Title: Spatio-temporal model reduces species misidentification bias of spawning eggs in stock assessment of spotted mackerel in the western North Pacific

Yuki Kanamori^{1,3*}, Shota Nishijima¹, Hiroshi Okamura¹, Ryuji Yukami¹, Mikio Watai¹, and Akinori Takasuka²

¹ National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan

² Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

Present address

³ Tohoku National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency, 25-259 Shimomekurakubo, Samemachi, Hachinohe, Aomori, 031-0841, Japan

* Corresponding author

Email: kana.yuki@fra.affrc.go.jp

Abstract

Species identification based on morphological characteristics includes species misidentification, leading to estimation bias of population size. The eggs of spotted mackerel *Scomber australicus* and chub mackerel *S. japonicus* in the western North Pacific has been identified based on egg diameter. Recent density of spotted mackerel was considerably high despite its low stock biomass. A possibility of this phenomenon is due to overestimation because the difference in egg diameter has become ambiguous between two species. However, we cannot test this possibility using DNA analysis because the eggs are fixed with formalin. Here, we estimated the index of egg density of spotted mackerel using a spatio-temporal model that incorporates the effect of egg density of chub mackerel on the catchability of spotted mackerel, using 15 years data of spawning eggs. We then examined how retrospective biases in estimated stock abundance were reduced when using the index from the model. The index estimated from the model decreased temporal fluctuation and showed smooth patterns. Especially, the recent index was considerably revised down rather than the nominal index. Additionally, the retrospective bias decreased ca. half compared with the nominal index. Therefore, incorporating species misidentification bias should be an essential process for improving stock assessment.

Keywords

species identification, stock assessment, retrospective bias, small pelagic fish

1 Introduction

2 Species identification based on morphological characteristics in field surveys is a major
3 method in ecology, despite the increasing use of DNA techniques in recent years. Although
4 most surveys are conducted under the assumption that species will be identified perfectly,
5 this is not always the case (Elphic, 2008). Species misidentification can lead to serious bias
6 in the inference of population size, resulting in a misunderstanding of the ecological
7 processes that drive population dynamics. Therefore, removing the bias due to species
8 misidentification as much as possible is essential in ecology, but such bias has drawn
9 considerably less research attention compared with detection bias (e.g., MacKenzie et al.,
10 2002; Williams, Nichols & Conroy, 2002).

11 Accurate species identification of fish eggs and larvae is essential for elucidating the
12 ecology of the early life–history of fish, including the location and timing of fish spawning,
13 hatching, and migration (Ko et al., 2013). Such information can improve the inference and
14 forecasting of fish population size. Morphological characteristics used for species
15 identification have traditionally been the size and oil globules of eggs, and the body shape,
16 pigmentation, and meristic count of larvae (e.g., Matarese & Sandknop, 1984; Ko et al.,
17 2013). However, species identification based on these morphological characteristics leads to
18 species misidentification because these morphological characteristics are likely to overlap
19 among species in early life–history (e.g., Victor et al., 2009; Ko et al., 2013). For example,
20 when we use size of eggs as a morphological measure, we often classify eggs by whether
21 their diameters are greater than or less than a predetermined value. However, because
22 distributions of diameter are likely to overlap among species, some eggs may be erroneously

classified as different species. In addition, morphological characteristics can change during developments, so that individuals of the same species at different development stages can be misidentified as a different species (Ko et al., 2013).

Spotted mackerel *Scomber australasicus* and chub mackerel *Scomber japonicus* are small pelagic fish that are widely distributed in the western North Pacific (ca. 120 – 150°E, Fig. 1; Watanabe & Yatsu, 2006). These species spawn in waters near the Kuroshio Current from winter to summer (e.g., Watanabe, 1970; Watanabe et al., 1999; Watanabe & Yatsu, 2006), after which the adults and their offspring are transported to their feeding ground by the Kuroshio Current (e.g., Watanabe & Nishida, 2002). Because Nishida (2001) suggested that there was the difference in egg diameter between two species, species identification based on egg diameter has been conducted routinely since 2005; eggs smaller than 1.1 mm of diameter were classified as chub mackerel and vice versa. These eggs, which were identified according to this basis, have been used as the indices of spawning stock biomass of spotted mackerel and chub mackerel for stock assessment. However, recent egg density of spotted mackerel was considerably high although stock biomass and spawning stock biomass has been low (Yukami et al. 2019). This considerable increase of the egg density of spotted mackerel is likely the result of overestimation because the difference in egg diameter has become ambiguous according to increase of egg density of chub mackerel and the distributions of egg diameter between species have overlapped (Yukami et al., 2019). From the possibility of overestimation, it is problematic to use a yearly trend simply estimated from the egg density data as a spawning stock biomass index for stock assessment, which could lead to bias sources in stock assessment.

There are two straightforward approaches to solving this problem. The first approach

46 is DNA analysis. However, Egg samples are fixed with formalin to preserve their
47 morphological characteristics and this results in DNA fragmentation and protein
48 cross-linking, which makes DNA extraction difficult or impossible (e.g., Goelz et al., 1985;
49 Impraim et al., 1987). The second approach is to use a mixture distribution of the eggs of
50 chub mackerel and spotted mackerel which contains the temporal changes in egg diameters
51 of two species. However, this is difficult on a practical level because complexly intertwined
52 factors such as spawning times within a given year, age, water temperature, and body
53 condition affect egg diameter, and these may be difficult to obtain by field surveys alone
54 (e.g., spawning times). As another solution, we modelled the species identification error by
55 linking the catchability of egg density of spotted mackerel to the egg density of chub
56 mackerel, because the recent increase of chub mackerel abundance may give rise to the
57 identification error for spotted mackerel egg. That is, an unexpected increase of the egg
58 density of spotted mackerel is virtually replaced by the increase of catchability of the
59 spotted mackerel eggs.

60 In this paper, we demonstrate a pretty good handling of identification error by using
61 the state-of-the-art spatio-temporal standardization method (Thorson 2019). Our new
62 method substantially reduced the bias that would have been caused by species
63 misidentification of spawning eggs between chub mackerel and spotted mackerel and led to
64 considerable improvement in the stock assessment of spotted mackerel in the western North
65 Pacific. To quantify the effect of species misidentification, we estimated the indices of egg
66 density of spotted mackerel with/without incorporation of the effect of the egg density of
67 chub mackerel on the catchability of spotted mackerel, using 15 years data of spawning
68 eggs. We then examined how retrospective biases of three measurements of stock abundance

(total number of individuals, total stock biomass, and spawning stock biomass; SSB) changed when we used the estimated indices for a stock assessment model. We tested the hypothesis that the retrospective bias should be lower in the spotted mackerel stock assessment with the egg–abundance index standardized by the spatio–temporal model incorporating chub mackerel egg density as a catchability covariate.

74

2 Materials and Methods

2.1 Data sets

Survey and data

The egg density data with 30' latitude $\times$ 30' longitude horizontal square resolution in the areas from 122°E to 150°E and 24°N to 43°N was used. The egg density data set was derived from monthly egg surveys off the Pacific coast of Japan from January to June, 2005–2019 (Takasuka et al., 2008a, 2019). The aim of the surveys was to monitor the egg abundance of major small pelagic fish species, including chub mackerel and spotted mackerel, so that the spatial area and survey month of the data largely covered the major spawning grounds and spawning season. While some sampling locations were fixed, others varied for various reasons (e.g., environmental conditions). Accordingly, the survey design changed slightly each year (Kanamori et al., 2019). Although the sampling efforts were approximately consistent year-round, the efforts tended to be more intensive during early spring; effort was highest in February and decreased gradually thereafter (Takasuka et al., 2008b).

The egg surveys were conducted by 18 prefectural experimental stations or fisheries research institutes and two national research institutes of the Japan Fisheries Research and Education Agency, following the consistent sampling designs, as a part of the stock assessment project. In the surveys, plankton nets were towed vertically from a depth of 150 m to the surface (if the depth was ≤ 150 m, nets were lowered to just above the bottom). This range of depths covers the vertical distributions of eggs of small pelagic fish. During the period from 2005 to 2019, the surveys used a plankton net with a mouth ring diameter of 0.45 m and a mesh size of 0.335 (partially 0.330 mm in 2015) (Takasuka et al., 2017). The samples were fixed with 5% formalin immediately after collection. In the laboratory, the samples were identified and sorted into eggs and larvae of different small pelagic species, based on the morphological characteristics (e.g., egg shape and size, number of oil globules, segmented yolk, perivitelline space ranging, yolk diameter, oil globule diameter). For the mackerel eggs, the egg diameters were measured to the nearest 0.025 mm by a micrometer for the maximum number of 100 individuals per sample (station or tow). Eggs with diameters >1.1 mm were identified as spotted mackerel, whereas those with diameters ≤ 1.0 mm were identified as chub mackerel, according to Nishida et al. (2001). For any sample of >100 individuals, the proportion of the two species among the randomly selected 100 individuals was assumed to be the same for the whole sample.

2.2 Data analyses

Indices of egg density

In this study, we used the three indices of egg density; nominal, chub $-$, and chub $+$. The nominal index was the arithmetic mean of egg density for each year. The chub $-$ index was

the estimated egg density by considering sampling effects (i.e., spatio—temporal changes in survey design). The chub+ index was the estimated egg density by considering sampling effects and the effect of egg density of chub mackerel on the catchability of egg density of chub mackerel. The process for estimating chub— and the chub+ is described in the following section.

Estimation of the indices of egg density

To estimate the chub— and the chub+ indices of egg density by considering sampling effects (i.e., spatio—temporal changes in survey design) as well as the effect of egg density of chub mackerel on the catchability of egg density of chub mackerel, we used the multivariate vector autoregressive spatio-temporal (VAST) model (Thorson & Barnett, 2017), which accounts for spatio-temporal changes in survey design, survey effort, and observation rates and can accurately estimate relative local densities at high resolution by standardizing sampling designs (Thorson & Barnett, 2017; Thorson, 2019). The model includes two potential components because it is designed to support delta-models: (i) the encounter probability p_i for each sample i and (ii) the expected egg density d_i for each sample i when spawning occurs (i.e., egg density is not zero). The encounter probability p_i and the expected egg density d_i are, respectively, approximated using a logit-linked linear predictor and a log-linked linear predictor as follows (Thorson & Barnett, 2017):

$$\text{logit } p_i = \beta_p(t_i) + \omega_p(s_i) + \varepsilon_p(s_i, t_i) + \eta_p(v_i) + \lambda_p Q(i)$$

$$\log d_i = \beta_d(t_i) + \omega_d(s_i) + \varepsilon_d(s_i, t_i) + \eta_d(v_i) + \lambda_d Q(i)$$

131 where $\beta(t_i)$ is the intercept for year t , and $\omega(s_i)$ and $\varepsilon(s_i, t_i)$ are the spatial and
 132 spatio-temporal random effects for year t and location s , respectively. $\eta(v_i)$ is
 133 overdispersion random effect of factor v_i which is the interaction of year and month. λ is the
 134 effect of the catchability covariate $Q(i)$, where
 135 $Q(i) = \log(\text{chub mackerel egg density}(s_i) + 0.1)$. That is, this term considers the effect of
 136 species misidentification between chub mackerel and spotted mackerel; as mentioned
 137 earlier, we suspected overestimation of egg density of spotted mackerel because the
 138 difference in egg diameter has become ambiguous according to increase of egg density of
 139 chub mackerel and the distributions of egg diameter between species have overlapped
 140 (Yukami et al., 2019). The subscripts for each term on the right side, p and d , represent the
 141 encounter probability and the expected egg density, respectively.

142 The probability density function of $\omega(\cdot)$ is a multivariate normal distribution
 143 $\text{MVN}(0, \mathbf{R})$, where the variance-covariance matrix $\mathbf{R}$ is a Matérn correlation function. The
 144 probability density function of $\varepsilon(s_i, t_i)$ is

$$\varepsilon(\cdot, t_i) \sim \begin{cases} \text{MVN}(0, \mathbf{R}), & \text{if } t = 1 \\ \text{MVN}(\rho_\varepsilon \varepsilon(\cdot, t - 1_i), \mathbf{R}), & \text{if } t > 1 \end{cases}.$$

145 Here, $\rho_\varepsilon = 0$ because we assumed that the year was independent. Therefore, the probability
 146 density function of $\eta(v_i)$ is $\eta(v_i) \sim \text{N}(0, 1)$.

147 For computational reasons, the spatio-temporal variation $\varepsilon_p(s_i, t_i)$ was approximated
 148 as being piecewise constant at a fine spatial scale. We used a k-means algorithm to identify
 149 200 locations (termed “knots”) to minimize the total distance between the location of

150 sampling data (Thorson et al., 2015) using R-INLA software (Lindgren, 2012). The number
 151 of knots was increased to the greatest extent possible, and similar results were obtained for
 152 low knots (= 100; Akaike information criterion [AIC] = 6773.01) and high knots (= 200;
 153 AIC = 6676.25).

154 Parameters in the VAST model were estimated using the VAST package (Thorson et
 155 al., 2015,2016a) in R 3.6.1 (R Development Core Team, 2019). Bias-correction for random
 156 effects (Thorson and Kristensen, 2016) was applied when estimating the derived parameters.
 157 We confirmed the model diagnostics plots and found no serious problems. The relative egg
 158 density in year t at location s , $\hat{d}(s, t)$ and the index of egg density in year t , $\hat{D}(t)$, were
 159 estimated using the predicted values for random effects as follows (Thorson et al., 2017):

$$\hat{d}(s, t) = \text{logit}^{-1}[\beta_p(t_i) + \omega_p(s_i) + \varepsilon_p(s_i, t_i) + \eta_p(v_i) + \lambda_p Q(i)]$$

160

$$\times \exp[\beta_d(t_i) + \omega_d(s_i) + \varepsilon_d(s_i, t_i) + \eta_d(v_i) + \lambda_d Q(i)],$$

161

$$\hat{D}(t) = \sum_s a(s) \times \hat{d}(s, t)$$

162 where $a(s)$ is the area of location s .

163 **Estimation of stock abundance**

164 To examine the validity of the three indices (i.e., nominal index, chub- index, and chub+
165 index), we estimated the three measurements of stock abundance (total number of
166 individuals, total stock biomass, and SSB) using a tuned virtual population analysis (VPA).

167 This model is an age-based cohort analysis for estimating the historical abundance and
168 fishing mortality rates from catch-at-age data and has been applied to spotted mackerel in
169 Japan (Yukami et al., 2019). In addition to the three indices of egg density, we used
170 catch-at-age, weight-at-age, maturity-at-age, the natural mortality coefficient, and a
171 recruitment index following stock assessment in Japan (Yukami et al., 2019). The fishing
172 mortality coefficients other than the terminal age in the terminal year were estimated under
173 the assumption that the selectivity in the latest year was equal to the average selectivity of
174 the prior 5 years (Ichinokawa & Okamura, 2014; Mori & Hiyama, 2014). We confirmed that
175 this assumption did not change our results when using the prior 3 years average of
176 selectivity as the selectivity in the latest year. The fishing mortality coefficient at each age in

the terminal year was estimated by a maximum likelihood method as follows:

$$\sum_k \sum_y \left[\frac{\{\log(I_{k,y}) - \log(q_k X_{k,y})\}^2}{2\sigma_k^2} - \log\left(\frac{1}{\sqrt{2\pi\sigma_k^2}}\right) \right],$$

where $I_{k,y}$ is the value of index k in year y , q_k is a proportionality constant, $X_{k,y}$ is the abundance estimate in VPA for index k (i.e., recruitment, and the three indices of egg density), σ_k^2 is the variance in fitting the abundance estimate to the index, and y_k is the first year of index k .

Retrospective analysis

Stock abundance in the terminal year estimated by VPA is notoriously inaccurate and imprecise compared with historical abundance estimates (Okamura et al. 2017). One of the most serious problems is that the stock abundance estimate in the terminal year has temporally systematic bias, i.e., retrospective bias (Hurtado-Ferro et al. 2015). Retrospective analysis is therefore a useful method for detecting such a systematic bias in stock abundance estimate in the terminal year. Dropping the most recent year's data sequentially and then comparing the estimates from a full-year data model and removed data model reveals presence or absence of systematic bias (Mohn 1999). Herein, we conduct a retrospective analysis to evaluate the relative goodness of the three indices of egg density.

To examine improvements in estimations of the three measurements of stock abundance when using the estimated indices of egg density from VAST with considering the chub mackerel's effect, we performed a retrospective analysis by sequentially removing the five most recent years of data from the full data set. Retrospective analysis is usually used in stock assessment models such as VPA to examine the reliability and predictability of stock

assessments (e.g., Mohn, 1999; Hashimoto et al., 2018). We calculated Mohn's rho to estimate the biases of the indices of egg density as follows (Mohn, 1999):

$$\rho = \frac{1}{c} \sum_i^c \left(\frac{I_{y-i}^R - I_{y-i}}{I_{y-i}} \right),$$

where I_{y-i} is the value of the year $y - i$ estimate using the full data and I_{y-i}^R is the estimate using the data up to year $y - i$. c is the maximum number of removed years (i.e., $c = 5$). A positive ρ means that the estimate in the terminal year tends to be positively biased on average, and vice versa. Moreover, a ρ close to 0 means no serious retrospective bias and greatly improved estimation of the stock abundance.

3 Results

Temporal trend in the indices of egg density

When comparing the standardized indices to the nominal index, the standardized indices reduced temporal fluctuation and showed smooth patterns (Fig. 2). Whereas the nominal index increased substantially in 2018, the standardized indices were revised downward to a considerable degree. Moreover, the standardized indices of some years, such as 2008, 2009, and 2012, were revised upward.

The model with the effect of chub mackerel's egg density on the catchability of spotted mackerel was more suitable model rather than the model without the effect of chub mackerel's, which based on AIC criteria (chub+, AIC = 8250.12; chub-, AIC = 8978.81).

215 The coefficient of the effect of chub mackerel's on the catchability of spotted mackerel, λ ,
 216 represents a positive effect ($\lambda = 0.17$). The estimated index with the chub mackerel's effect
 217 reached a peak in 2008 and then gradually decreased. The value of this index in 2019 was
 218 the lowest since 2005 (Fig. 2).

219 **Spatial distribution of the relative egg density**

220 The relative egg density with the effect of chub mackerel was high off the coast of Kyushu,
 221 Shikoku, and the Izu Islands (Fig. 3). In addition, the relative egg density was slightly high
 222 off the coast of the Tohoku region. These tendencies were consistent during the study
 223 period. There was no area where the relative egg density clearly increased or decreased
 224 during this study period.

225 **Retrospective analysis**

226 Recent estimated values of stock abundance (i.e., total numbers of individuals, total
 227 biomass, and SSB) were distinct depending on what indices were used, whereas the
 228 directions of retrospective bias were sometimes not, depending on the indices used (Fig. 4).
 229 In all the three measurements of stock abundance, the recent estimated values were higher
 230 when using the nominal and estimated index without the chub mackerel's effect rather
 231 compared with using the estimated index with the chub mackerel's effect. The directions
 232 of retrospective bias were always positive and were independent if the indices used.

233 In all the three measurements of stock abundance (i.e., total numbers of individuals,
 234 total biomass, and SSB), retrospective biases were clearly improved when using the
 235 estimated index with the chub mackerel's effect (Table 1). Mohn's rho, which represents the
 236 magnitude and direction of retrospective bias, had similar values between when using

nominal index as when using the estimated index without the chub mackerel's effect (Table 1). In contrast, Mohn's rho decreased when using the estimated index with the chub mackerel effect. The directions of the retrospective bias did not change depending on the indices used because the values of Mohn's rho were always positive.

4 Discussion

We modelled the species identification error by linking the catchability of egg density of spotted mackerel to the egg density of chub mackerel. We found that the model incorporating the effect of the egg density of chub mackerel was the better model, based on AIC (Fig. 2). In addition, the model showed a positive effect of the egg density of chub mackerel on the catchability of spotted mackerel. These results suggest the necessity of incorporating the effect of the egg density of chub mackerel when standardizing the egg density of spotted mackerel.

Methods that reduce the bias in species misidentification are needed for accurate stock assessment because inaccurate estimates of stock size may lead to incorrect management decisions and endanger exploited populations in the long term (Marko et al., 2004; Garcia-Vazquez et al., 2012). The retrospective biases in all the three measurements of stock abundance were clearly improved when using the estimated index with the chub mackerel effect; the magnitude of the retrospective biases decreased by about half compared with when the other indices were used (Fig. 4 and Table 1). These results suggest that our new method is effective for reducing the bias in species misidentification and greatly improves

the stock estimation especially of pelagic eggs, which have less significant differences in shape and size for species identification. Species samples for preserving morphological characteristics are usually fixed with formalin because of some advantages such as small shrinks of tissue and low cost than with ethanol. However, it is difficult to extract DNA from formalin-fixed samples due to DNA fragmentation and protein cross-linking (e.g., Goelz et al., 1985; Impraim et al., 1987), and so DNA analysis of these samples for species identification is difficult, if not impossible. Accordingly, species samples which were collected prior to development of DNA techniques cannot used for DNA analysis. In contrast, our new method requires only the geographic locations and “prior-” information, such as the species name (which can be based on some morphological characteristics), to be able to use various data such as the survey data of eggs and larvae collected in the ICES area. Thus, our method should be of great benefit to fisheries science.

Our results can play an important role on actual management of spotted mackerel. The stock status and management of this species is the focus of much attention in Japan because this species is one of the nine TAC (total allowable catch) species, whose catches are strictly managed according to output control. In fact, a new harvest control rule based on maximum sustainable yield (MSY) was implemented in 2020 (Yukami et al. 2020). The stock abundance of spotted mackerel has been decreasing in recent years, and positive retrospective bias caused overestimation of abundance in the terminal year in previous stock assessment using the nominal index of spawning egg (Yukami et al. 2019). This indicates that the allowable biological catch (ABC) was also overestimated, and this may have led to overfishing. The present study found that the retrospective bias was considerably mitigated by incorporating the effect of mixing of chub mackerel’ s eggs on spotted mackerel’ s egg

281 and, thus, would contribute to the derivation of ABC at an adequate level. Although the
282 current status is overfishing and overfished (Yukami et al. 2020), it is expected that the
283 Pacific stock of spotted mackerel will show a recovery to a level that produces MSY, using
284 our assessment method and the new Harvest Control Rules.

285 The geographic location of spawning grounds did not change in spotted mackerel
286 (Fig. 3), whereas the geographical location of spawning grounds has been shifted northward
287 in chub mackerel (Kanamori et al., 2019). This difference in change of spawning ground
288 between the two species may make it more difficult to perform species identification based
289 on egg diameter because the diameter of marine fish eggs generally increases in higher
290 latitudes (Llanos–Rivera & Castro, 2004). In other words, the egg diameter of chub
291 mackerel may increase as their spawning ground shifts northward, making it closer in size to
292 that of the spotted mackerel. This suggests that rising sea temperatures associated with
293 climate change may affect not only spatio–temporal patterns of organisms, such as
294 phenology and spatial distribution, but also an estimation of population abundance.

295 Although detailed information on spawning grounds is necessary for understanding of
296 the fluctuations in recruitment as well as a basis for stock management, prior data on the
297 spotted mackerel has not been reliable. For example, some studies have reported that the
298 waters around the Izu Islands may not be a suitable spawning ground for spotted mackerel
299 because few eggs have been observed (Yukami et al. 2019). In contrast, it is possible that the
300 spotted mackerel spawns around the Izu Islands because the estimated hatch day and the
301 spatial distribution of spotted mackerel at the Kuroshio–Oyashio transition area were similar
302 to those of chub mackerel, which spawns around mainly the Izu Islands (Takahashi et al.,
303 2010). The present study showed that the relative egg density, which was estimated using

the better model, was equally high off the coast of Kyushu, Shikoku, and the Izu Islands (Fig. 3), providing direct evidence that the waters around the Izu Islands are also a major spawning ground of spotted mackerel. One reason that spotted mackerel spawn in the waters around the Izu Islands is that spotted mackerel are not sensitive to rising water temperatures because they are generally distributed farther south than chub mackerel (Mitani et al., 2002). Indeed, although both spotted mackerel and chub mackerel spawn at the same time around the Izu Islands (Tanoue et al., 1960; Hanai & Meguro, 1997), the reproductive phenology of chub mackerel has changed due to rising sea surface temperatures associated with climate change; chub mackerel have been migrating to their feeding ground earlier and spawning farther northward since 2000 (Kanamori et al., 2019).

Understanding migration patterns is necessary for conducting stock assessments (Crossin et al., 2017). It has been assumed that spotted mackerel changes their spawning ground with age; spotted mackerel migrates from around the Izu Islands to the Kuroshio–Oyashio transition area to feed before spawning at 2 years of age (Nishida et al., 2000; Kawabata et al. 2008). Adults that have spawned gradually migrate westward, using the spawning grounds off the coast of Kyushu and Shikoku (Hanai, 1999; Nishida et al., 2006). Although the number of recruits was substantially high in 2004 and 2009 (Yukami et al., 2019), we did not find a tendency toward increased the relative egg density around the Izu Islands in 2006 and in 2011 or the other spawning grounds after 2007 and 2012 (Fig. 3). One explanation for this is the possibility that the migration range of spotted mackerel is narrower than we assumed. Previous studies have reported that spotted mackerel has retention around the Izu Islands and off the coast of Shikoku (Hanai, 1999; Nishida et al., 2006). Another explanation is that part of a strong year may remain in another area due to

the expansion of spatial distribution resulting from an increased number of recruitments. For example, Kawabata et al. (2008) reported that the 2004 year class migrated for feeding and overwintering until at least 3 years old over the Emperor Seamounts (around 165 – 170°E and 30 – 55°N). Testing these hypotheses will be the subject of future research and should improve our understanding of the migratory patterns of the spotted mackerel, which in turn should improve stock assessment and management.

Conclusion

This study showed that the indices of egg density of spotted mackerel, which were standardized using a spatio-temporal model, reduced temporal fluctuation and showed smooth patterns. In particular, the standardized indices in 2018 were revised downward to a considerable degree compared with the nominal index. The model incorporating the effect of chub mackerel egg density on the catchability of spotted mackerel (i.e., the model incorporating species misidentification bias) was the better model according to the AIC criteria. In addition, the retrospective bias decreased by about half when using the egg density index from the better model. These results suggest that incorporating species misidentification bias should be an essential process in improving stock assessment.

Acknowledgments

This research was financially supported by the grants from the Japan Society for the Promotion of Science (JSPS) (19K15905, 20392904).

Literature cited

- Crossin GT, Cooke SJ, Goldbogen JA, Phillips RA (2014) Tracking fitness in marine vertebrates: current knowledge and opportunities for future research. *Mar Ecol Prog Ser* 496:1-17
- Elphick CS (2008) How you count counts: the importance of methods research in applied ecology. *J Appl Ecol* 45:1313-1320
- Garcia-Vazquez E, Machado-Schiaffino G, Campo D, Juanes F (2012) Species misidentification in mixed hake fisheries may lead to overexploitation and population bottlenecks. *Fish Res* 114:52-55
- Goelz SE, Hamilton SR, Vogelstein B (1985) Purification of DNA from formaldehyde fixed and paraffin embedded human tissue. *Biochem Biophys Res Commun* 130:118 - 126
- Hashimoto M, Nishijima S, Yukami R, Watanabe C, Kamimura Y, Furuichi S, Ichinokawa M, Okamura H (2019) Spatiotemporal dynamics of the Pacific chub mackerel revealed by standardized abundance indices. *Fish Res* 219:105315
- Hashimoto M, Okamura H, Ichinokawa M, Hiramatsu K, Yamakawa T (2018) Impacts of the nonlinear relationship between abundance and its index in a tuned virtual population analysis. *Fish Sci* 84:335-347
- Hurtado-Ferro F, Szuwalski CS, Valero JL, Andderson SC, Cunningham CJ, Johnson KF, Licandeo RL, McGilliard CR, Monnahan CC, Muradian ML, Ono K, Vert-Pre KA, Whitten AR, Punt AE (2015) Looking in the review mirror: bias and retrospective patterns in integrated, age-structured stock assessment models. *ICES J Mar Sci* 72:99-110
- Ichinokawa M, Okamura H (2014) Review of stock evaluation methods using VPA for

372 fishery stocks in Japan: implementation with R. Bull Jpn Soc Fish Oceanogr
373 78:104-113 (in Japanese with English abstract)

374 Impraim CC, Saiki RK, Erlich HA, Teplitz RL (1987) Analysis of DNA extracted from
375 formalin-fixed, paraffin-embedded tissues by enzymatic amplification and
376 hybridization with sequence-specific oligonucleotides. Biochem Biophys Res
377 Commun 142:710 - 716

378 Kanamori Y, Takasuka A, Nishijima S, Okamura H (2019) Climate change shifts the
379 spawning ground northward and extends the spawning period of chub mackerel in the
380 western North Pacific. Mar Ecol Prog Ser 624:155-166

381 Ko HL, Wang YT, Chiu TS, Lee MA, Leu MY, Chang KZ et al. (2013) Evaluating the
382 accuracy of morphological identification of larval fishes by applying DNA barcoding.
383 PLoS ONE 8:e53451

384 Lindgren F (2012) Continuous domain spatial models in R-INLA. ISBA Bull 19:14-20

385 MacKenzie DI, Nichols JD, Lanchman GB, Droege S, Royle JA, Langtimm CA (2002)
386 Estimating site occupancy rates when detection probabilities are less than one.
387 Ecology 83:2248-2255

388 Marko PB, Lee SC, Rice AM, Gramling JM, Fitzhenry TM, McAlister JS, Harper GR,
389 Moran AL (2004) Mislabelling of a depleted reef fish. Nature 430:309-310

390 Matarese AC, Spies IB, Busby MS, Orr JW (2011) Early larvae of *Zesticelus profundorum*
391 (family Cottidae) identified using DNA barcoding. Ichthyol Res 58: 170-174

392 Mohn R (1999) The retrospective problem in sequential population analysis: an
393 investigation using cod fishery and simulated data. ICES J Mar Sci 56:473-488

394 Mori K, Hiyama Y (2014) Stock assessment and management for walleye pollock in Japan.

395 Fish Sci 80:161-172

396 Nishida H, Wada T, Oozeki Y, Sezaki K, Saito M (2001) Possibility of identifying chub
397 mackerel and spotted mackerel by measuring diameter of mackerel eggs. Nippon
398 Suisan Gakkaishi, 67: 102-104

399 Okamura H, Yamashita Y, Ichinokawa M (2017) Ridge virtual population analysis to reduce
400 the instability of fishing mortalities in the terminal year. ICES J Mar Sci 74:2427-2436

401 R Development Core Team (2019) R: a language and envi- ronment for statistical
402 computing. R Foundation for Sta- tistical Computing, Vienna

403 Takahashi M, Takagi K, Kawabata A, Watanabe C, Nishida H, Yamashita N, Mori K,
404 Suyama S, Nakagami M, Ueno Y, Saito M (2010) Estimated hatching season of the
405 Pacific stock of chub mackerel *Scomber japonicus* and spotted mackerel *S.*
406 *australasicus* in 2007. Fisheries biology and oceanography in the Kuroshio 11:49-54
407 (in Japanese)

408 Takasuka A, Kubota H, Oozeki Y (2008a) Spawning overlap of anchovy and sardine in the
409 western North Pacific. Mar Ecol Prog Ser 366:231-244

410 Takasuka A, Oozeki Y, Kubota H (2008b) Multi-species regime shifts reflected in spawning
411 temperature optima of small pelagic fish in the western North Pacific. Mar Ecol Prog
412 Ser 360:211-217

413 Takasuka A, Tadokoro K, Okazaki Y, Ichikawa T, Sugisaki H, Kuroda H, Oozeki Y (2017)
414 In situ filtering rate vari- ability in egg and larval surveys off the Pacific coast of
415 Japan: Do plankton nets clog or over-filter in the sea? Deep-Sea Res I 120:132 – 137

416 Takasuka A, Yoneda M, Oozeki Y (2019) Density depend- ence in total egg production per
417 spawner for marine fish. Fish Fish 20:125 – 137

- 418 Thorson JT (2019) Guidance for decisions using the Vector Autoregressive Spatio-Temporal
419 (VAST) package in stock, ecosystem, habitat and climate assessments. *Fish Res*
420 210:143-161
- 421 Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and distribution
422 shifts using single- and multispecies models of fishes and biogenic habitat. *ICES J*
423 *Mar Sci* 74:1311 – 1321
- 424 Thorson JT, Kristensen K (2016) Implementing a generic method for bias correction in
425 statistical models using ran- dom effects, with spatial and population dynamics exam-
426 ples. *Fish Res* 175: 66 - 74
- 427 Thorson JT, Shelton AO, Ward EJ, Skaug HJ (2015) Geostatistical delta-generalized linear
428 mixed models improve precision for estimated abundance indices for West Coast
429 groundfishes. *ICES J Mar Sci* 72:1297 – 1310
- 430 Victor BC, Hanner R, Shivji M, Hyde J, Caldow C (2009) Identification of the larval and
431 juvenile stages of the cubera snapper, *Lutignus cyanopterus*, using DNA barcoding.
432 *Zootaxa* 2215:24-36
- 433 Watanabe C, Hanai T, Meguro K, Ogino R, Kubota Y, Kimura R (1999) Spawning biomass
434 estimates of chub mackerel *Scomber japonicus* of Pacific subpopulation off central
435 Japan by a daily egg production method. *Nippon Suisan Gakkaishi* 65: 695-702 (in
436 Japanese with English abstract)
- 437 Watanabe C, Nishida H (2002) Development of assessment techniques for pelagic fish
438 stocks: applications of daily egg production method and pelagic trawl in the
439 northwestern Pacific Ocean. *Fish Sci* 68:97-100
- 440 Watanabe C, Yatsu A (2006) Long-tem changes in maturity at age of chub mackerel

441 (*Scomber japonicus*) in relation to population declines in the waters off northeastern
 442 Japan. Fish Res 78:323-332

443 Watanabe T (1970) Morphology and ecology of early stages of life in Japanese common
 444 mackerel, *Scomber japonicus* HOUTTUYN, with special reference to fluctuation of
 445 population. Bull Tokai Reg Fish Res Lab 62:1-283 (in Japanese with English abstract)

446 Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal
 447 population. Academic Press, New York

448 Yukami R, Isu S, Watanabe C, Kamimura Y, Furuichi S (2019) Stock assessment and
 449 evaluation for the Pacific stock of spotted mackerel (fiscal year 2018). In: Marine
 450 fisheries stock assessment and evaluation for Japanese waters (2018/ 2019). Fisheries
 451 Agency and Fisheries Research Agency of Japan, Yokohama, Kanagawa, p 248 —
 452 278 (in Japanese)

453 Yukami R, Isu S, Kamimura Y, Furuichi S, Watanabe R, Kanamori Y (2020) Stock
 454 assessment and evaluation for the Pacific stock of spotted mackerel (fiscal year 2019).
 455 In: Marine fisheries stock assessment and evaluation for Japanese waters (2019/
 456 2020). Fisheries Agency and Fisheries Research Agency of Japan, Yokohama,
 457 Kanagawa (in Japanese)

Fig. 1: Study area. Spotted mackerel *Scomber australasicus* in the western North Pacific spawns around Kyushu, Shikoku, and the Izu Islands in Japan. Adults and their offspring are then transported to their feeding ground by the Kuroshio Current.

Fig. 2: Temporal trend of the indices of egg density. The grey line represents the scaled nominal index, the blue line represents the estimated index without the chub mackerel effect, and the red line represents the estimated index with chub mackerel effect. Vertical bars are 95% confidence intervals of the estimated indices.

Fig. 3: Temporal changes in the spatial distribution of relative egg density, which estimated by using the model with chub mackerel effect.

Fig. 4: Retrospective patterns of total numbers of individuals, total biomass, and spawning stock biomass (SSB).

Table 1: Mohn's rho for each index of total numbers of individuals, total biomass, and spawning stock biomass (SSB).

Index	Mohn's rho		
	Numbers	Biomass	SSB
Nominal	0.47	0.45	0.44
Chub –	0.51	0.48	0.45
Chub +	0.28	0.24	0.19

458