Recevied: 22 & 28 August 2015

Update of standardized CPUE of blue shark (*Prionace glauca*) in the Indian Ocean estimated from Japanese observer data in the period between 1992 and 2014

Yasuko Semba[2], Minoru Kanaiwa1,and Kotaro Yokawa[2]

[1]National Research Institute of Far Seas
Fisheries, Fishery Research Agency
5-7-1 Orido, Shimizu-ku, Shizuoka 424-8633, JAPAN

[2]Tokyo University of Agriculture, Faculty of Aquatic bioscience
196 Yasaka, Abashiri, Hokkaido Japan 099-2493

Summary

This document provided the update of standardized CPUE (catch number per 1000 hooks) of blue shark caught by Japanese longline fishery in the Indian Ocean, based on Japanese observer data conducted between 1992 and 2014. As the operation observed in 2013 strongly biased to certain area, the standardization was conducted without the data of 2013. The model selection based on information criteria and statistical test suggested the zero-inflated negative binomial GLM was the best model among three type of GLM (Poisson FLM, zero-inflated Poisson GLM and zero-inflated negative binomial GLM). Throughout the period analyzed, the standardized CPUE indicated relatively stable trend except fluctuation between 1998 and 2000. The estimate of 2013 was not obtained in this study, however, neither continuously increasing nor decreasing trend of abundance was suggested in this analysis.

Key words

Blue shark, standardized CPUE, zero inflated model, Japanese longline fishery

Introduction

Blue shark (*Prionace glauca*) is one of the popular and important bycatch shark species for Japanese tuna longline fishery in the Indian Ocean. In the past, Mastunaga (2007), Hiraoka and Yokawa (2011 and 2012) estimated the abundance index of blue shark caught by Japanese longliners in the Indian Ocean, using filtered log-book data of commercial boat. The evaluation of filtering method for sharks in the Indian Ocean has been left to be done, which was addressed by Kai and Yokawa (2015) based on comparison between commercial logbook data and observer data. The analysis of observer data provides the reliable index of abundance because the data includes all discards and released individuals. Kanaiwa et al. (2014) estimated the abundance index of blue shark using observer data collected by Japanese national observer program of CCSBT. CCSBT observer program started in 1992 and its data widely covers high latitudinal area in the south Indian Ocean where blue shark abundantly distributes. This document updated the standardized CPUE of blue shark estimated by Kanaiwa et al. (2014) using the data of 2013 and 2014.

Material and Method

1) Data set

Catch and effort data used in this analysis was provided from the Japanese longline fishery statics compiled at the

National Research Institute of Far Seas Fisheries for 1992-2014 through the Japanese national observer program of CCSBT. The number of catch, the number of hooks, spatio-temporal information of each operation (year, month, day, latitude and longitude) and the number of branch lines between floats (hooks par basket: HPB) were used for this analysis.

2) Data filtering

The data which does not have latitude or longitude or hooks or catch or HPB was removed from this analysis. The data of 2013 was removed because of small observation number and bias of spatial distribution. The data whose HPB is larger than 14 and more northern than 25°S was removed from this analysis to keep constancy of fishery. Because the fishery season of Southern bluefin tuna is between April and December, these seasons are used for this analysis.

3) Model description

Three standardized models were used for this analysis, i.e. Poisson GLM, zero-inflated Poisson GLM and zero-inflated negative binomial GLM. The models structures are below.

Poisson GLM:

$Catch = \alpha_1 \cdot year + \alpha_2 \cdot area + \alpha_3 \cdot season + \alpha_4 \cdot year : area + \alpha_5 \cdot area : season + intercept + \varepsilon$ Here, α_1 ～ α_5 are coefficients for each factors, $year$ denotes year factor, $area$ denotes area where eastern than 90° E (area 1) or western (area 0), $season$ denotes season which is season 1 (April – July) or season 2 (August – December), respectively. $year : area$ and $area : season$ denote each interaction, respectively. ε denotes error terms followed by Poisson distribution. Link function is logarithm and log(number of hooks) was used as offset term.

zero-inflated Poisson and Negative binomial GLM:

$$Count\ process's\ catch = \beta_1 \cdot year + \beta_2 \cdot area + \beta_3 \cdot season + \beta_4 \cdot year : area + \beta_5 \cdot area : season + intercept + \varepsilon_1$$
$$False\ zero\ prob = \beta_6 \cdot year + \beta_7 \cdot area + intercept + \varepsilon_2$$

Here, β_1 ～ β_7 are coefficients for each factors. ε_1 denotes error terms followed by Poisson or Negative binomial distribution and ε_2 denotes error terms followed by binomial distribution.

Former model's link function is log and later models link function is logit. Log(number of hooks) was used as offset term.

4) Model evaluations

Person residuals for each category were used for the model evaluations. Vuong Non-Nested Hypothesis Test was used to compare the fitting between predicted and observed data by each model. AIC and BIC were also used to evaluate predictive ability by each model.

For the selected model, the 95% confidence interval for the estimates of annual CPUE was estimated by bootstrap with one thousand replicates for the best-fit model.

Results and Discussions

In the present study, CPUE (catch number / 1000 hooks) of blue shark caught by Japanese longliners was standardized using CCSBT observer data, which consists of operations more or less southern bluefin tuna (*Thunnus maccoyii*) was targeted. Sometimes Japanese longliners conduct temporal switch of their target (i.e., southern bluefin tuna) to other species such as albacore (*Thunnus alalunga*) and bigeye tuna (*Thunnus obesus*) when the catch rate of southern bluefin tuna is lower than those of aforementioned species.

As a result of update of data in 2013 and 2014, GLM models did not converge due to the spatial distribution of operation which was skewed toward a particular area (i.e., 111 operations in eastern area and one operation in western area) in 2013. The skewed distribution of observer data would be partly caused by the decrease of amount of observer effort and flexibility of operation plan by longline vessels due to the increase of catch rate of southern bluefin tuna (Yamazaki et al. 2015). It is suggested that this skewed distribution of operation in terms of area prevented the interaction term between year and area to be included into the model. For the consistency with the model structure of past analysis (Kanaiwa et al. 2014), the calculation was conducted with the removal of 2013 data. Therefore, the estimate of 2013 is not obtained and not shown in the figures and tables.

In the CPUE analysis, evaluation by both vuong non-nested hypothesis test and information criteria (i.e., AIC and BIC) supported the zero-inflated negative binomial GLM as the best model (Table 1, 2). Although the zero catch ratio of the observer data selected for CPUE analysis is generally low (Fig. 1), Kanaiwa et al. (2014) suggests that treatment of zero catch produce better results even in the case of lower zero catch ratio when zero catch ration fluctuates. Comparison of annual trend of standardized CPUE among three types of GLM model was shown in Fig. 2.

The estimated trend of abundance for blue shark shows general stabilized trend with some fluctuations in the period analyzed (Fig.3). Large value in 1999 was suggested to be caused by few observations in which more than 100 sharks were recorded in one operation. Although the reason for this observation is left to be investigated, it is suggested that the effect of these large catch could not be removed by the current model. Considering the productivity of blue shark, which is suggested to be lower than tunas and billfishes, large jump of abundance level in single year is quite unrealistic and thus the observed spike of abundance index in 1999 should better not to be interpreted as it is and lower weight should be put for this value in the stock assessment model. Given this situation, the results of this study indicates that the level of blue shark stock in the south Indian Ocean does not change largely during the period analyzed.

As pointed out previously, the trend of CPUE for blue shark caught in the area where Japanese longliners mainly target southern bluefin tuna (i.e., temperate area) is suggested to reflect the dynamics of main population of this species in the Indian Ocean, because blue shark is known to be abundant in higher latitudinal area than tropical area. According to Coelho et al. (2015), large individuals tend to occur in both tropical area and higher latitudinal part of subtropical area while smaller individuals tend to occur in temperate waters as well as higher latitudinal part of subtropical area in the Indian Ocean. Given this assumption, the result of this document indicates the historical trend of abundance for both adults and subadults.

References

Coelho, R, Yokawa, K, Liu, KM, Romanov, E, da Silva, C, Lino, PG, Oshimo, S, Tsai, WP, and Santos, MN. 2015. Distribution patterns of sizes and sex-ratios of blue shark in the Indian Ocean. IOTC-2015-WPEB11-22

Hiraoka, Y. and K. Yokawa 2011. Standardized CPUE for blue sharks caught by Japanese tuna longline fishery in the Indian Ocean, 1971-1993 and 1994-2010. IOTC–2011–WPEB07–33, 11p.

Hiraoka, Y. and K. Yokawa 2012. Update of CPUE of blue shark caught by Japanese longliner and estimation of annual catch series in the Indian Ocean. IOTC–2012–WPEB08–28, 15p.

IOTC 2012. Report of the eighth session of the IOTC working party on ecosystems and bycatch, Cape Town, South Africa, 17 – 19 September, 2012. IOTC-2012-WPEB08-R[E]. 77p.

Kai, M., and K. Yokawa. 2015. Estimation of appropriate reporting ratio for the blue shark caught by Japanese longlinser in the Indian Ocean. IOTC-2015-WPEB11-YY

Kanaiwa, M., Y. Semba. and K. Yokawa. 2014. Standardized CPUE of blue shark in the Indian Ocean estimated from observer data in the period between 1992 and 2012. IOTC–2014–WPEB010-26.

Matsunaga, H. 2007. Standardized CPUE for blue sharks caught by the Japanese tuna longline fishery in the Indian Ocean, 1971-2005. IOTC-2007-WPEB-17, 5p

Yamazaki, I., T. Itoh., H. Minami., and H. Matsunaga. 2015. Report of Japanese scientific observer activities for southern bluefin tuna fishery in 2013 and 2014. CCSBT-ERS/1503/BGD/XX, 17p

Table 1. List of statistical tests conducted in the CPUE analysis of blue shark caught by Japanese longliners.

model1: GLM with Poisson
model2: zero-inflated with Poisson
Vuong Non-Nested Hypothesis Test-Statistic: -21.42533
(test-statistic is asymptotically distributed N(0,1) under the
null that the models are indistinguishible) in this case:
model2 > model1, with p-value 3.879023e-102

model1: zero-inflated with Poisson
model2: zero-inflated with Negative Binomial
Vuong Non-Nested Hypothesis Test-Statistic: -21.9522
(test-statistic is asymptotically distributed N(0,1) under the
null that the models are indistinguishible) in this case:
model2 > model1, with p-value 4.125667e-107

model1: GLM with Poisson
model2: zero-inflated with Negative Binomial
Vuong Non-Nested Hypothesis Test-Statistic: -24.7925
(test-statistic is asymptotically distributed N(0,1) under the
null that the models are indistinguishible) in this case:
model2 > model1, with p-value 5.400666e-136

Table 2. AIC values for three model analysis of CPUE of blue shark. The model produced smallest AIC selected as one for base case.

	Poisson GLM	zero-inflated Poisson GLM	zero-inflated NB GLM
AIC	91821.97	82224.96	45841.43
BIC	92141.42	82704.13	46327.54

Table 3. Estimated abundance index and its CV of blue shark caught by Japanese longliners targeting southern bluefin tuna in 1992 – 2014.

	Median of standardized CPUE	C.V.
1992	1.5484	0.0765
1993	2.0201	0.0826
1994	2.9026	0.1113
1995	2.5564	0.0857
1996	3.7686	0.0572
1997	1.8683	0.0765
1998	3.4975	0.0754
1999	5.9774	0.0785
2000	3.1970	0.1187
2001	3.4050	0.0989
2002	3.1842	0.0721
2003	3.8944	0.0522
2004	1.8877	0.0514
2005	2.6710	0.0843
2006	2.1925	0.0596
2007	2.2322	0.0851
2008	2.2209	0.0546
2009	3.9174	0.0688
2010	1.6861	0.0874
2011	2.4278	0.0737
2012	3.3426	0.0596
2014	3.0920	0.0779

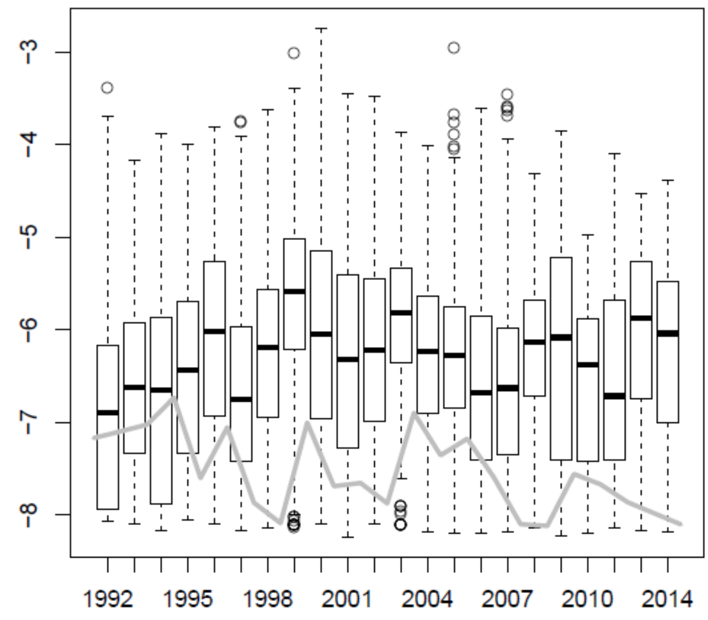


Fig. 1. Annual trend of zero catch ratio (grey line) and positive CPUE (box plot: log scale, n / hooks) of blue shark caught by Japanese longliners obtained by Japanese national observer program of CCSBT. Unit of Y axis is log(CPUE).

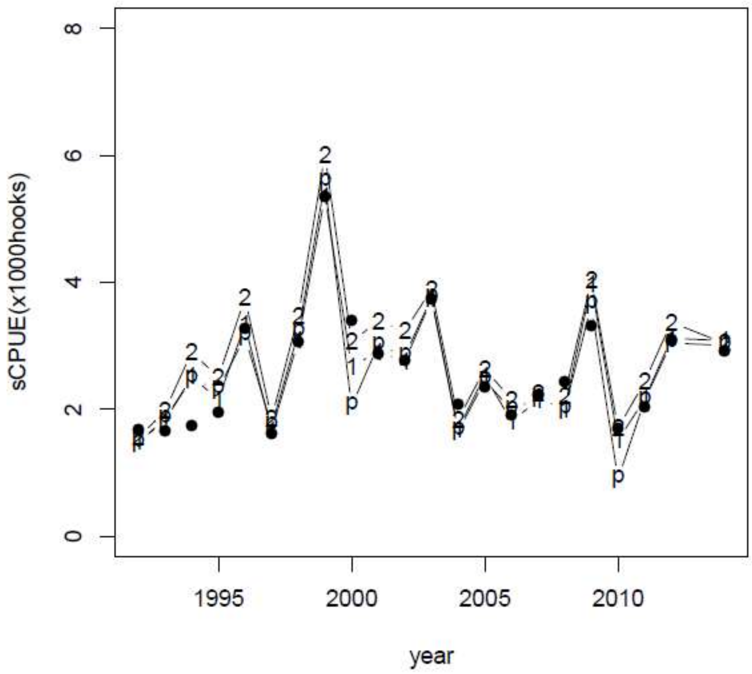


Fig. 2 Annual trend of CPUE of blue shark standardized by Poisson GLM (p), Zero-inflated Poisson GLM (1), Zero inflated Negative binominal GLM, and nominal one (closed circle) in the period between 1992 and 2014. Note that data of 2013 was not included in the standardization.

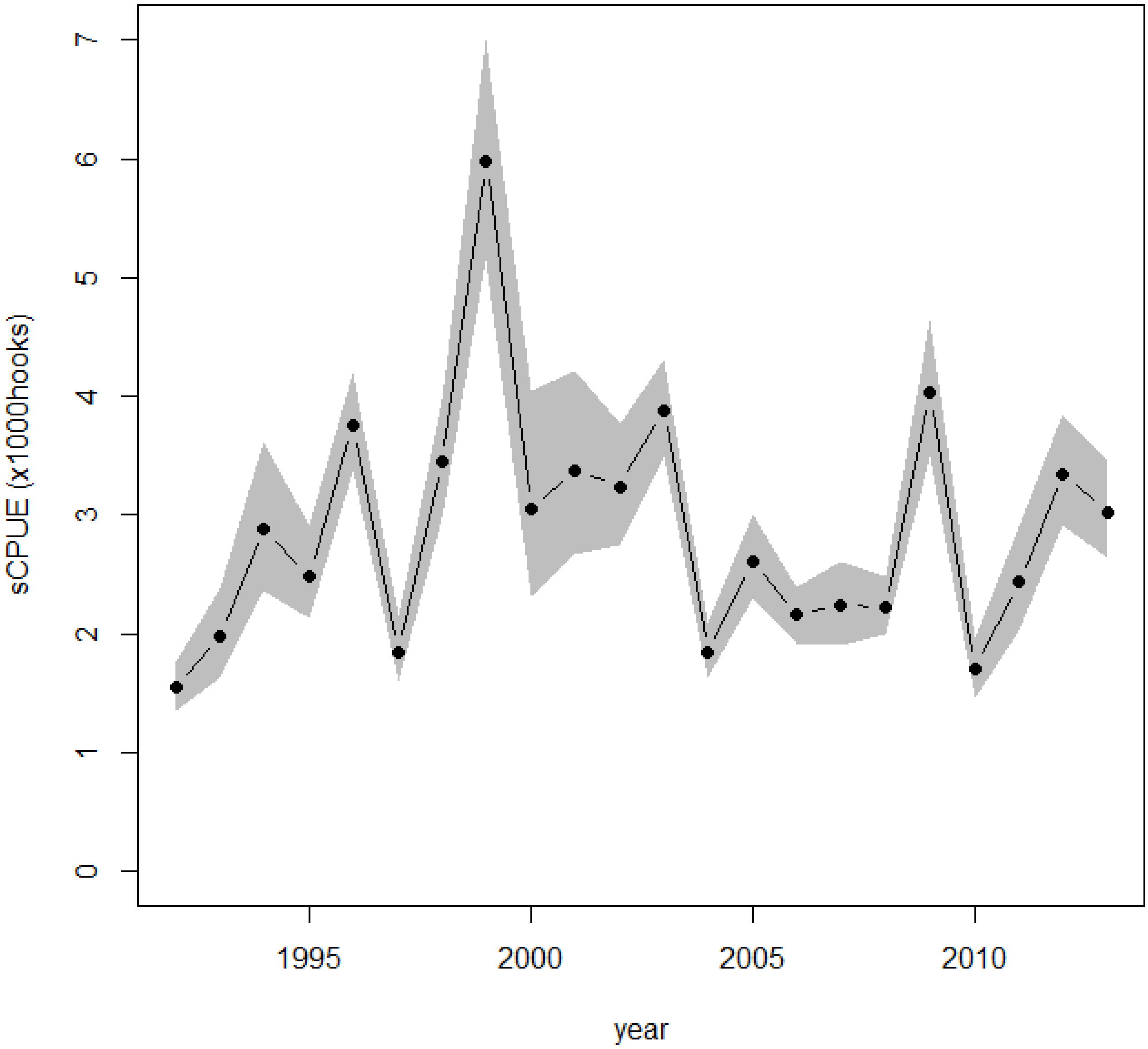
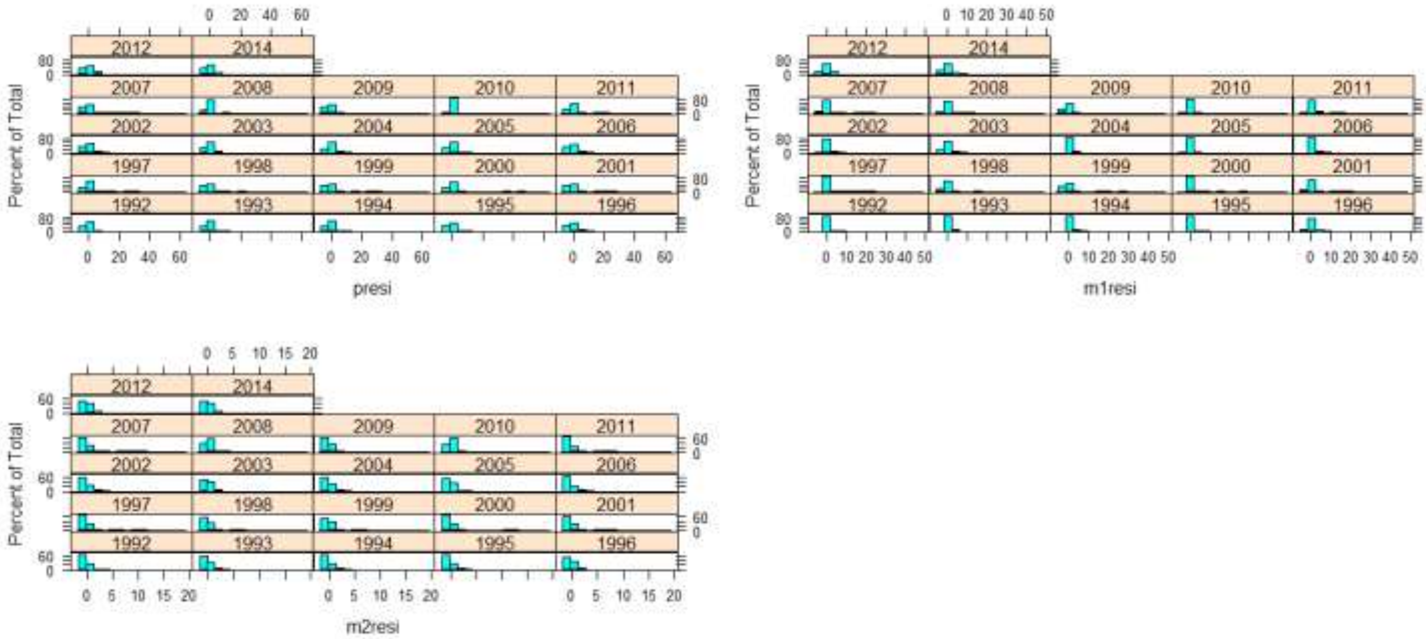
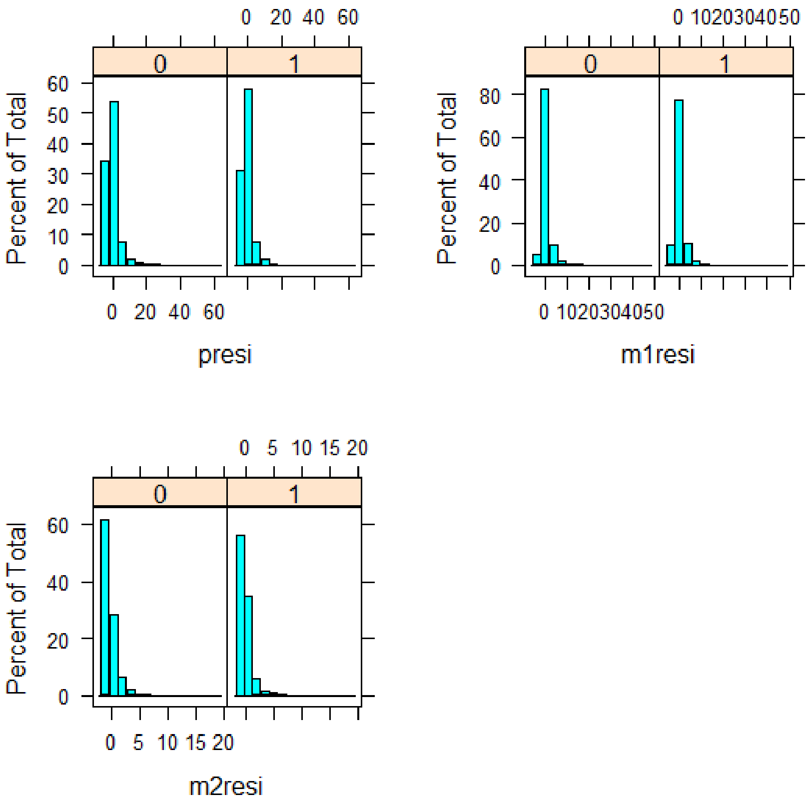


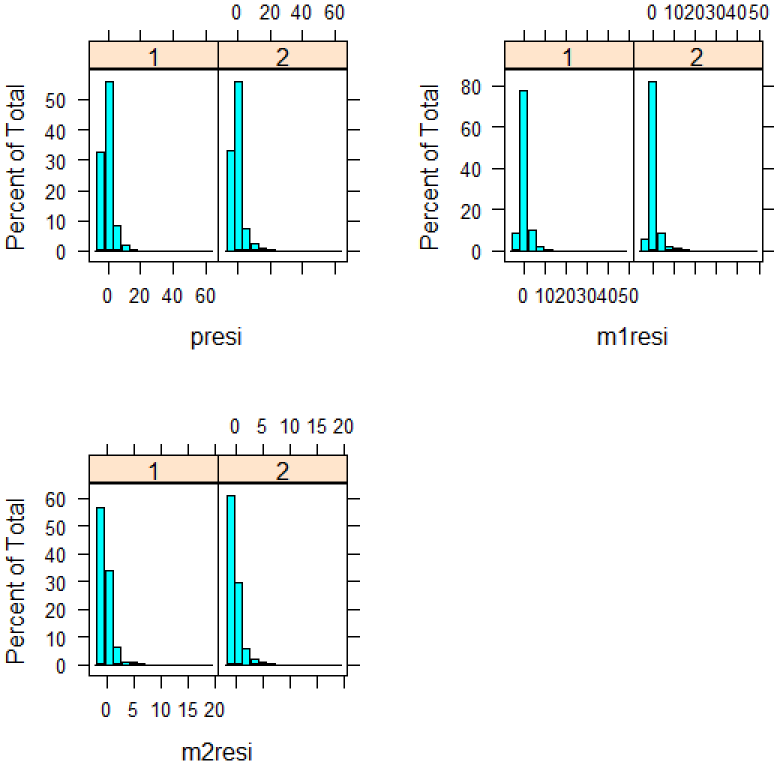
Fig. 3 Estimated abundance index of blue shark caught by Japanese longliners targeting southern bluefin tuna in 1992 – 2014. Observe collected catch and effort data was selected and standardized by Zero-Inflated negative binominal model.



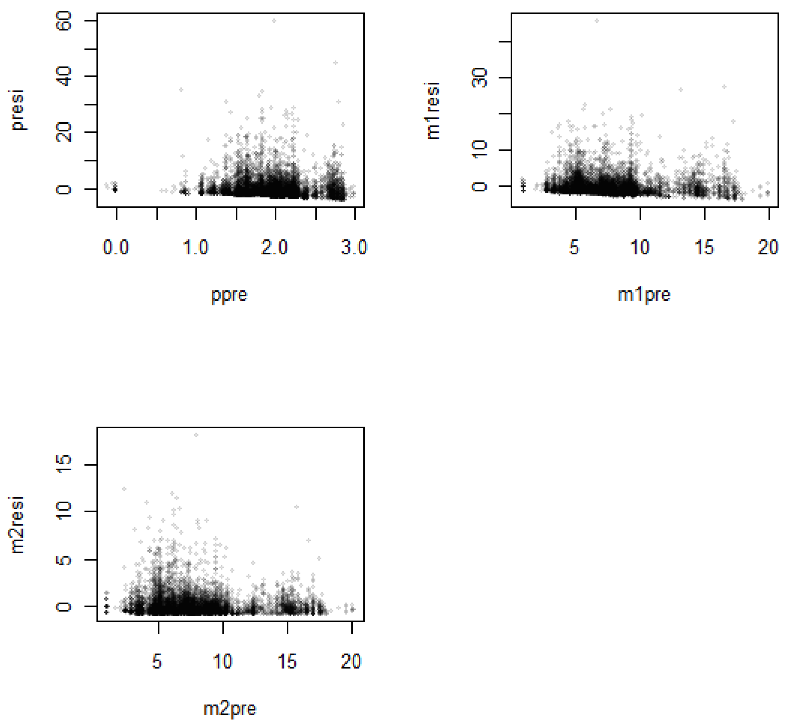
Appendix Fig.1 Annual residuals pattern for standardized CPUE of blue shark caught by Japanese longliners targeting for southern bluefin tuna. Top left is person residuals pattern for Poisson model, top right is residuals pattern for Zero-inflated Poisson model and bottom left is Zero-inflated negative binominal model.



Appendix Fig.2 Area specific residuals pattern of analysis of CPUE of blue shark caught by Japanese longliners targeting for southern bluefin tuna. Top left is person residuals pattern for Poisson model, top right is residuals pattern for Zero-inflated Poisson model and bottom left is Zero-inflated negative binominal model. In both three panels, left graph shows pattern of area 1 and right is area 2.



Appendix Fig.3. Season specific residuals pattern of analysis of CPUE of blue shark caught by Japanese longliners targeting for southern bluefin tuna. Top left is person residuals pattern for Poisson model, top right is residuals pattern for Zero-inflated Poisson model and bottom left is Zero-inflated negative binominal model. In both three panels, left graph shows pattern of season 1 and right is season 2.



Appendix Fig. 4. Comparison between observed and predicted CPUEs in the analysis of CPUE of blue shark caught by Japanese longliners targeting for southern bluefin tuna. Top left is comparison by Poisson model, top right is one by Zero-inflated Poisson model and bottom left is one by negative binominal model.

Appendix; Output of model analysis

Poisson model

Call:

```
glm(formula = oblk_n ~ as.factor(oyer) * as.factor(area) + as.factor(area) *
    as.factor(season) + offset(log(othk)), family = poisson,
    data = odata)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-5.9380	-2.5582	-1.1977	0.6933	27.2613

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-6.09693	0.02613	-233.293	< 2e-16
as.factor(oyer)1993	-0.32525	0.04100	-7.932	2.15e-15
as.factor(oyer)1994	-0.26878	0.03424	-7.850	4.17e-15
as.factor(oyer)1995	-0.02934	0.03216	-0.912	0.361644
as.factor(oyer)1996	-0.02759	0.03663	-0.753	0.451308
as.factor(oyer)1997	-0.22287	0.03557	-6.266	3.71e-10
as.factor(oyer)1998	0.56686	0.03320	17.072	< 2e-16
as.factor(oyer)1999	1.07492	0.03295	32.621	< 2e-16
as.factor(oyer)2000	-0.84563	0.08623	-9.806	< 2e-16
as.factor(oyer)2001	0.50953	0.03779	13.483	< 2e-16
as.factor(oyer)2002	0.24411	0.04288	5.693	1.25e-08
as.factor(oyer)2003	0.43233	0.03750	11.529	< 2e-16
as.factor(oyer)2004	-0.52025	0.05955	-8.736	< 2e-16
as.factor(oyer)2005	0.26740	0.03444	7.764	8.24e-15
as.factor(oyer)2006	0.10517	0.03360	3.131	0.001744
as.factor(oyer)2007	-0.04658	0.04366	-1.067	0.286027
as.factor(oyer)2008	0.31534	0.03985	7.914	2.49e-15
as.factor(oyer)2009	0.16760	0.04320	3.880	0.000104
as.factor(oyer)2010	0.38350	0.04774	8.033	9.53e-16
as.factor(oyer)2011	-0.14736	0.04155	-3.547	0.000390
as.factor(oyer)2012	0.44879	0.03838	11.693	< 2e-16
as.factor(oyer)2014	0.26456	0.03384	7.818	5.35e-15
as.factor(area)1	-0.68191	0.05161	-13.213	< 2e-16
as.factor(season)2	-0.25450	0.02126	-11.968	< 2e-16
as.factor(oyer)1993:as.factor(area)1	1.12205	0.07574	14.815	< 2e-16
as.factor(oyer)1994:as.factor(area)1	1.58017	0.07132	22.155	< 2e-16
as.factor(oyer)1995:as.factor(area)1	0.97039	0.06431	15.089	< 2e-16

```
as.factor(oyer)1996:as.factor(area)1  1.57887   0.06049   26.102  < 2e-16
as.factor(oyer)1997:as.factor(area)1  0.77903   0.06397   12.179  < 2e-16
as.factor(oyer)1998:as.factor(area)1  0.42627   0.06443    6.616 3.69e-11
as.factor(oyer)1999:as.factor(area)1  0.51835   0.06013    8.620  < 2e-16
as.factor(oyer)2000:as.factor(area)1  2.35686   0.10042   23.470  < 2e-16
as.factor(oyer)2001:as.factor(area)1  0.41640   0.06154    6.766 1.32e-11
as.factor(oyer)2002:as.factor(area)1  0.83144   0.06796   12.234  < 2e-16
as.factor(oyer)2003:as.factor(area)1  1.01896   0.06258   16.282  < 2e-16
as.factor(oyer)2004:as.factor(area)1  1.27550   0.07696   16.573  < 2e-16
as.factor(oyer)2005:as.factor(area)1  0.48870   0.05901    8.281  < 2e-16
as.factor(oyer)2006:as.factor(area)1  0.40466   0.05855    6.912 4.79e-12
as.factor(oyer)2007:as.factor(area)1  0.87814   0.06694   13.118  < 2e-16
as.factor(oyer)2008:as.factor(area)1 -0.01039   0.45119   -0.023 0.981621
as.factor(oyer)2009:as.factor(area)1  1.48209   0.07009   21.145  < 2e-16
as.factor(oyer)2010:as.factor(area)1 -1.74183   0.17108  -10.181  < 2e-16
as.factor(oyer)2011:as.factor(area)1  1.05162   0.07467   14.083  < 2e-16
as.factor(oyer)2012:as.factor(area)1  0.56191   0.07022    8.002 1.22e-15
as.factor(oyer)2014:as.factor(area)1  0.90420   0.07091   12.752  < 2e-16
as.factor(area)1:as.factor(season)2   0.16456   0.02811    5.854 4.80e-09

(Intercept)                          ***
as.factor(oyer)1993                  ***
as.factor(oyer)1994                  ***
as.factor(oyer)1995
as.factor(oyer)1996
as.factor(oyer)1997                  ***
as.factor(oyer)1998                  ***
as.factor(oyer)1999                  ***
as.factor(oyer)2000                  ***
as.factor(oyer)2001                  ***
as.factor(oyer)2002                  ***
as.factor(oyer)2003                  ***
as.factor(oyer)2004                  ***
as.factor(oyer)2005                  ***
as.factor(oyer)2006                  **
as.factor(oyer)2007
as.factor(oyer)2008                  ***
as.factor(oyer)2009                  ***
as.factor(oyer)2010                  ***
as.factor(oyer)2011                  ***
```

```
as.factor(oyer)2012                ***
as.factor(oyer)2014                ***
as.factor(area)1                   ***
as.factor(season)2                 ***
as.factor(oyer)1993:as.factor(area)1 ***
as.factor(oyer)1994:as.factor(area)1 ***
as.factor(oyer)1995:as.factor(area)1 ***
as.factor(oyer)1996:as.factor(area)1 ***
as.factor(oyer)1997:as.factor(area)1 ***
as.factor(oyer)1998:as.factor(area)1 ***
as.factor(oyer)1999:as.factor(area)1 ***
as.factor(oyer)2000:as.factor(area)1 ***
as.factor(oyer)2001:as.factor(area)1 ***
as.factor(oyer)2002:as.factor(area)1 ***
as.factor(oyer)2003:as.factor(area)1 ***
as.factor(oyer)2004:as.factor(area)1 ***
as.factor(oyer)2005:as.factor(area)1 ***
as.factor(oyer)2006:as.factor(area)1 ***
as.factor(oyer)2007:as.factor(area)1 ***
as.factor(oyer)2008:as.factor(area)1
as.factor(oyer)2009:as.factor(area)1 ***
as.factor(oyer)2010:as.factor(area)1 ***
as.factor(oyer)2011:as.factor(area)1 ***
as.factor(oyer)2012:as.factor(area)1 ***
as.factor(oyer)2014:as.factor(area)1 ***
as.factor(area)1:as.factor(season)2    ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 78974  on 7665  degrees of freedom
Residual deviance: 68892  on 7620  degrees of freedom
AIC: 91822

Number of Fisher Scoring iterations: 6
```

Zero Inflated - Poisson model

```
Call:
zeroinfl(formula = oblk_n ~ as.factor(oyer) * as.factor(area) + as.factor(area) *
    as.factor(season) | as.factor(oyer) + as.factor(area), data = odata,
    offset = log(othk), dist = "poisson")

Pearson residuals:
    Min      1Q  Median      3Q     Max
-3.7309 -1.3561 -0.7404  0.5210 45.8648

Count model coefficients (poisson with log link):
                                    Estimate Std. Error  z value Pr(>|z|)
(Intercept)                        -5.929677   0.025625 -231.404  < 2e-16
as.factor(oyer)1993                -0.268869   0.041402   -6.494 8.36e-11
as.factor(oyer)1994                -0.239241   0.034520   -6.930 4.20e-12
as.factor(oyer)1995                 0.079113   0.032457    2.438 0.014789
as.factor(oyer)1996                -0.096722   0.037060   -2.610 0.009058
as.factor(oyer)1997                -0.090580   0.035888   -2.524 0.011604
as.factor(oyer)1998                 0.380164   0.033509   11.345  < 2e-16
as.factor(oyer)1999                 0.814959   0.033256   24.505  < 2e-16
as.factor(oyer)2000                -0.273376   0.088992   -3.072 0.002127
as.factor(oyer)2001                 0.406886   0.038059   10.691  < 2e-16
as.factor(oyer)2002                 0.063548   0.043138    1.473 0.140716
as.factor(oyer)2003                 0.216096   0.037823    5.713 1.11e-08
as.factor(oyer)2004                -0.366816   0.060731   -6.040 1.54e-09
as.factor(oyer)2005                 0.441214   0.034736   12.702  < 2e-16
as.factor(oyer)2006                -0.116456   0.033858   -3.440 0.000583
as.factor(oyer)2007                -0.233471   0.044001   -5.306 1.12e-07
as.factor(oyer)2008                 0.062130   0.040108    1.549 0.121367
as.factor(oyer)2009                -0.082188   0.043513   -1.889 0.058917
as.factor(oyer)2010                 0.095299   0.047953    1.987 0.046885
as.factor(oyer)2011                -0.222086   0.041606   -5.338 9.41e-08
as.factor(oyer)2012                 0.226730   0.038327    5.916 3.30e-09
as.factor(oyer)2014                 0.101695   0.033488    3.037 0.002391
as.factor(area)1                   -0.745819   0.052883  -14.103  < 2e-16
as.factor(season)2                 -0.133548   0.021210   -6.296 3.05e-10
as.factor(oyer)1993:as.factor(area)1  0.994134   0.077008   12.909  < 2e-16
as.factor(oyer)1994:as.factor(area)1  1.447289   0.072565   19.945  < 2e-16
as.factor(oyer)1995:as.factor(area)1  0.807563   0.065686   12.294  < 2e-16
```

as.factor(oyer)1996:as.factor(area)1	1.559537	0.062047	25.135	< 2e-16
as.factor(oyer)1997:as.factor(area)1	0.575813	0.065400	8.804	< 2e-16
as.factor(oyer)1998:as.factor(area)1	0.531813	0.065811	8.081	6.43e-16
as.factor(oyer)1999:as.factor(area)1	0.704184	0.061608	11.430	< 2e-16
as.factor(oyer)2000:as.factor(area)1	1.681261	0.103565	16.234	< 2e-16
as.factor(oyer)2001:as.factor(area)1	0.495029	0.063000	7.858	3.92e-15
as.factor(oyer)2002:as.factor(area)1	1.022206	0.069339	14.742	< 2e-16
as.factor(oyer)2003:as.factor(area)1	1.201613	0.063947	18.791	< 2e-16
as.factor(oyer)2004:as.factor(area)1	1.256971	0.078895	15.932	< 2e-16
as.factor(oyer)2005:as.factor(area)1	0.301236	0.060521	4.977	6.45e-07
as.factor(oyer)2006:as.factor(area)1	0.839997	0.060066	13.985	< 2e-16
as.factor(oyer)2007:as.factor(area)1	1.138678	0.068302	16.671	< 2e-16
as.factor(oyer)2008:as.factor(area)1	0.139476	0.451385	0.309	0.757325
as.factor(oyer)2009:as.factor(area)1	1.667462	0.071349	23.370	< 2e-16
as.factor(oyer)2010:as.factor(area)1	-1.547914	0.171602	-9.020	< 2e-16
as.factor(oyer)2011:as.factor(area)1	1.057630	0.075769	13.959	< 2e-16
as.factor(oyer)2012:as.factor(area)1	0.866367	0.071318	12.148	< 2e-16
as.factor(oyer)2014:as.factor(area)1	0.992442	0.071806	13.821	< 2e-16
as.factor(area)1:as.factor(season)2	-0.005188	0.027964	-0.186	0.852824

(Intercept)	***
as.factor(oyer)1993	***
as.factor(oyer)1994	***
as.factor(oyer)1995	*
as.factor(oyer)1996	**
as.factor(oyer)1997	*
as.factor(oyer)1998	***
as.factor(oyer)1999	***
as.factor(oyer)2000	**
as.factor(oyer)2001	***
as.factor(oyer)2002	
as.factor(oyer)2003	***
as.factor(oyer)2004	***
as.factor(oyer)2005	***
as.factor(oyer)2006	***
as.factor(oyer)2007	***
as.factor(oyer)2008	
as.factor(oyer)2009	.
as.factor(oyer)2010	*
as.factor(oyer)2011	***

as.factor(oyer)2012 ***

as.factor(oyer)2014 **

as.factor(area)1 ***

as.factor(season)2 ***

as.factor(oyer)1993:as.factor(area)1 ***

as.factor(oyer)1994:as.factor(area)1 ***

as.factor(oyer)1995:as.factor(area)1 ***

as.factor(oyer)1996:as.factor(area)1 ***

as.factor(oyer)1997:as.factor(area)1 ***

as.factor(oyer)1998:as.factor(area)1 ***

as.factor(oyer)1999:as.factor(area)1 ***

as.factor(oyer)2000:as.factor(area)1 ***

as.factor(oyer)2001:as.factor(area)1 ***

as.factor(oyer)2002:as.factor(area)1 ***

as.factor(oyer)2003:as.factor(area)1 ***

as.factor(oyer)2004:as.factor(area)1 ***

as.factor(oyer)2005:as.factor(area)1 ***

as.factor(oyer)2006:as.factor(area)1 ***

as.factor(oyer)2007:as.factor(area)1 ***

as.factor(oyer)2008:as.factor(area)1

as.factor(oyer)2009:as.factor(area)1 ***

as.factor(oyer)2010:as.factor(area)1 ***

as.factor(oyer)2011:as.factor(area)1 ***

as.factor(oyer)2012:as.factor(area)1 ***

as.factor(oyer)2014:as.factor(area)1 ***

as.factor(area)1:as.factor(season)2

Zero-inflation model coefficients (binomial with logit link):

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.24555	0.11592	-10.745	< 2e-16	***
as.factor(oyer)1993	0.06781	0.19316	0.351	0.725537	
as.factor(oyer)1994	0.05383	0.17076	0.315	0.752557	
as.factor(oyer)1995	0.42712	0.15340	2.784	0.005365	**
as.factor(oyer)1996	-0.45627	0.19081	-2.391	0.016791	*
as.factor(oyer)1997	0.26451	0.15984	1.655	0.097955	.
as.factor(oyer)1998	-1.12553	0.25976	-4.333	1.47e-05	***
as.factor(oyer)1999	-1.97049	0.43081	-4.574	4.79e-06	***
as.factor(oyer)2000	0.50964	0.22784	2.237	0.025297	*
as.factor(oyer)2001	-0.37117	0.20169	-1.840	0.065717	.
as.factor(oyer)2002	-0.46164	0.23884	-1.933	0.053258	.

```
as.factor(oyer)2003    -0.99355      0.25671    -3.870 0.000109 ***
as.factor(oyer)2004     0.76568      0.16605     4.611 4.00e-06 ***
as.factor(oyer)2005     0.18081      0.15981     1.131 0.257862
as.factor(oyer)2006     0.40554      0.15192     2.669 0.007597 **
as.factor(oyer)2007    -0.22167      0.19879    -1.115 0.264809
as.factor(oyer)2008    -2.42420      0.60248    -4.024 5.73e-05 ***
as.factor(oyer)2009    -2.28072      0.52869    -4.314 1.60e-05 ***
as.factor(oyer)2010 -15.02668    419.14087    -0.036 0.971401
as.factor(oyer)2011    -0.71172      0.25642    -2.776 0.005510 **
as.factor(oyer)2012    -1.06667      0.32217    -3.311 0.000930 ***
as.factor(oyer)2014    -2.31148      0.43110    -5.362 8.24e-08 ***
as.factor(area)1       -0.92689      0.07702 -12.034   < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of iterations in BFGS optimization: 90
Log-likelihood: -4.104e+04 on 69 Df
```

Zero Inflated negative binominal

Call:

```
zeroinfl(formula = oblk_n ~ as.factor(oyer) * as.factor(area) + as.factor(area) *
    as.factor(season) | as.factor(oyer) + as.factor(area), data = odata,
    offset = log(othk), dist = "negbin")
```

Pearson residuals:

```
    Min      1Q  Median      3Q     Max
-0.9251 -0.6845 -0.3721  0.2297 18.3300
```

Count model coefficients (negbin with log link):

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-6.01563	0.07237	-83.122	< 2e-16
as.factor(oyer)1993	-0.34120	0.11535	-2.958	0.00310
as.factor(oyer)1994	-0.27771	0.09801	-2.834	0.00460
as.factor(oyer)1995	0.20632	0.10147	2.033	0.04202
as.factor(oyer)1996	0.03897	0.11119	0.350	0.72597
as.factor(oyer)1997	0.06643	0.10953	0.606	0.54419
as.factor(oyer)1998	0.61870	0.11058	5.595	2.21e-08
as.factor(oyer)1999	1.10822	0.12787	8.667	< 2e-16
as.factor(oyer)2000	-0.15378	0.23742	-0.648	0.51715
as.factor(oyer)2001	0.66906	0.13367	5.005	5.58e-07
as.factor(oyer)2002	0.27627	0.13149	2.101	0.03563
as.factor(oyer)2003	0.47625	0.12014	3.964	7.37e-05
as.factor(oyer)2004	-0.33653	0.15805	-2.129	0.03323
as.factor(oyer)2005	0.67822	0.12276	5.525	3.30e-08
as.factor(oyer)2006	0.16159	0.10518	1.536	0.12444
as.factor(oyer)2007	-0.02198	0.12583	-0.175	0.86135
as.factor(oyer)2008	0.33471	0.12590	2.659	0.00785
as.factor(oyer)2009	0.18829	0.13268	1.419	0.15584
as.factor(oyer)2010	0.41149	0.15782	2.607	0.00913
as.factor(oyer)2011	-0.04427	0.11731	-0.377	0.70589
as.factor(oyer)2012	0.51295	0.12973	3.954	7.69e-05
as.factor(oyer)2014	0.23708	0.10359	2.289	0.02210
as.factor(area)1	-0.75874	0.12027	-6.308	2.82e-10
as.factor(season)2	-0.36566	0.06443	-5.675	1.39e-08
as.factor(oyer)1993:as.factor(area)1	1.14705	0.20496	5.597	2.19e-08
as.factor(oyer)1994:as.factor(area)1	1.60225	0.21466	7.464	8.39e-14
as.factor(oyer)1995:as.factor(area)1	0.75021	0.17683	4.243	2.21e-05
as.factor(oyer)1996:as.factor(area)1	1.51234	0.16590	9.116	< 2e-16

as.factor(oyer)1997:as.factor(area)1	0.47263	0.16584	2.850	0.00437
as.factor(oyer)1998:as.factor(area)1	0.37396	0.18119	2.064	0.03903
as.factor(oyer)1999:as.factor(area)1	0.50411	0.19040	2.648	0.00811
as.factor(oyer)2000:as.factor(area)1	1.66297	0.27863	5.968	2.40e-09
as.factor(oyer)2001:as.factor(area)1	0.31103	0.17594	1.768	0.07710
as.factor(oyer)2002:as.factor(area)1	0.90463	0.18781	4.817	1.46e-06
as.factor(oyer)2003:as.factor(area)1	0.87994	0.17542	5.016	5.27e-07
as.factor(oyer)2004:as.factor(area)1	1.09112	0.19461	5.607	2.06e-08
as.factor(oyer)2005:as.factor(area)1	0.06514	0.16423	0.397	0.69164
as.factor(oyer)2006:as.factor(area)1	0.33432	0.15066	2.219	0.02648
as.factor(oyer)2007:as.factor(area)1	0.78927	0.17340	4.552	5.32e-06
as.factor(oyer)2008:as.factor(area)1	-0.03424	1.15682	-0.030	0.97638
as.factor(oyer)2009:as.factor(area)1	1.39071	0.20872	6.663	2.68e-11
as.factor(oyer)2010:as.factor(area)1	-1.79391	0.29386	-6.105	1.03e-09
as.factor(oyer)2011:as.factor(area)1	0.96607	0.20495	4.714	2.43e-06
as.factor(oyer)2012:as.factor(area)1	0.53975	0.20740	2.602	0.00926
as.factor(oyer)2014:as.factor(area)1	0.86488	0.21688	3.988	6.67e-05
as.factor(area)1:as.factor(season)2	0.37629	0.08361	4.501	6.77e-06
Log(theta)	-0.10721	0.02035	-5.269	1.37e-07

(Intercept)	***
as.factor(oyer)1993	**
as.factor(oyer)1994	**
as.factor(oyer)1995	*
as.factor(oyer)1996	
as.factor(oyer)1997	
as.factor(oyer)1998	***
as.factor(oyer)1999	***
as.factor(oyer)2000	
as.factor(oyer)2001	***
as.factor(oyer)2002	*
as.factor(oyer)2003	***
as.factor(oyer)2004	*
as.factor(oyer)2005	***
as.factor(oyer)2006	
as.factor(oyer)2007	
as.factor(oyer)2008	**
as.factor(oyer)2009	
as.factor(oyer)2010	**
as.factor(oyer)2011	

```
as.factor(oyer)2012                      ***
as.factor(oyer)2014                      *
as.factor(area)1                         ***
as.factor(season)2                       ***
as.factor(oyer)1993:as.factor(area)1 ***
as.factor(oyer)1994:as.factor(area)1 ***
as.factor(oyer)1995:as.factor(area)1 ***
as.factor(oyer)1996:as.factor(area)1 ***
as.factor(oyer)1997:as.factor(area)1 **
as.factor(oyer)1998:as.factor(area)1 *
as.factor(oyer)1999:as.factor(area)1 **
as.factor(oyer)2000:as.factor(area)1 ***
as.factor(oyer)2001:as.factor(area)1 .
as.factor(oyer)2002:as.factor(area)1 ***
as.factor(oyer)2003:as.factor(area)1 ***
as.factor(oyer)2004:as.factor(area)1 ***
as.factor(oyer)2005:as.factor(area)1
as.factor(oyer)2006:as.factor(area)1 *
as.factor(oyer)2007:as.factor(area)1 ***
as.factor(oyer)2008:as.factor(area)1
as.factor(oyer)2009:as.factor(area)1 ***
as.factor(oyer)2010:as.factor(area)1 ***
as.factor(oyer)2011:as.factor(area)1 ***
as.factor(oyer)2012:as.factor(area)1 **
as.factor(oyer)2014:as.factor(area)1 ***
as.factor(area)1:as.factor(season)2    ***
Log(theta)                               ***

Zero-inflation model coefficients (binomial with logit link):
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)          -2.858e+00   5.773e-01   -4.951 7.37e-07 ***
as.factor(oyer)1993   3.484e-02   9.964e-01    0.035 0.972107
as.factor(oyer)1994 -1.163e-01   9.022e-01   -0.129 0.897410
as.factor(oyer)1995   1.508e+00   6.006e-01    2.511 0.012046 *
as.factor(oyer)1996 -6.263e-01   1.300e+00   -0.482 0.629952
as.factor(oyer)1997   1.542e+00   6.085e-01    2.534 0.011276 *
as.factor(oyer)1998 -1.403e+01   9.839e+02   -0.014 0.988623
as.factor(oyer)1999 -1.918e+01   7.486e+03   -0.003 0.997956
as.factor(oyer)2000   2.766e+00   6.610e-01    4.184 2.86e-05 ***
as.factor(oyer)2001   3.679e-01   7.954e-01    0.463 0.643705
```

```
as.factor(oyer)2002 -1.523e+01    1.554e+03    -0.010 0.992178
as.factor(oyer)2003 -1.625e+01    1.790e+03    -0.009 0.992754
as.factor(oyer)2004    1.192e+00    7.525e-01      1.584 0.113291
as.factor(oyer)2005    2.006e+00    6.032e-01      3.326 0.000881 ***
as.factor(oyer)2006 -1.945e+01    5.697e+03    -0.003 0.997276
as.factor(oyer)2007 -1.613e+01    1.732e+03    -0.009 0.992572
as.factor(oyer)2008 -2.271e+01    3.637e+04    -0.001 0.999502
as.factor(oyer)2009 -1.996e+01    1.027e+04    -0.002 0.998449
as.factor(oyer)2010 -1.646e+01    1.961e+03    -0.008 0.993302
as.factor(oyer)2011 -1.455e+01    1.414e+03    -0.010 0.991786
as.factor(oyer)2012 -1.834e+01    4.170e+03    -0.004 0.996490
as.factor(oyer)2014 -2.051e+01    9.919e+03    -0.002 0.998350
as.factor(area)1        -2.342e+01    7.882e+03    -0.003 0.997629
---
Signif. codes:    0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.8983
Number of iterations in BFGS optimization: 91
Log-likelihood: -2.285e+04 on 70 Df
```