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by consumption of common minke whales
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ABSTRACT

A statistical analysis was conducted to assess predation impacts of the common minke whales on the sandlance population off Sanriku region. A state-space delay-difference model, which is a two-stage population dynamics model with a stock-recruitment relationship, was used for the sandlance population to employ two independent time series indices for the juvenile and mature population sizes as well as catch and age-composition data. Predation impacts on the sandlance were assessed through minke whales' consumption expressed as a functional response. To take into account several stochastic flexibilities such as process errors, a Bayesian method was used to estimate the parameters and latent variables in the model. The results showed that the predation by the common minke whales accounts for a certain proportion of the current adult biomass for the sandlance population although the level of proportion is sensitive to the model assumption.

KEYWORDS: COMMON MINKE WHALES, DELAY-DIFFERENCE MODEL, PREDATION, SANDLANCE

INTRODUCTION

The sandlance off Sanriku, which is the western North Pacific region of Japan, is one of commercially valuable fishery populations in that area. The sandlance is also one of prey species for the western North Pacific common minke whales, and therefore an interaction between fishery and predation by the common minke whales is of interest for better understanding of the sandlance population.

The life history of sandlances is illustrated in Figure 1. The peak spawning season is an early period in the calendar year, and then the fishery by dip nets starts in February for adult sandlances, which continues until June, and that for juvenile sandlances comes next from March to May. As an atypical ecological life history of this species, they have an aestivation period after the fishing season, and a sampling experiment has been conducted to collect its size-distribution, which is converted to the age-composition data.

Fishery for this species has a long history but the data of catch and population index are poor until 1960. Also, stock indices are available only since mid-1990 although separate indices are available for juvenile and adult sandlances. To exploit this merit and also to employ a moderate complexity of model, we will use a delay-difference model (*e.g.* Hilborn and Walters, 1992; Meyer and Millar, 1999). A state-space model is constructed to take account for both the observation and process errors.

MATERIALS AND METHODS

Data

- 1) Catch series of juvenile sandlances by lift nets with light fishery from 1960-2015 (Figure 2)
- 2) Catch series of adult sandlances by dip nets fishery from 1960-2015 (Figure 2)
- 3) CPUE series of juvenile sandlances by lift nets with light fishery from 1994-2015 (Figure 3)
- 4) CPUE series of adult sandlances by dip nets fishery from 1994-2015 (Figure 3)
- 5) Time series data for age composition from 2002-2013
- 6) Consumption of sandlances by common minke whales in 2005, 2006 and 2012 (Table 1; see Tamura *et al.*, 2016: SC/F16/JR17 for more details)
- 7) Time series of abundance estimates in Sanriku region for the common minke whales in 2004, 2005,

2006 and 2012 (Table 2; see Hakamada *et al.*, 2016: SC/F16/JR11 for more details)

Notation	Definition	Note
Parameters		
r	Resilience	U(0.01, 2)
K_J	Recruitment at carrying capacity	$f K_A$
K_A	Carrying capacity of adult abundance (1000ton)	U(1,100)
D_A	Depletion level in 1960	U(0.01, 0.99)
z	Exponent of density dependence	Fixed at 1
f	Fecundity at the carrying capacity	Derived by (4)
S_J	Juvenile survival rate	U(0.01, 0.99)
S_A	Adult survival rate	U(0.01, 0.99)
q_J	Juvenile survival rate	U(0.00001, 0.99)
q_A	Adult survival rate	U(0.00001, 0.99)
F_J	Exploitation rate for juveniles	U(0.01, 0.99)
F_A	Exploitation rate for adult	U(0.01, 0.99)
σ_J, σ_A etc.	Residuals	U(0.001, 1) for all SDs
α	Growth intercept	Fixed at 9.519
ρ	Growth slope	Fixed at 0.234
w_0	Weight at age 0	Fixed at 3.264 (g)
w_1	Weight at age 1	Fixed at 10.33 (g)
c_{\max}	Per capita maximum consumption	U(0.001,100)
B_H	Parameter in functional response	U(1,1000)
Estimated in the model		
$N_{J,t}$	Juvenile sand lance abundance in year t	Log normal process error
$N_{A,t}$	Adult sand lance abundance in year t	Log normal process error
$B_{J,t}$	Juvenile sand lance biomass in year t	
$B_{A,t}$	Adult sand lance biomass in year t	
Data		
$I_{J,t}$	Observed CPUE for juvenile sand lances	Log normal
$I_{A,t}$	Observed CPUE for adult sand lances	Log normal
$C_{J,t}$	Observed CPUE for juvenile sand lances	Log normal
$C_{A,t}$	Observed CPUE for adult sand lances	Log normal
Neff	Effective sample size	Assumed
$n_t = (n_{0,t}, n_{1,t}, n_{2+,t})$	Age composition adjusted by Neff	Multinomial
\hat{P}_t	Number of migrant minke whales off Sanriku	Log normal
Y_t	Consumption of sand lances by minke whales	Log normal

State-space Population Dynamics Models for sandlances (Model I)

We employ a delay-difference model with juvenile and adult stages. The list above summarizes notations used in this paper. The number of juvenile sandlances is assumed to be expressed as a density dependent stock-recruitment model with a process error as follows:

$$N_{J,t} = f N_{A,t} \left\{ 1 + r \left(1 - \left(\frac{N_{A,t}}{K_A} \right)^z \right) \right\} e^{u_{J,t}}, \quad u_{J,t} \sim N(0, \sigma_J^2). \quad (1)$$

The number of adult sandlances is expressed as a sum of survived juveniles and adults as follows:

$$N_{A,t} = \left[(1 - F_{A,period(t-1)}) S_A N_{A,t-1} + (1 - F_{J,period(t-1)}) S_J^{1/2} S_A^{1/2} N_{J,t-1} \right] e^{u_{A,t}}, \quad u_{A,t} \sim N(0, \sigma_A^2) \quad (2)$$

As in other population dynamics models, a simultaneous equation for the equilibrium conditions at the carrying capacity (say K_J and K_A),

$$\begin{cases} K_J = f K_A \left\{ 1 + r \left(1 - \frac{K_A}{K_A} \right) \right\}, \\ K_A = S_A K_A + S_J^{1/2} S_A^{1/2} K_J \end{cases} \quad (3)$$

produces an explicit solution for the fecundity, f , as

$$f = \frac{1 - S_A}{S_J^{1/2} S_A^{1/2}}. \quad (4)$$

The biomass of juvenile and adult sandlances can be given by the following formulas:

$$\begin{aligned} B_{J,t} &= w_0 N_{J,t} \\ B_{A,t} &= w_1 N_{A,t} \end{aligned} \quad (5)$$

Using a relationship

$$B_{A,t} = w_1 N_{A,t} = w_1 (1 - F_{A,t}) S_A N_{A,t} + w_0 (1 - F_{J,t}) S_J^{1/2} S_A^{1/2} N_{J,t} \quad (6)$$

and Ford-Brody

$$w_1 N_{A,t} = \alpha N_{A,t} + \rho B_{A,t}, \quad (7)$$

which is derived from a general assumption of growth for fish of age a

$$w_a N_{a,t} = (\alpha + \rho w_{a-1}) N_{a,t} = \left[\alpha N_{a-1,t} + \rho w_{a-1} N_{a-1,t} \right] (1 - F_a) S_a, \quad (8)$$

the following recursive formula is obtained:

$$B_{A,t} = (\alpha N_{A,t-1} + \rho B_{A,t-1}) (1 - F_{A,period(t)}) S_A + w_1 (1 - F_{J,period(t)}) S_A^{1/2} S_J^{1/2} N_{J,t-1}. \quad (9)$$

State-space Population Dynamics Models for sandlances with whale consumption (Model II)

In case that the mortality by the minke whale predation is taken into account, then the following model is proposed, where g is a function for functional response:

$$N_{A,t} = \left[(1 - F_{A,period(t-1)}) S_A N_{A,t-1} - \frac{1}{w_1} g(B_{A,t-1}) P_t + (1 - F_{J,period(t-1)}) S_J^{1/2} S_A^{1/2} N_{J,t-1} \right] e^{u_{A,t}}, \quad (10)$$

where the functional response is generally given by

$$g(B_{A,t}) = \frac{c_{\max} B_{A,t}^m}{B_H^m + B_{A,t}^m}, \quad (11)$$

though we here assume only $m=1$ (Type II functional response).

Observation models

CPUE data (tons/vessel) are available for juvenile and adult sandlances. Here, neither of hyperstability nor hyperdepletion is considered for both the fisheries.

$$\begin{aligned} \log I_{J,t} &\sim N(\log(q_{J,period(t)} B_{J,t}), \tau_J^2) \\ \log I_{A,t} &\sim N(\log(q_{A,period(t)} B_{A,t}), \tau_A^2) \end{aligned} \quad (12)$$

The total catch and age-composition data are also available for estimation of parameters as follows:

$$\begin{aligned} \log C_{J,t} &\sim N(\log(F_{J,period(t)} B_{J,t}), \gamma_J^2) \\ \log C_{A,t} &\sim N(\log(F_{A,period(t)} B_{A,t}), \gamma_A^2) \end{aligned} \quad (13)$$

and

$$n_t = (n_{0,t}, n_{1,t}, n_{2+,t}) \sim \text{Multinomial}(N_t, (p_{0,t}, p_{1,t}, p_{2+,t})), \quad (14)$$

where

$$\begin{aligned} p_{0,t} &\propto (1 - F_{J,t}) S_J^{1/2} N_{J,t} \\ p_{1,t} &\propto (1 - F_{A,t}) S_A (1 - F_{J,t-1}) S_J^{1/2} N_{J,t-1} \\ p_{2+,t} &\propto (1 - F_{A,t}) S_A (1 - F_{A,t-1}) S_A^{1/2} N_{A,t-1} \end{aligned} \quad (15)$$

and $n_t = (n_{0,t}, n_{1,t}, n_{2+,t})$ is a vector for the age-composition of sampled individuals ($N_t = n_{0,t} + n_{1,t} + n_{2+,t}$). We here assume an effective sample size (Neff) as 100 for all the years.

The total consumption of sandlance by the common minke whales and the population size of minke whales contributed to the likelihood in Model II.

$$\begin{aligned} \log \hat{P}_t &\sim N(\log P_t, \hat{C}V_t^2) \\ \log P_t &\sim (iid)N(\log \bar{P}, \lambda^2) \end{aligned} \quad (16)$$

$$\log Y_t \sim N(\log(g(B_{A,t})P_t), cv_t^2) \quad (17)$$

Statistical estimation

Due to a large number of parameters are included in the model, achievement of convergence might be difficult when the likelihood is tried to be maximized. Also, usually it is hard to distinguish the process error variance from observation error variance. Therefore, when the process error is estimated, a Bayesian method is applied. Also in theory the Bayesian method has a benefit when a hierarchical structure such as smooth changes in the fishing mortality is incorporating into the model.

A Markov Chain Monte Carlo method (*e.g.* Gelman *et al.*, 2013) was employed for generating posterior distribution. A software WinBUGS (Speigelhalter, 2003) was used for this computation.

RESULTS AND DISCUSSION

Model Fitting and Parameter estimates

Figure 4 shows the posterior distributions of key estimated parameters in Model I, and Figure 5 presents fitness in CPUE as well as the estimated population trajectories for juveniles and adults in that model. Also, Figure 6 and 7 provide the same information for Model II. The posterior distributions are almost unimodal except for some parameters with bounds, but the original assumption of prior shapes and the generated posterior distributions indicated that all the parameters were well-updated using information of observed data. However, in most recent years, the predicted CPUEs tend to be greater than observed values. This might be attributed to changes in the fishery; the less fishing efforts compared to the prequake level.

The total biomass level of sandlances is estimated differently in Models I and II, respectively. The results showed that the predation by the common minke whales accounts for a certain proportion of the current adult biomass for the sandlance population although the level of proportion is sensitive to the model assumption.

Potential sensitivity tests and extensions

We applied a Bayesian method for estimation parameters, but further analyses should be conducted to examine sensitivities of the results to the assumption of prior distributions.

Regarding the modelling, we only consider a Type II functional response to link between preys and predators in the model. Another functional form and/or multiple-prey functional response with krill and anchovy are worth investigation. Also, it is possible to extend the model by incorporating more hierarchical structures such as assumption of smooth changes in fishery coefficients. Bayesian methods have benefits of these sorts of extensions.

How weights are allocated to likelihood components is a matter of interest these days especially in the forum of integrated models, which tend to use a multiple sources of information/data. Usually, due to a nature of fishery population, the actual samples for age composition are not independent and therefore the reduced sample size, so-called the effective sample size (which is less than the original sample size), is assumed to relatively down-weight the likelihood of age/size composition data to the CPUE data etc. A more careful examination will be addressed in the future.

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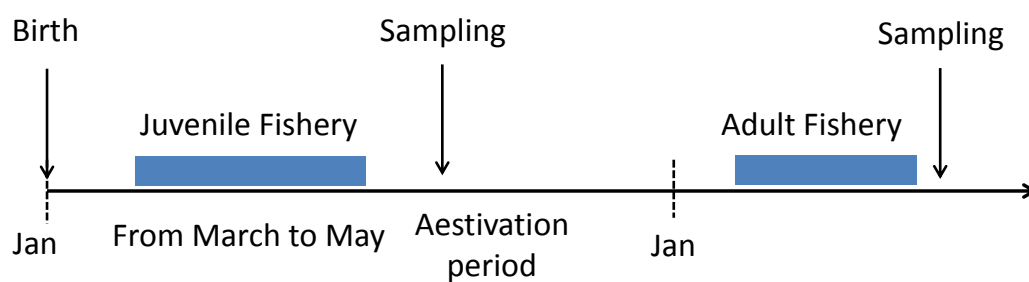
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Table 1. Consumption of sandlances by common minke whales.

Year	Sandlance consumption (ton)	CV
2005	3,709	0.16
2006	1,522	0.18
2012	683	0.22

Table 2. Time series of abundance estimates in Sanriku region for the common minke whales

Year	Minke whale abundance	CV
2004	260	0.56
2005	401	0.32
2006	216	0.41
2012	124	0.37

**Figure 1.** Life history of sandlance population.

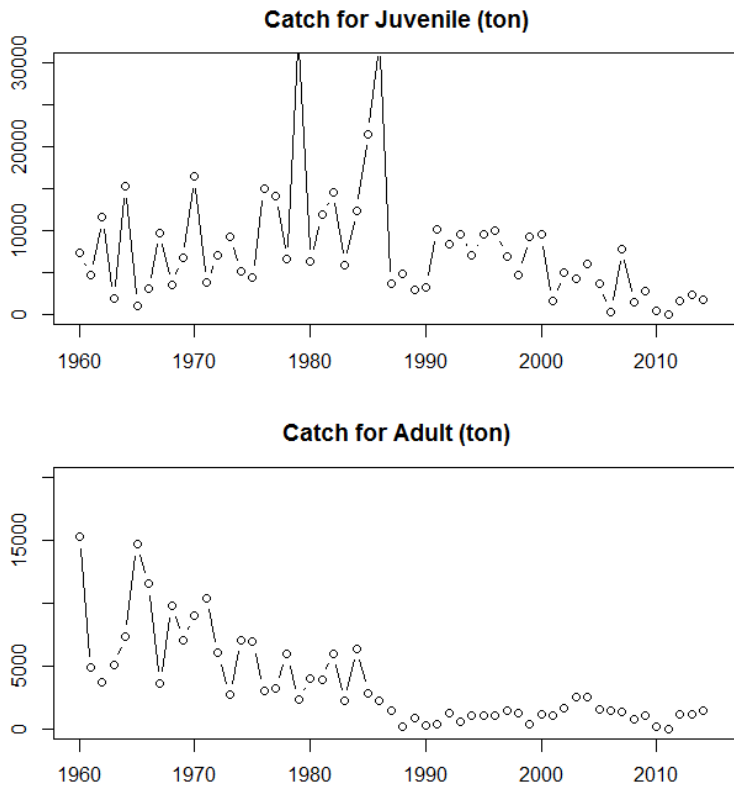


Figure 2. Time series of catch for juvenile and adult sandlances.

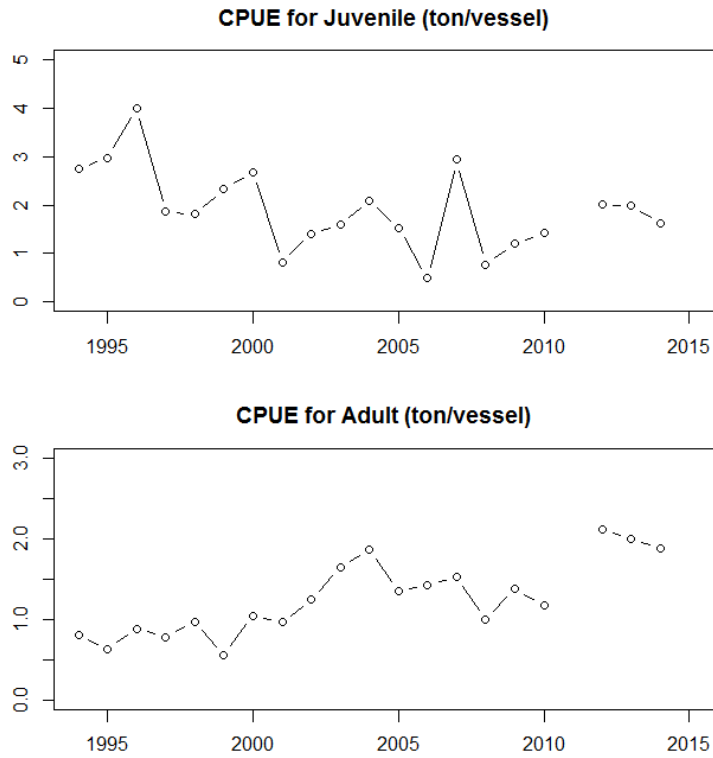


Figure 3. Time series of CPUE for juvenile and adult sandlances.

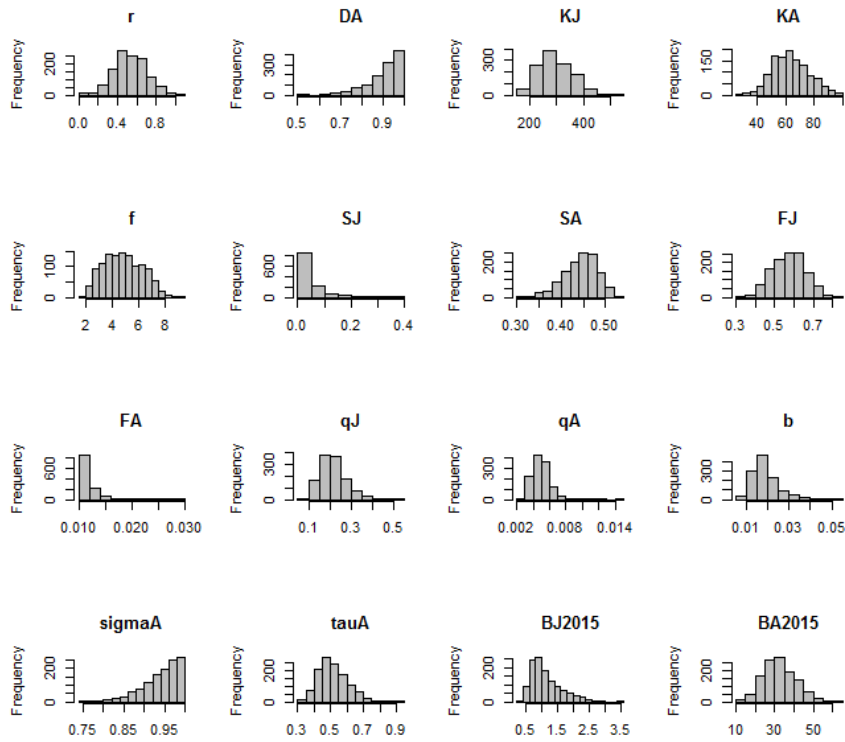


Figure 4. Posterior distributions of key estimated parameters in Model I.

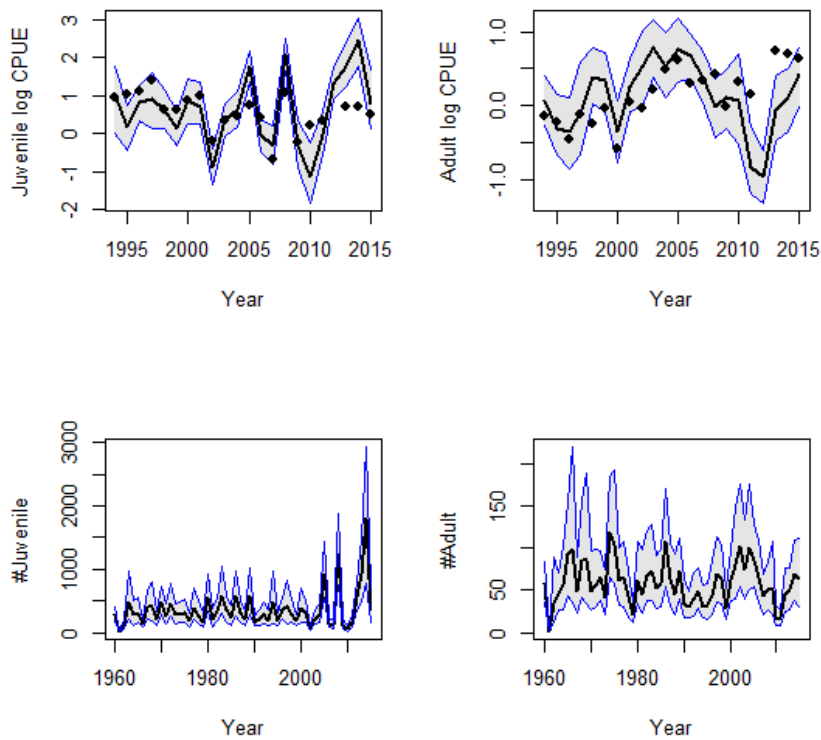


Figure 5. Fitness in CPUE and estimated population trajectories with 95% credible region for juveniles and adults for Model I.

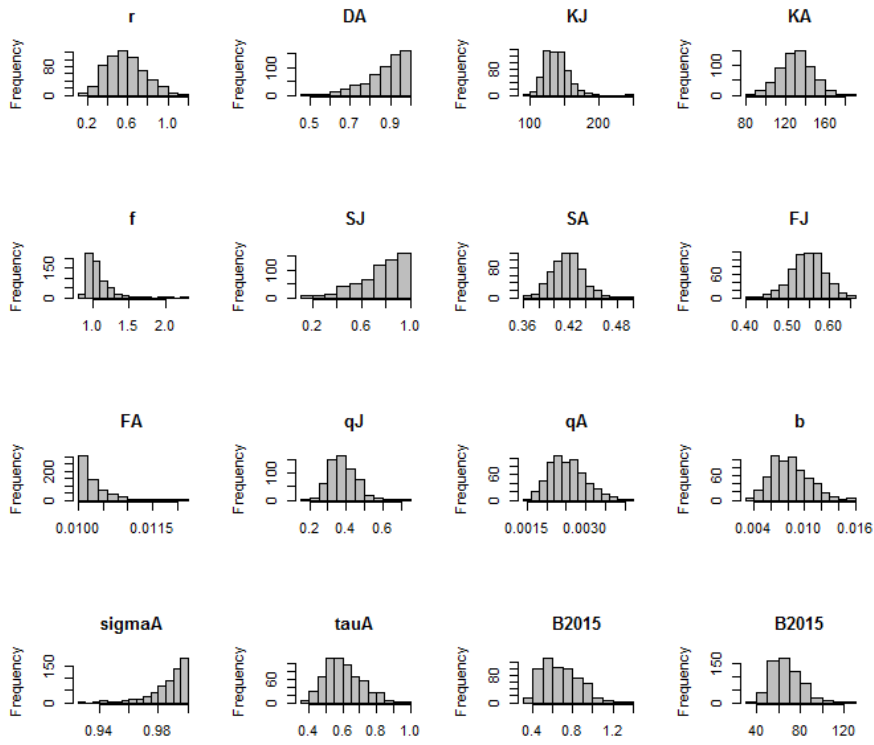


Figure 6. Posterior distributions of key estimated parameters in Model II.

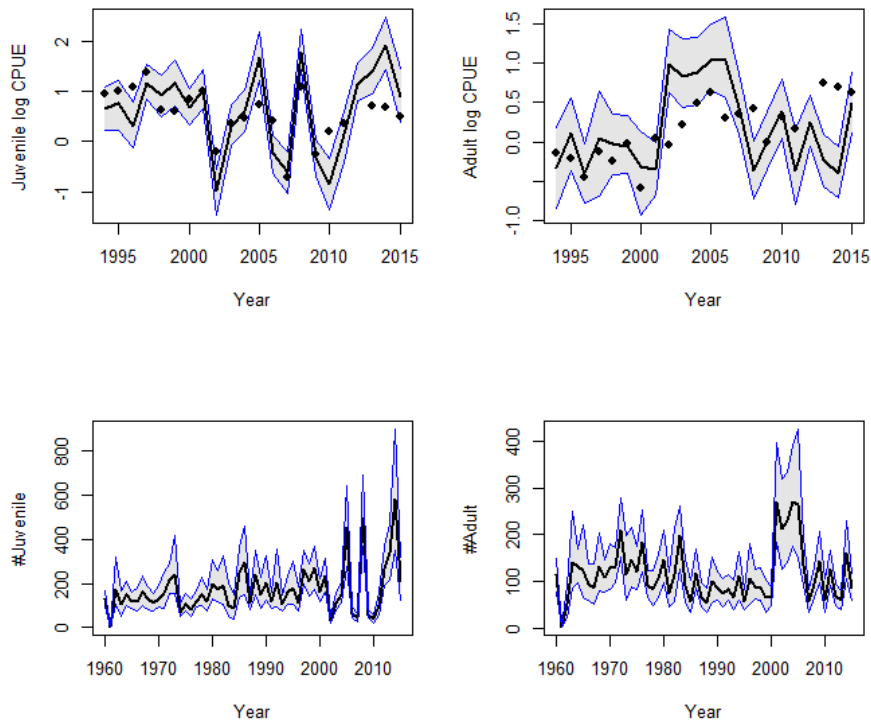


Figure 7. Fitness in CPUE and estimated population trajectories for juveniles and adults for Model II.