a satisfies $a(T + \alpha_2)^{-\alpha_3} = \alpha_1$. Furthermore, S05

use $\alpha_3 = -2$ as a fixed quantity. S05 transform α_1 and α_2 to β_1 and β_2 , and give estimates of the latter in their Table 3. We need α_2 which is given as $-10 + \beta_1\beta_2$. Based on their Table 3, α_2 is fixed at the different stages as:

Parameter	Stage	Fixed value
α_2	R	4
α_2	CH	9
α_2	PA	2
α_2	Am and Af	not used

Let $p = \exp(\eta_{ta}^d)/(1 + \exp(\eta_{ta}^d))$ denote the first term in the equation for the development rate. S05 assumes that the development rate is 0 until a certain time point, and then increase to a constant ν . As mentioned above, this happens when the energetic variable x_{ta}^e is equal to α_1 . We assume instead that the development rate increase for values of x_{ta}^e around α_1 . This means that $p = 0.5$ when $x_{ta}^e = \alpha_1$, which further means that $\text{logit}(0.5) = \log(0.5/(1 - 0.5)) = 0 = \beta_0^d + \beta_1^d\alpha_1$. Thus, β_0^d can be expressed as

$$\beta_0^d = -\beta_1^d\alpha_1. \quad (24)$$

Plausible values for α_1 (see below) can be found from Table 3 in S05 ($\alpha_1 = \beta_1^2$).

If β_1^d in our model goes to infinity, the development rate changes from 0 to ν instantaneously as in the model of S05. However, we want to allow for a more smooth transition (i.e. β_1^d less than infinity), but not too smooth. Therefore we require that $p \leq 0.01$ when $x_{ta}^e = \alpha_1/2$. This gives

$$\beta_1^d \geq -2\text{logit}(0.01)/\alpha_1 = 9.19/\alpha_1. \quad (25)$$

We set

$$\beta_1^d = 9.19/\alpha_1 + \tilde{\beta}_1^d, \quad (26)$$

Development from the R stage to the CO stage corresponds to development first from egg to nauplius and then from nauplius to copepod in S05. The α_1 in the R stage is a sum of two constants from S05.

The parameters β_0^d and β_1^d are unrestricted and different for the three stages R, CH and PA.

Below are the plausible ranges for α_1 and β_1^d for the three stages R, CH and PA.

Parameter	Stage	Lower limit	Upper limit	Point estimate
α_1	R	1797	3037	2077
α_1	CH	55	201558	1686
α_1	PA	715	11705	2219
α_1	Am and Af	not used		
$\tilde{\beta}_1^d$	R	0		
$\tilde{\beta}_1^d$	CH	0		
$\tilde{\beta}_1^d$	PA	0		
$\tilde{\beta}_1^d$	Am and Af	not used		

S05 gives the following plausible ranges for the ν parameters for the CH and PA stages:

Parameter	Stage	Lower limit	Upper limit	Comment
ν	R	0	1	
ν	CH	0.24	0.89	
ν	PA	0.24	0.80	
ν	Am and Af			not used

Development rate for the CO stage:

The development rate for the COpepodit stage is cage-dependent and represents the copepodits that infect fish and thus develop into the CHalimus stage. The development rate does not depend on stage-age a , except that we assume that development may only happen for $a \geq 1$. This is modelled as

$$d_{tac}^{CO} = d_{tc}^{CO} = \exp[\beta_1^{CO}(\log(W_{tc}) - 0.55)]\beta_0^{CO}, \quad (27)$$

where A_{tc} and W_{tc} are the number (in millions) and the weight (in kg) respectively of fish in cage c at time t and 0.55 is roughly the mean of the natural logarithm of the weight of fish. . The parameters β_0^{CO} and β_1^{CO} are restricted to be non-negative. The sum over all cages of $d_{(t-1)c}^{CO}$ in Eq. (27) should always be less than 1. This is handled by restricting each d_{tc}^{CO} to be less than 0.1, and in optimum all values are much lower than this upper limit. The parameter β_0^{CO} controls how small development rate should be. Ideally, β_0^{CO} should depend on cage, since some cages are more exposed to infection than others due to sea current conditions, but to limit the number of parameters to estimate, they are assumed equal.

Parameter	Part of the model	Lower limit	Upper limit
β_0^{CO}	development CO		0
β_1^{CO}	development CO		0

Reproduction factor:

Female adults extrude pairs of egg strings. They can extrude a new set of egg strings within 24 hour after the previous set was hatched (S05, page 270), but hatching can take several days (S05, Figure 2). The number off eggs per string may increase further with the the extrusion number, which we approximate with stage-age. Finally, not all eggs are viable.

The reproduction factor from female adults and is thus modelled as

$$r_{ta} = \beta_0^r \cdot (a + 1)^{\beta_1^r} / [\alpha_1 \cdot (T + \alpha_2)^{-2} + 1]. \quad (28)$$

The parameters in equation Eq. (28) has ranges:

Parameter	Part of the model	Lower limit	Upper limit	Fixed value
β_0^r	reproduction	70	275	
β_1^r	reproduction			0.20
α_1	reproduction			$41.98^2 = 1762$
α_2	reproduction			4.2

The first term in the equation (28) represents the number of viable eggs for the first extrusion. The next term models how the number of viable eggs per extrusion increases by stage-age. The third term represents the hatching time, which is approximately the time between each egg extrusion.

Here, we estimate only β_0^r and fix the remaining parameters. S05 says that a female produce a set of two egg strings with 70-152 eggs per string for the fist set, which can be increased by a factor 1.9 (290/152) to the next set or by a factor 2.1 (150/70) to the fifth set. Furthermore, the proportion of viable eggs can be in the range 0.5-0.9. So the number of viable eggs may be in the range 70-275 for the fist set of egg strings, i.e. β_0^r is in the range 70-275.

S05 says that the number of eggs produced per extrusion can be increased by a factor 1.9 (290/152) to the second set or by a factor 2.1 (150/70) to the fifth set compared to the first set. Hatching take about 8.75 days when the temperature is 10 degrees Celsius (see below). Further assuming that it takes one more day to extrude a new set of egg strings, the fifth set of egg strings are extruded after $(4 \cdot (8.75 + 1) + 1) = 40$ days. A reasonable value for β_1^r is therefore $\log(2.1)/\log(40) = 0.20$, and we fix β_1^r at that value.

The hatching time is dominated by the minimum time to hatching, described by equation (7) in S05, i.e. $\alpha_1(T + \alpha_2)^{-2}$. In addition, it takes one day to extrude a new set of egg strings after hatching. The average time between each set of egg strings is therefore $1/[\alpha_1 \cdot (T + \alpha_2)^{-2} + 1]$. Based on Table 3 in S05 (and the relationships between α 's and β 's), α_1 is set to 42 and α_2 is set to 4.2.

External recruitment:

External recruitment is a part of the recruitment model, Eq. (7), and includes the proportionality parameter ϕ , which is non-negative.

Parameter	Part of the model	Lower limit	Upper limit
ϕ	external recruitment	0	

The proportion of recruited female adults:

q is defined as the proportion of recruited female adults. It is assumed that this quantity is not dependent on time and cage. It is a factor that divides the adults into a female and a male group. We assume that q is between 0.25 and 0.75.

Parameter	Part of the model	Lower limit	Upper limit
q	Adult females	0.25	0.75

7 Data model

Let

- Y_{tack}^s : the number of lice per fish in stage s , at the start of time t , at stage-age a , in cage c and fish k .

Then $Y_{tck}^s = \sum_a N_{tack}^s$ and $Y_{tc}^s = \sum_{k=1}^{n_{tc}} N_{tck}^s$.

We assume that lice are counted at the start of time t , before any development etcetera. Let

- n_{tc} : The number of fish investigated in cage c at time t
- Y_{tck}^{CH} : The number of chalimus lice counted from fish k , or the chalimus abundance.
- Y_{tck}^{Af} : The abundance of adult, female lice counted from fish k .
- Y_{tck}^{OM} : The abundance of other mobile lice counted from fish k .

Assume

$$Y_{tck}^s \sim NB(R_{tc}^s, P_{tc}^s), \quad (29)$$

where

$$E(Y_{tck}^s) = R_{tc}^s \cdot \frac{P_{tc}^s}{1 - P_{tc}^s}. \quad (30)$$

These variables also have expectations obtained from the population model

$$\begin{aligned} E(Y_{tck}^{CH}) &= \delta_{tc} \cdot \frac{N_{tck}^{CH}}{A_{tc}}, \\ E(Y_{tck}^{Af}) &= \frac{N_{tck}^{Af}}{A_{tc}}, \\ E(Y_{tck}^{OM}) &= \frac{N_{tck}^{PA} + N_{tck}^{Am}}{A_{tc}}. \end{aligned} \quad (31)$$

The role of the parameter δ_{tc} is to adjust for underreporting of chalimus lice, since they are more difficult to count for larger fish than for small fish. For small fish (0.1 kg, say) almost all chalimus are counted, but on large fish (3 kg, say) we expect that the proportion of counted chalimus is around 0.3-0.4 (personal communication with Solveig Gaasø, Marine Harvest). We model δ_{tc} as

$$\delta_{tc} = \exp(\eta_{tc}^{\delta}) / (1 + \exp(\eta_{tc}^{\delta})), \quad (32)$$

where

$$\eta_{tc}^{\delta} = \beta_0^{\delta} + \beta_1^{\delta}(W_{tc} - 2.4), \quad (33)$$

where W_{tc} as before is the mean weight of fish in cage c at time t and 2.4 is roughly the mean weight (in kg) of the fish. The limits for β_0^{δ} and β_1^{δ} given in the table below ensure roughly that δ_{tc} is above 0.9 for fish at weight 0.1 kg and above 0.2 for fish at weight 3 kg, which is slightly less strict than the limits mentioned above.

Parameter	Part of the model	Lower limit	Upper limit
β_0^{δ}	Chalimus counts	-2	3
β_1^{δ}	Chalimus counts	-2	0

Assume that the second parameter in the negative binomial distribution in (29) is constant for each stage, that is $P_{tc}^s = P^s$. This gives three more parameters, restricted to be between 0.001 and 0.999:

Parameter	Part of the model	Lower limit	Upper limit
P^{CH}	Chalimus counts	0.001	0.999
P^{Af}	Adult females counts	0.001	0.999
P^{OM}	Other Mobiles counts	0.001	0.999

The first parameter in the negative binomial distribution in (29) is given by equation (30)

$$R_{tc}^s = E(Y_{tck}^s) \cdot \frac{1 - P_{tc}^s}{P_{tc}^s}. \quad (34)$$

Since the number of lice are observed as a sum over all sampled fish, we need the distribution form of $Y_{tc}^s = \sum_{k=1}^{n_{tc}} Y_{tck}^s$. The sum of independent negative binomial distributed variables is also negative binomial giving

$$Y_{tc}^s \sim NB(n_{tc}R_{tc}^s, P_{tc}^s). \quad (35)$$

8 The likelihood function

The probability distribution of the negative binomial variable in (35) is

$$P(Y_{tc}^s = y_{tc}^s) = \frac{\Gamma(y_{tc}^s + n_{tc}R_{tc}^s)}{y_{tc}^s! \Gamma(n_{tc}R_{tc}^s)} (P_{tc}^s)^{y_{tc}^s} (1 - P_{tc}^s)^{n_{tc}R_{tc}^s}. \quad (36)$$

Let all the unknown parameters be gathered into one parameter vector θ . We observe at certain dates the number of louse in three stages in the different cages. We do not observe how old a louse is in a certain stage. We only observe Y_{tc}^s at certain time points (around every 7th day). Also assume that the number of lice in each stage is independent of each other. The log likelihood is then given by

$$\begin{aligned} ll(\theta) = & \sum_{s \in \{CH, PA, OM\}} \sum_c \sum_{t \in T_c} (\log(\Gamma(y_{tc}^s + n_{tc}R_{tc}^s)) - \log(\Gamma(n_{tc}R_{tc}^s))) \\ & + y_{tc}^s \log(P_{tc}^s) + n_{tc}R_{tc}^s \log(1 - P_{tc}^s), \end{aligned}$$

where T_c is the times for the lice counts in cage c and where the terms that do not depend on the parameters are dropped in the log likelihood. Note that (when y is a positive integer)

$$\log(\Gamma(y + R)) - \log(\Gamma(R)) = \sum_{j=0}^{y-1} \log(R + j). \quad (37)$$

The right hand side of equation (37) is easier to calculate numerically and can take higher values of R compared to the left hand side.

9 Results

The model was estimated by maximum likelihood using all available data. Table 1 gives an overview of all parameters, including fixed values, estimated values and lower and upper limits.

Figures 1 to 8 show the data and fitted values for each cage, separately for the chalimus larvae, Adult females and other mobiles. The data include lice counts, time when fish are stocked, time when fish are moved to new cages and time for and type of medical treatments. Figure 9 shows the same averages over all cages.

The two upper panels of Figure 10 show how external and internal recruitment vary over time. These are indexes where the maximum value of internal recruitment is set to 1. The lower panel of Figure 10 shows how the proportion of internal recruitment varies over time.

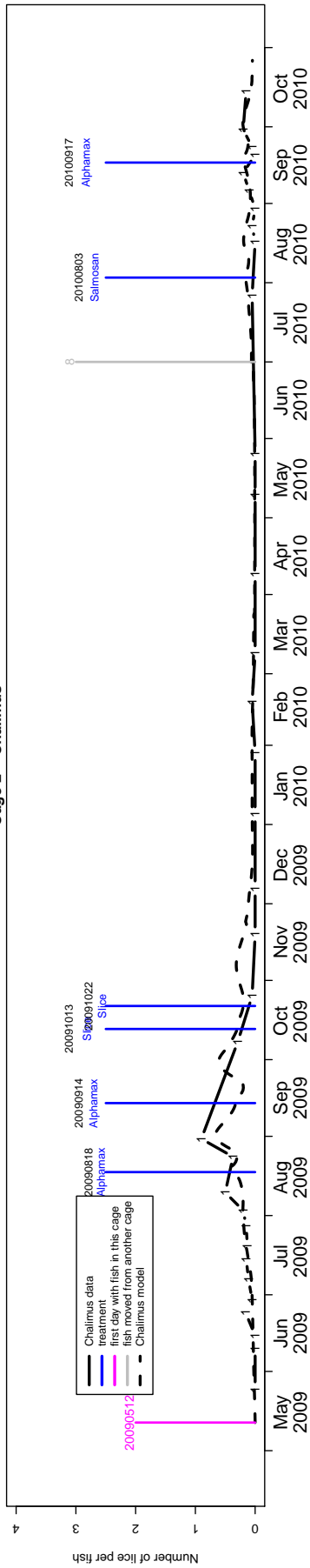
Finally, the model was re-estimated using lice counts only until 31. August 2010. The model was then used to predict the lice abundance from 1. September 2010 and on-

wards. Figure 11 shows the model fit from the re-estimated model and predictions from 1. September 2010.

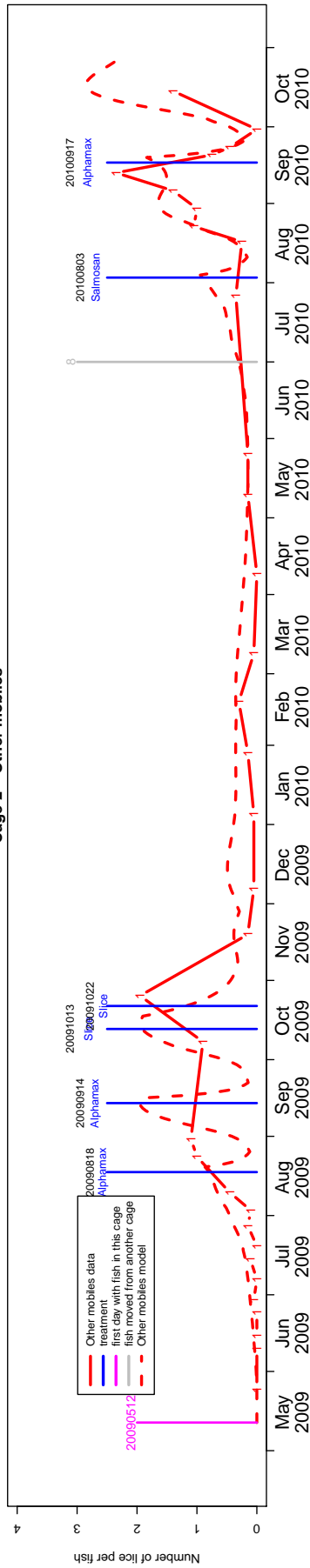
Table 1. Overview of all parameters, with estimated or fixed values and prior upper and lower limits.

Parameter description	Parameter symbol	Stage	Fixed value	Estimated value	Lower prior value	Upper prior value
mortality, intercept	β_0^m	R,CO		-1.59 =logit(0.17)	logit(0.17)	
mortality, intercept	β_0^m	CH		-4.60 =logit(0.01)	logit(0.002)	logit(0.01)
mortality, intercept	β_0^m	PA		-3.90 =logit(0.020)	logit(0.020)	logit(0.18)
mortality, intercept	β_0^m	Af, Am		-3.90 =logit(0.020)	logit(0.020)	logit(0.06)
mortality, effect of Alphamax	β_1^{mt}	CH, PA, Af, Am		3.44	0	
mortality, effect of Slice	β_2^{mt}	CH, PA, Af, Am		1.95	0	
mortality, effect of Salmosan	β_3^{mt}	CH, PA, Af, Am		3.17	0	
mortality, effect of H_2O_2	β_4^{mt}	CH, PA, Af, Am		5.92	0	
constant in development rates	α_2	R	4			
constant in development rates	α_2	CH	9			
constant in development rates	α_2	PA	2			
development rates, typical energetic value	α_1	R		1797	1797	3037
development rates, typical energetic value	α_1	CH		3602	55	201558
development rates, typical energetic value	α_1	PA		1789	715	11705
development rates, coefficient	$\tilde{\beta}_1^d$	R		0	0	
development rates, coefficient	$\tilde{\beta}_1^d$	CH		1.84	0	
development rates, coefficient	$\tilde{\beta}_1^d$	PA		0	0	
development rates, maximum value	ν	R		1	0	1
development rates, maximum value	ν	CH		0.24	0.24	0.89
development rates, maximum value	ν	PA		0.24	0.24	0.80
development rates, factor	β_0^{CO}	CO		0.0326	0	
development rates, coefficient	β_1^{CO}	CO		0	0	
reproduction, factor	β_0^r			70	70	275
reproduction, exponent	β_1^r		0.20			
reproduction	α_1		41.98 ² = 1762			
reproduction	α_2		4.2			
external recruitment, factor	ϕ			54.5·10 ³	0	
proportion female adults	q			0.540	0.25	0.75
chalimus counts, intercept	β_0^δ			-1.58	-2	3
chalimus counts, coefficient	β_1^δ			-0.427	-2	0
second parameter in NB distribution	P^{CH}	CH		0.776	0.001	0.999
second parameter in NB distribution	P^{Af}	Af		0.736	0.001	0.999
second parameter in NB distribution	P^{OM}	OM		0.880	0.001	0.999

Cage 2 – Chalmus



Cage 2 – Other mobiles



Cage 2 – Adult females

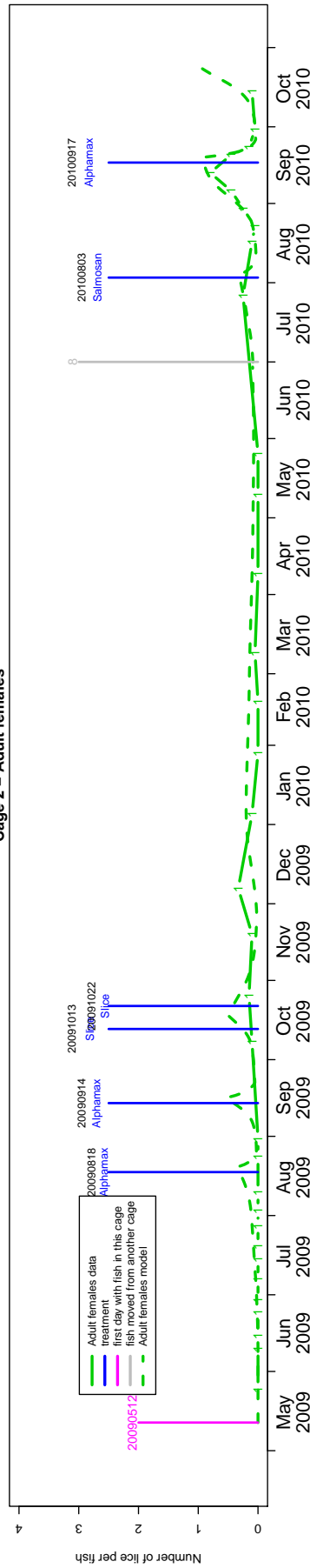
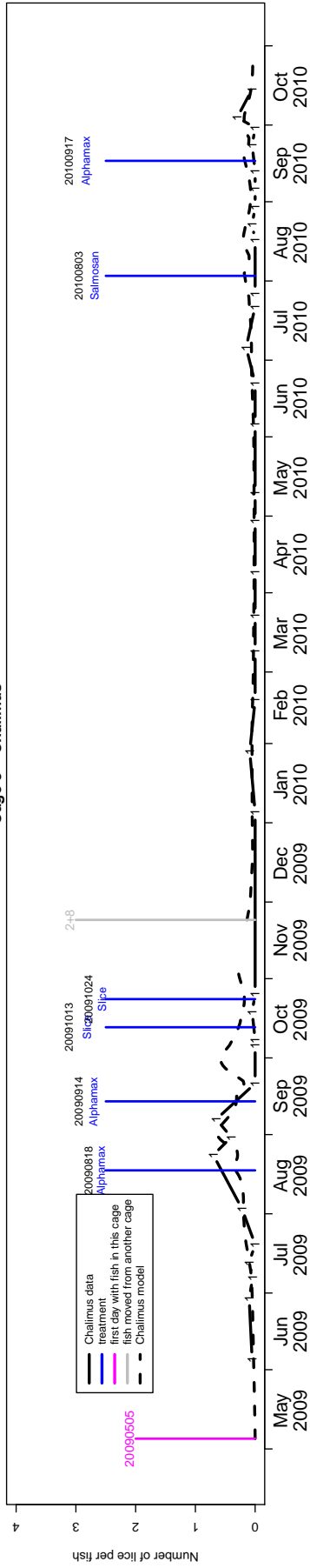
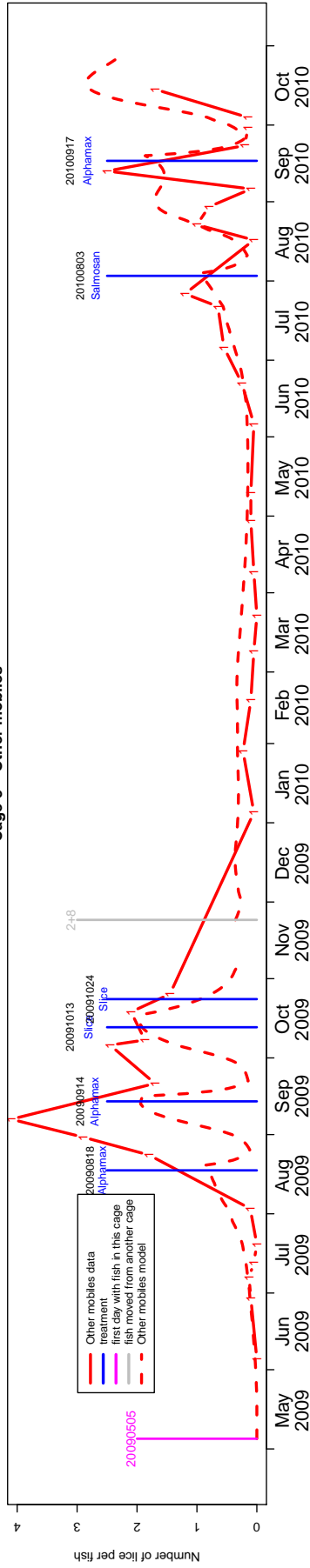


Figure 1. Data and model fit for cage 2.

Cage 3 – Chalimus



Cage 3 – Other mobiles



Cage 3 – Adult females

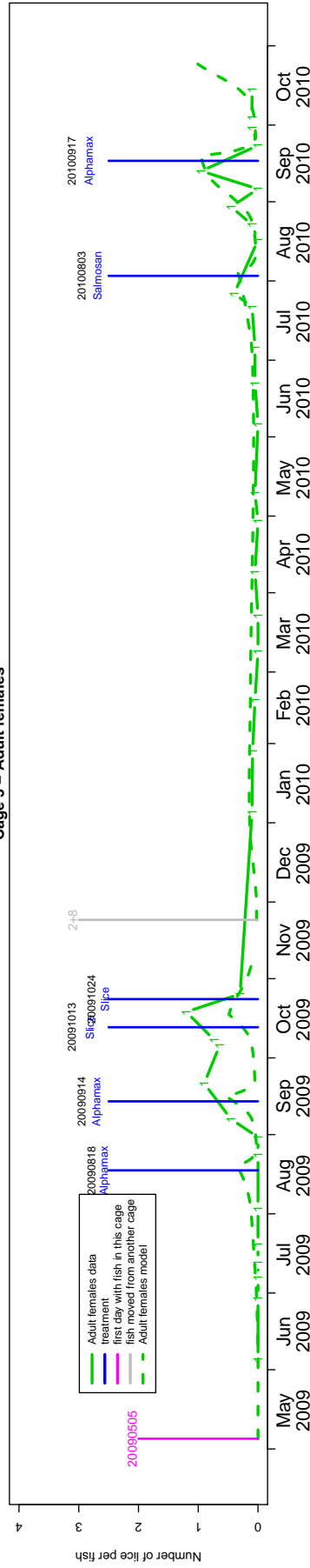
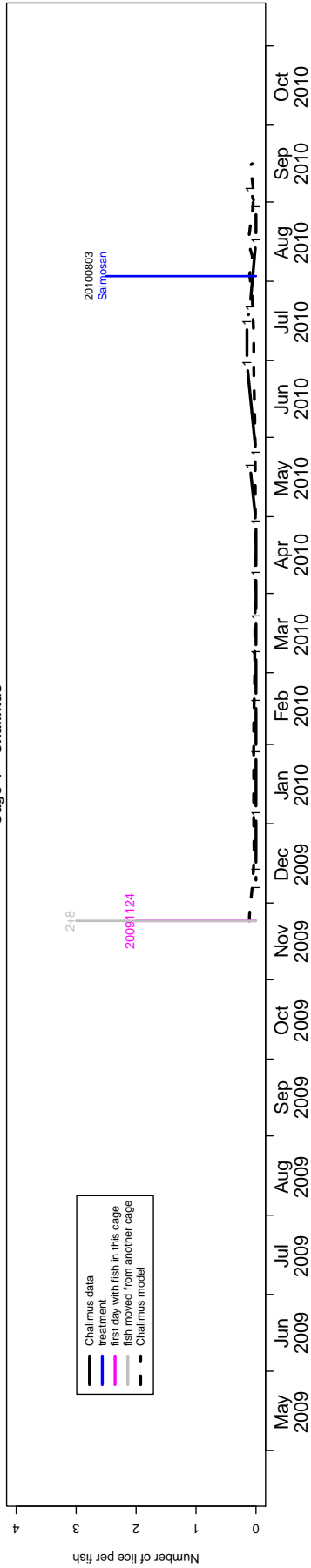
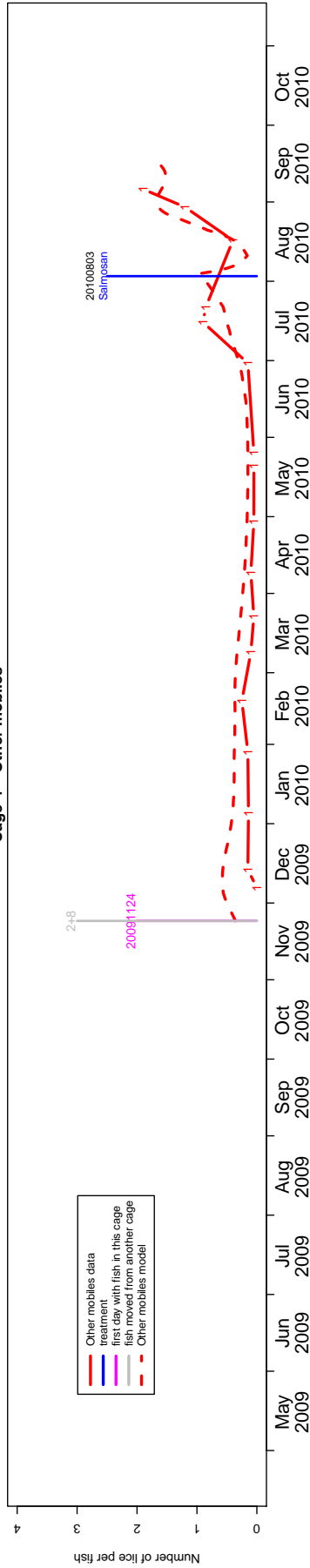


Figure 2. Data and model fit for cage 3.

Cage 4 – Chalimus



Cage 4 – Other mobiles



Cage 4 – Adult females

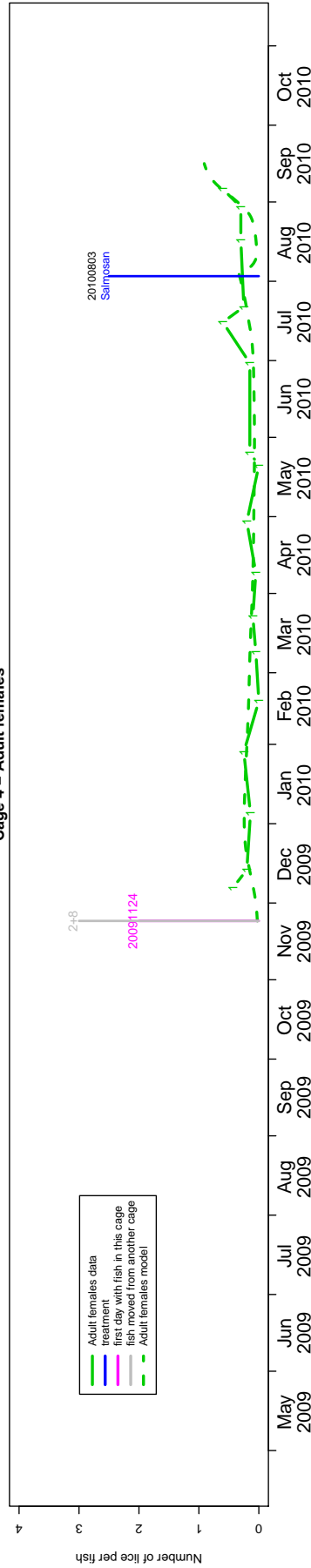
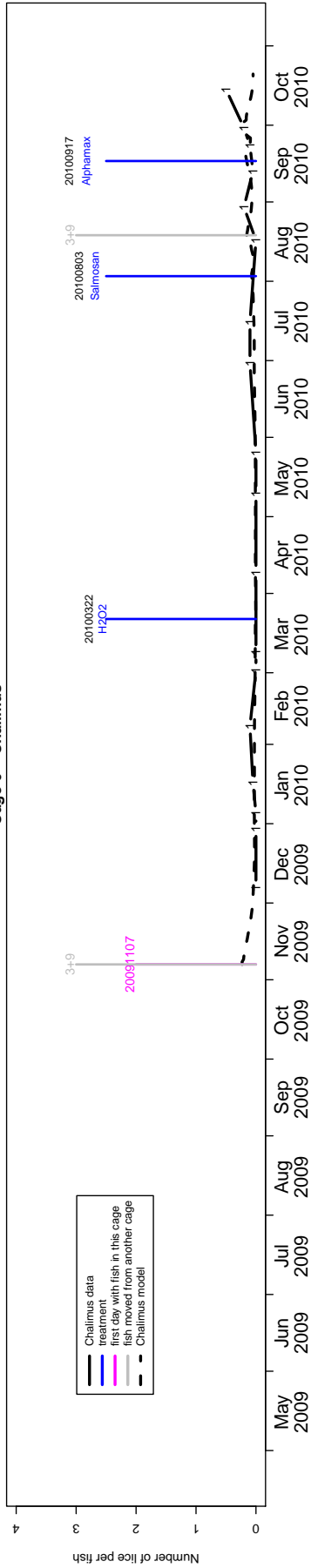
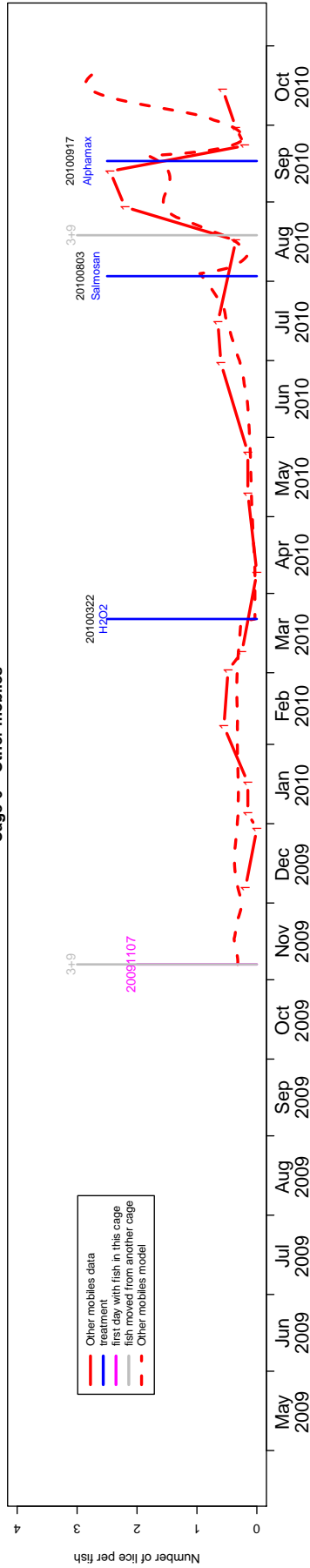


Figure 3. Data and model fit for cage 4.

Cage 6 – Chalimus



Cage 6 – Other mobiles



Cage 6 – Adult females

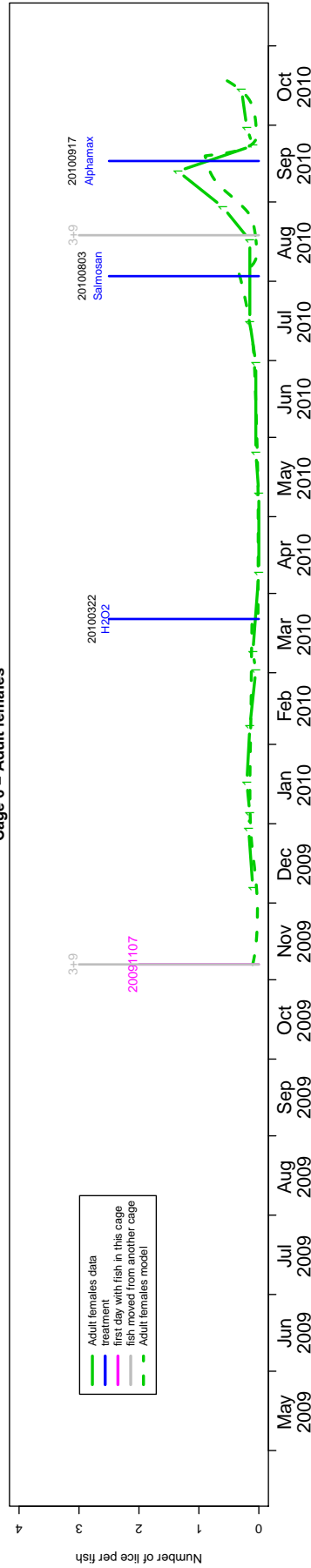
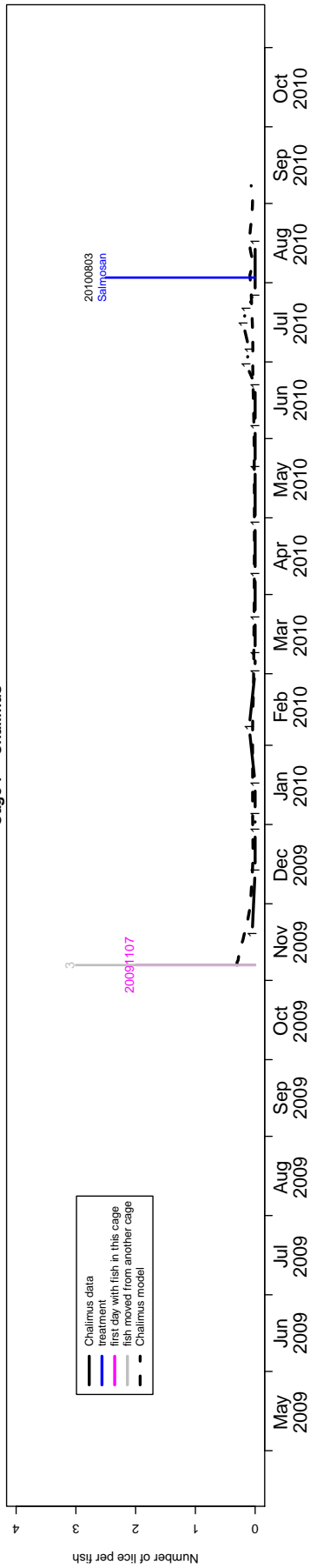
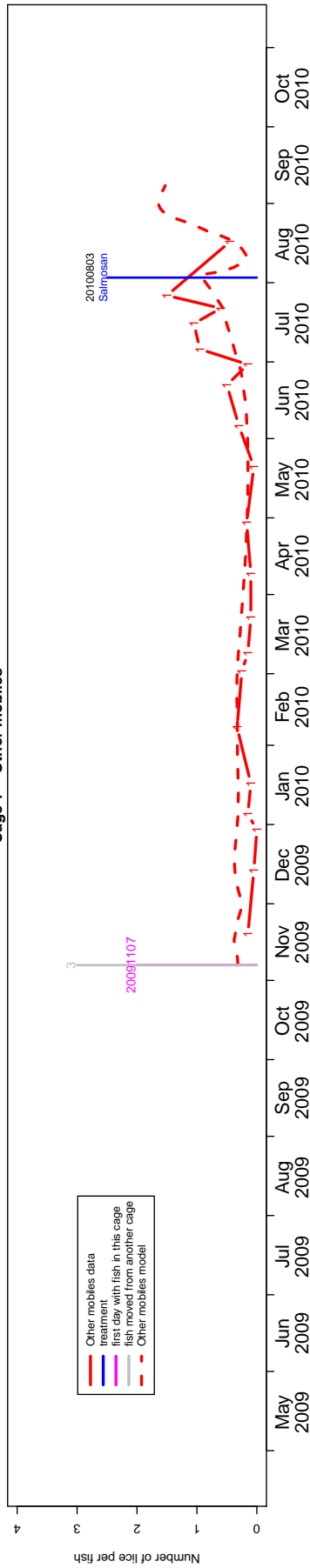


Figure 4. Data and model fit for cage 6.

Cage 7 – Chalimus



Cage 7 – Other mobiles



Cage 7 – Adult females

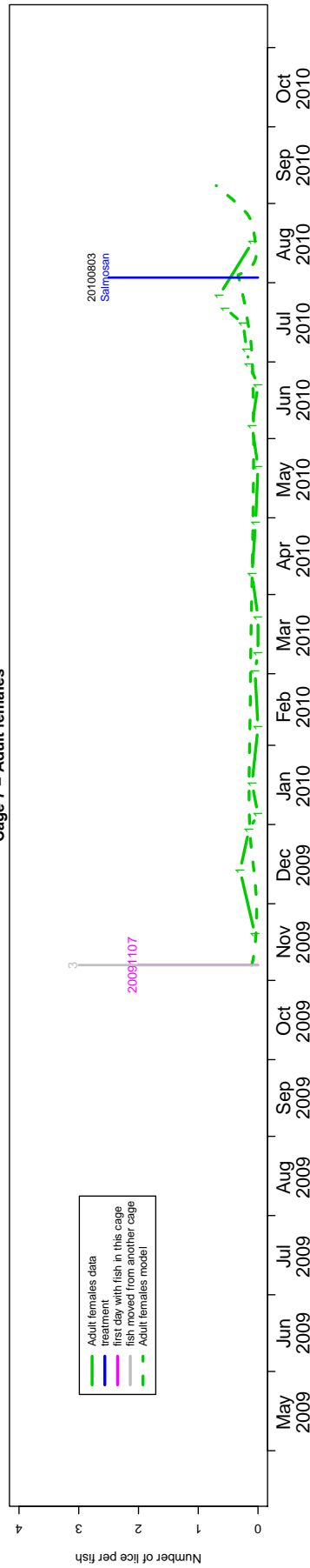
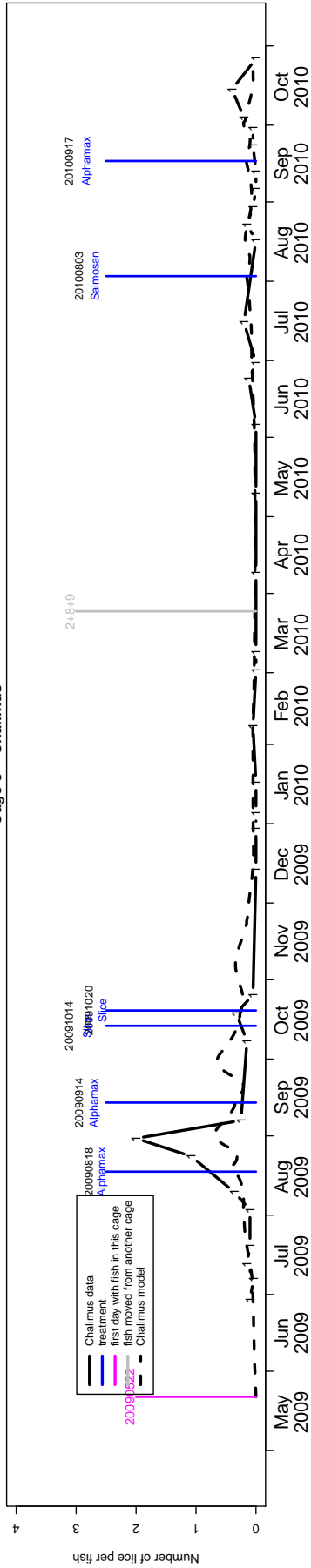
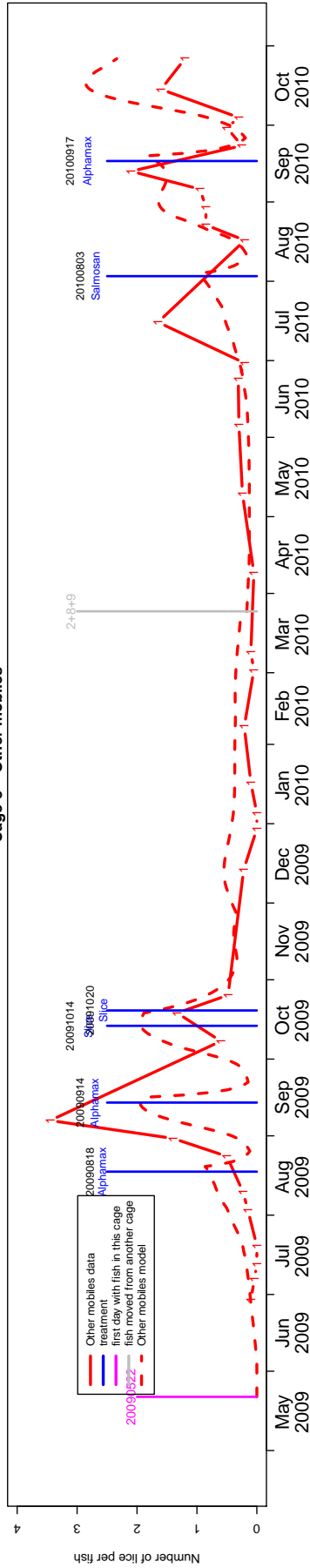


Figure 5. Data and model fit for cage 7.

Cage 8 – Chalmus



Cage 8 – Other mobiles



Cage 8 – Adult females

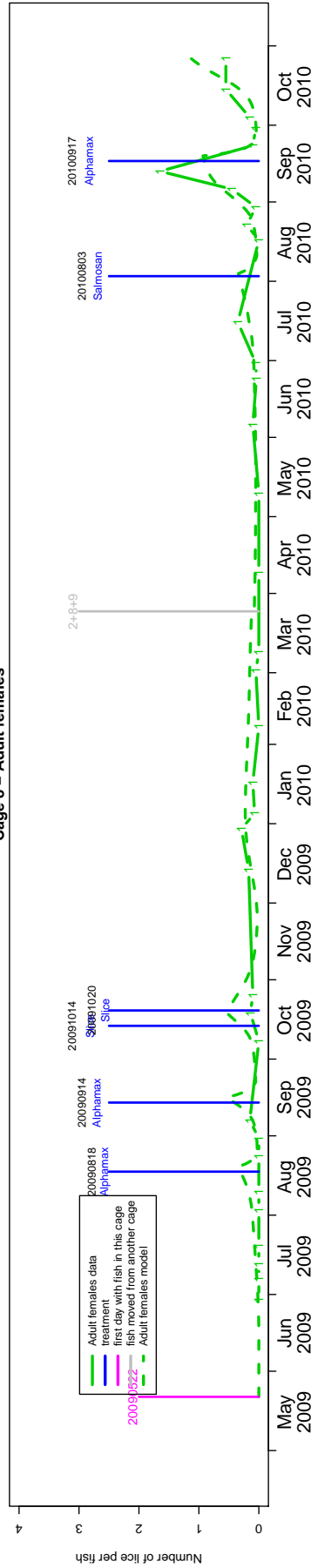
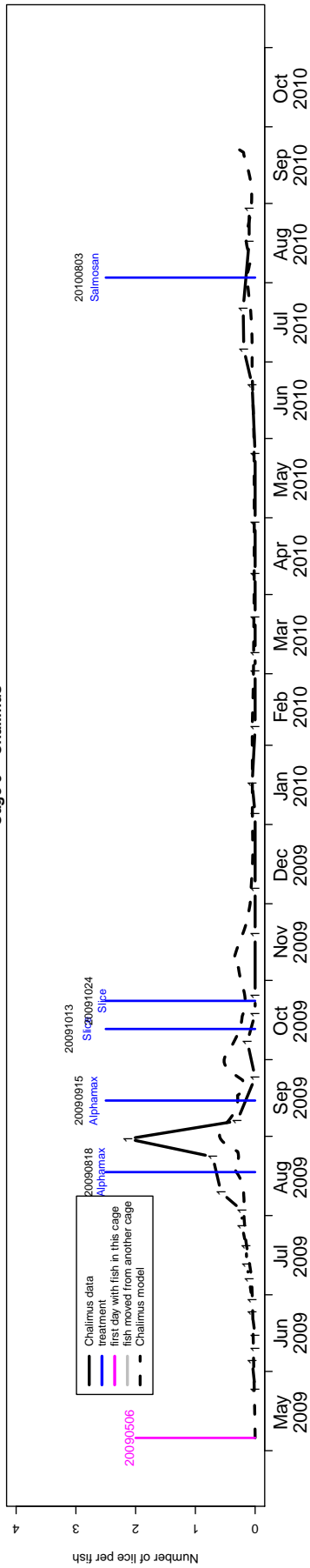


Figure 6. Data and model fit for cage 8.

Cage 9 – Chalmus



Cage 9 – Other mobiles



Cage 9 – Adult females

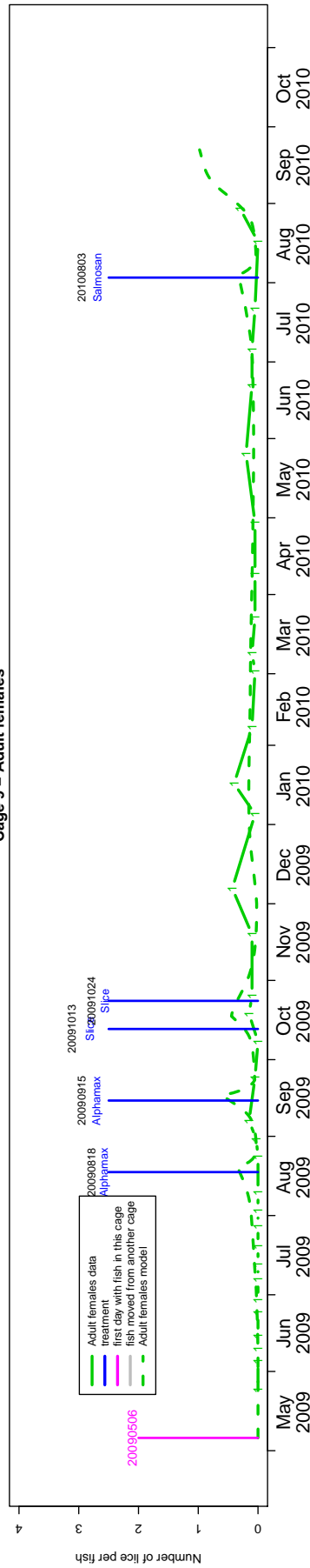
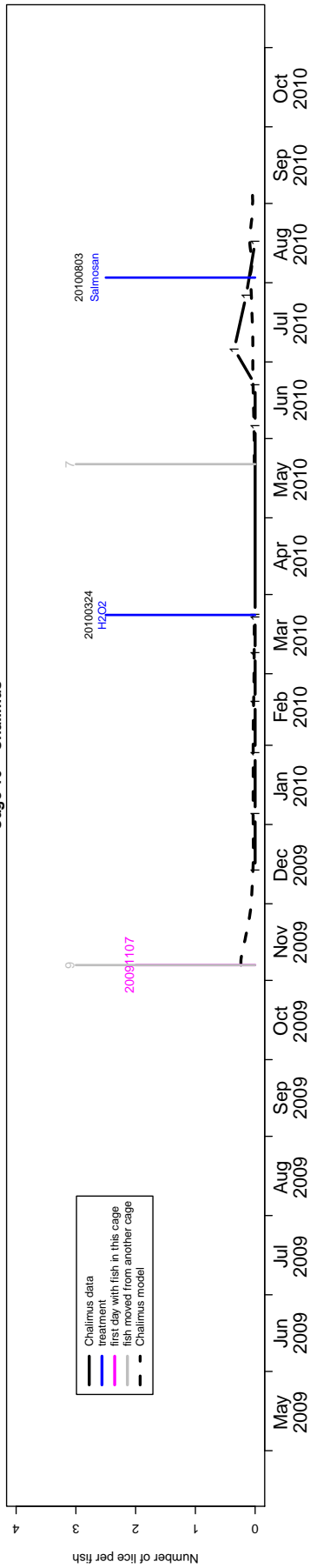
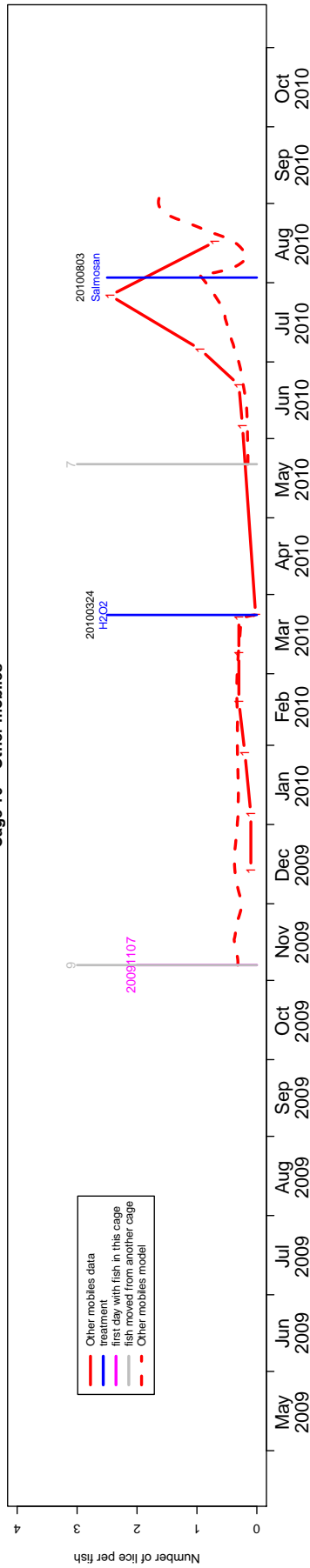


Figure 7. Data and model fit for cage 9.

Cage 10 – Chalmus



Cage 10 – Other mobiles



Cage 10 – Adult females

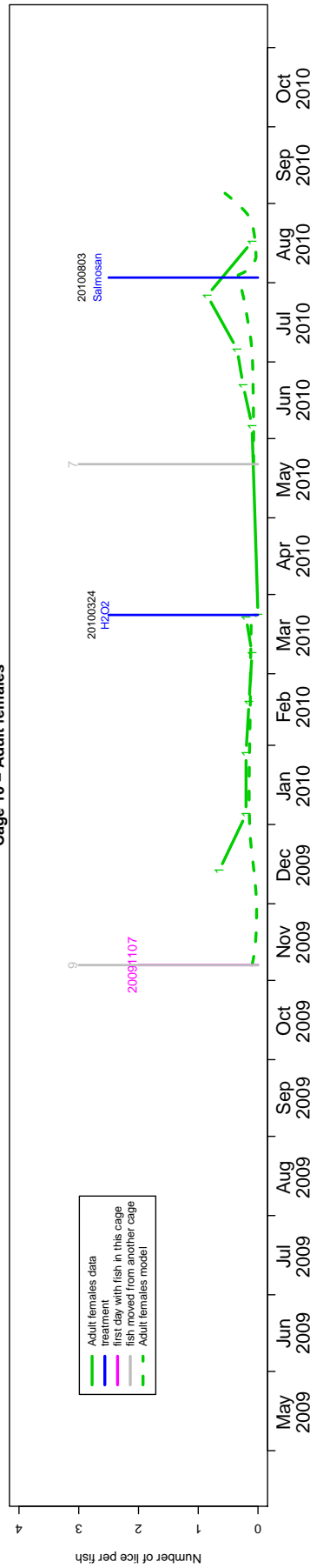


Figure 8. Data and model fit for cage 10.

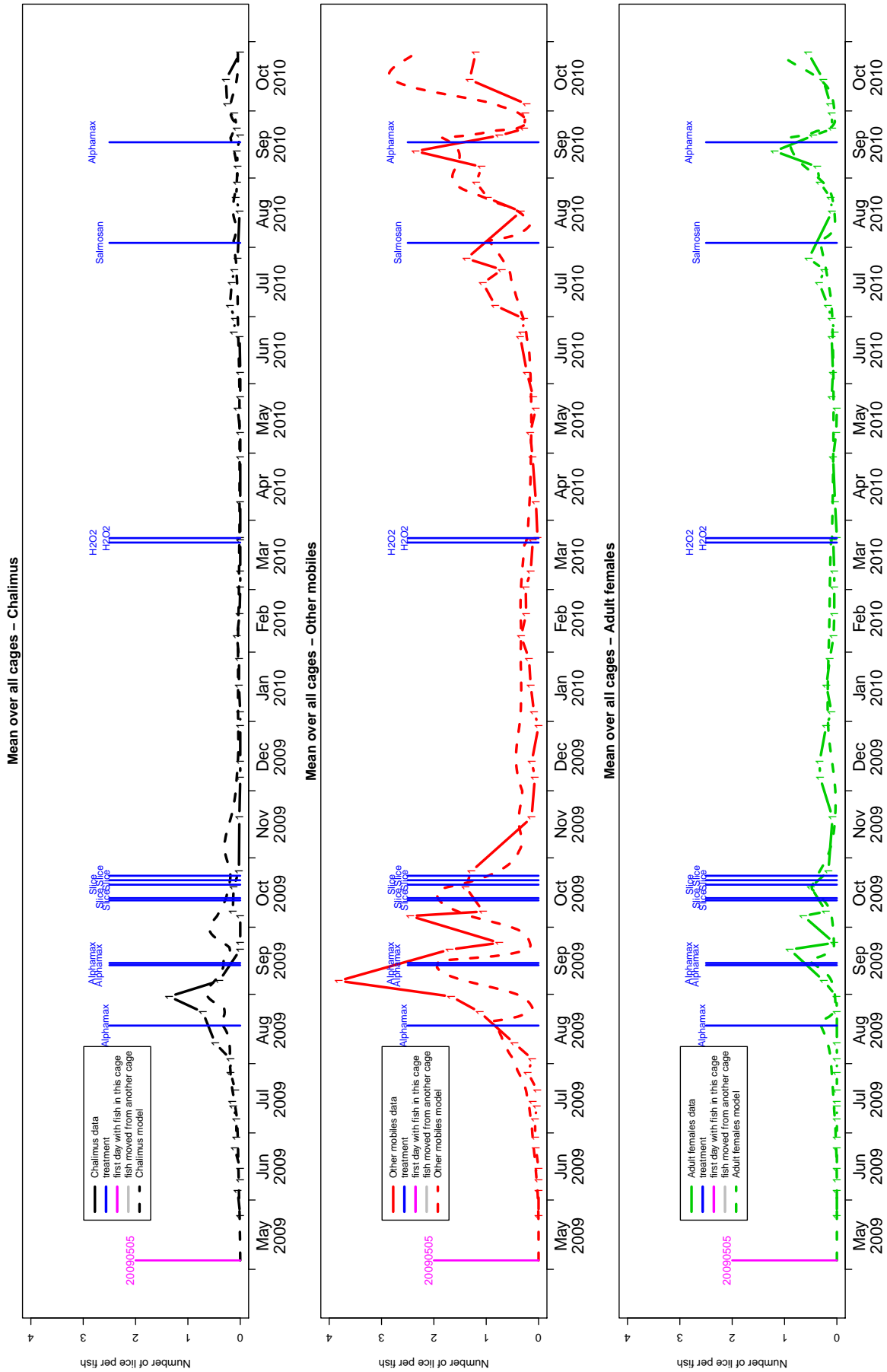


Figure 9. Data and model fit averaged over all cages.

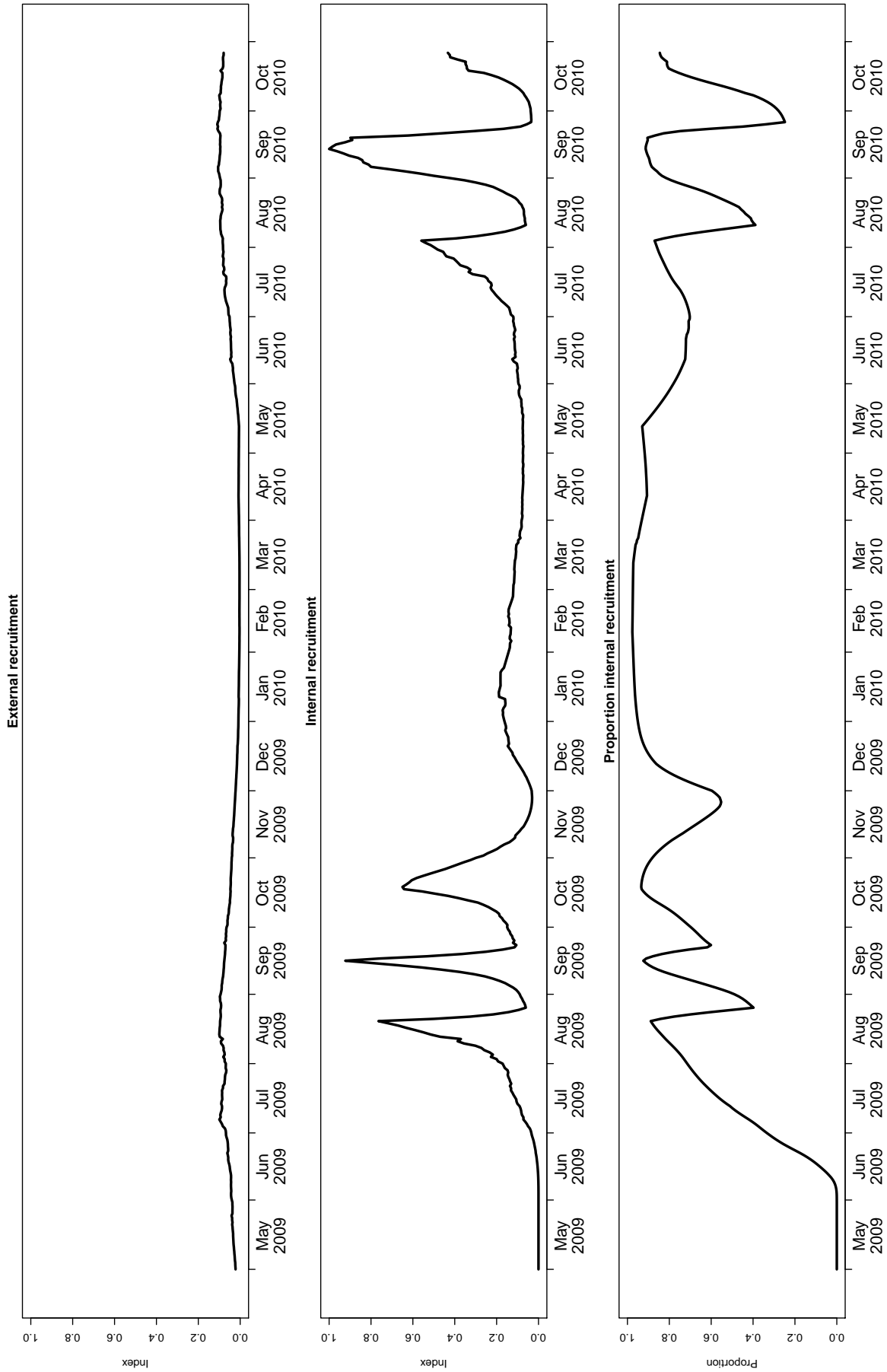


Figure 10. Indexes for external (upper panel) and internal (middle panel) recruitment, and proportion of internal recruitment (lower panel). The indexes for external and internal recruitment is scaled so the maximum value of internal recruitment is 1.

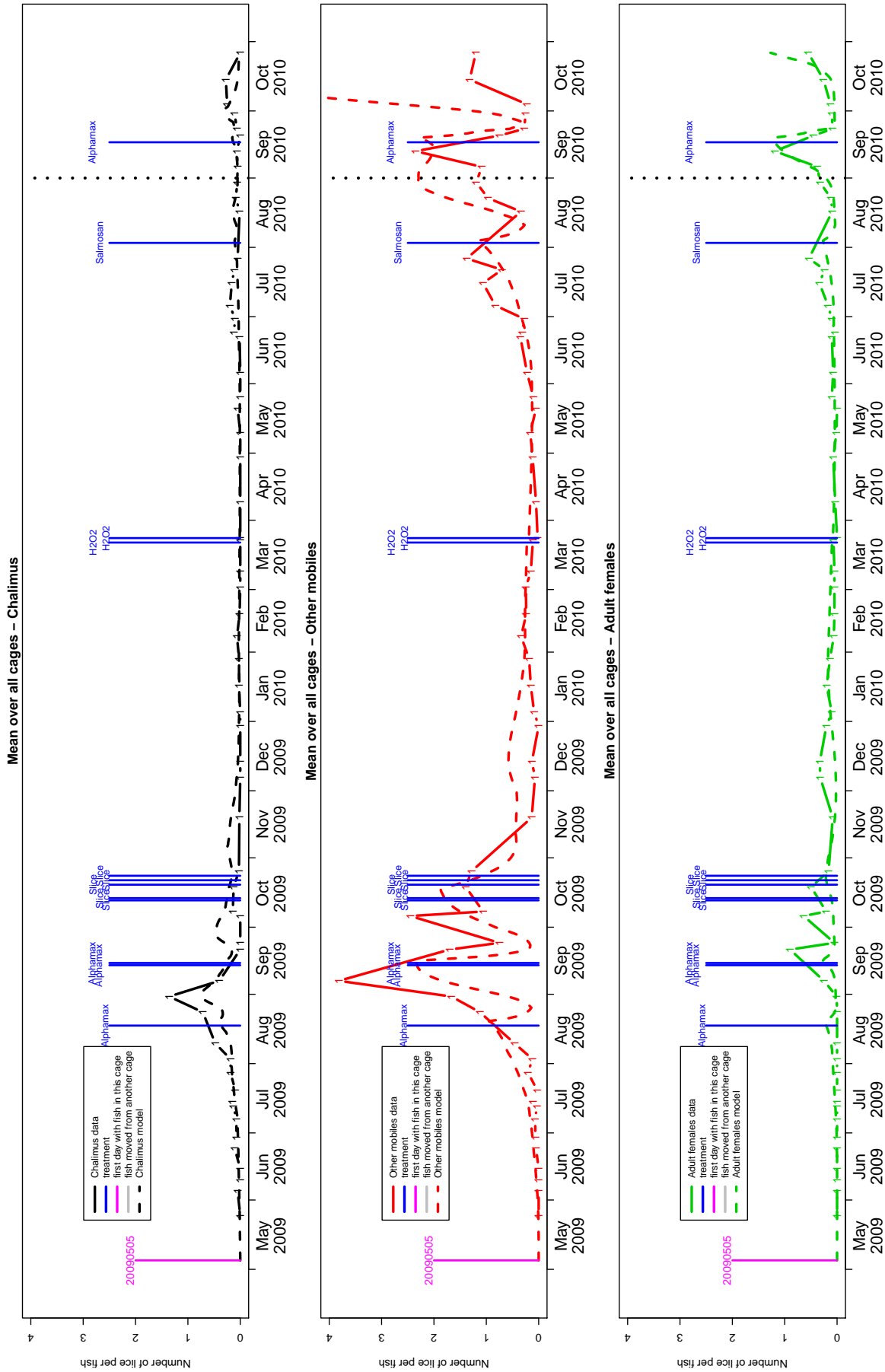


Figure 11. Data, model fit until 31 . August 2010 and predictions from 1. September 2010, averaged over all cages. The dashed horizontal line 1. September 2010 marks the start of the prediction period.

10 Conclusions

The model we have presented here constitutes a useful basis for a model that can be implemented and applied routinely at fish farms in the future, but it has to be improved and extended first.

The model is deterministic. It can be improved by introducing stochastic elements in parts of the model.

First, one could introduce a random error term in several parts of the model, where the error typically can be positively correlated over time. For instance, both the mortality rates and the development rates for each stage may be extended by an error term that follows an autoregressive process of order 1. Figure 9 shows that the model in periods is systematically higher or lower than the data, and this can be improved by introducing such error terms.

Furthermore, in the present model, the effect of a specific treatment is the same every time such treatments are applied. But by looking at the data, for instance in Figure 9, it seems that the treatment by Alphamax in August 2009 was not very successful, whereas it seemed to be very effective in September 2009 and September 2010. This can be handled by a random effect, where a specific treatment has an average effect, but that the effect can vary from one application to another.

When the model is extended, one also needs more data to estimate all the parameters. We suggest therefore that data for more than one farm are included when the model is developed further.

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