

Title: Integrated spatial model estimates the fish distribution using environmental DNA and catch data

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Abstract

Keywords

1 Introduction

Understanding of spatial distribution of species and underlying its mechanism is an essential issue in ecology. Field surveys using environmental DNA (eDNA) are widely used for detecting invasive or rare species and hotspot of biodiversity (面倒なのでレビュー論文を引用) because the surveys of eDNA are easy to detect presence/absence of target species, non-invasiveness, and high cost effectiveness rather than previous direct sampling method (Rees et al. 2014; Thomsen & Willerslev 2015). However, the presence/absence of eDNA includes many types of uncertainties due to relating to environmental factors such as temperature and advection (). For example, in aquatic habitats, it is not sure whether target species are in a location or not when eDNA of target species is detected because eDNA are transported passively. Therefore, the consideration to the influence of environmental factors on eDNA is necessary for estimation of species distribution when we use eDNA methods.

One step towards overcoming these uncertainties is a understanding of the "ecology of eDNA": (Barnes & Turner 2016). Previous studies

Integrated species distribution models are now common spatial model to predict spatial pattern of species (Issac et al. 2020). The model use the different type of data with strengths and weaknesses, such as scientific survey data which is restricted spatially and quantitatively and opportunistic citizen data which is widely collected and abundant, and combine in a single model (Isaac et al. 2020; Miller et al. 2019).

The models combine the different type of data with strengths and weaknesses in a single model (). For example, scientific survey data are high quality but less abundant due to restriction of spatially costly while opportunistic data such as citizen data are widely

23 collected and abundant but may be low quality due to not using consistent field methods.
24 Combining both types of data can capitalize on the strengths of each data and perform better
25 prediction than models when we use single data (Pacifi et al. 2017; Miller et al. 2019).

26 Tokyo Bay is a large enclosed coastal sea in Japan. In Tokyo Bay, there are many
27 useful species for fisheries that are called "Edomae" because these species have been used
28 for Sushi since Edo Era (about 400 years ago). Catch of some Edomae have been decreased
29 because of habitat modification due to urbanization (e.g., landfill of tidal flats and water
30 pollution). Catch statistics (total catch in each fish, efforts, and geographic location of
31 fishing) have been collected for stock assessment since 1990 by prefectures around Tokyo
32 Bay, which is widely collected and abundant. In addition, scientific survey of eDNA has
33 been conducted monthly in same points since 2018 for monitoring biodiversity (Hongo et
34 al., submitted).

35 In this paper, we demonstrate a method for reducing identification error by using the
36 state-of-the-art spatio-temporal standardization method (Thorson 2019). Our new
37 application substantially reduced the bias that would have been caused by the species
38 misidentification of spawning eggs between chub mackerel and spotted mackerel and led to
39 considerable improvement in the stock assessment of spotted mackerel in the western North
40 Pacific. To quantify the effect of species misidentification, we estimated the indices of egg
41 density for spotted mackerel both with and without incorporation of the effect of the egg
42 density of chub mackerel on the catchability of spotted mackerel, using 15 years data of
43 spawning eggs. We then examined how retrospective biases of three measurements of stock
44 abundance (total number of individuals, total stock biomass, and spawning stock biomass;
45 SSB) changed when we used the estimated indices for a stock assessment model. We tested

46 the hypothesis that the retrospective bias should be lower in the spotted mackerel stock
47 assessment with the egg–abundance index standardized by the spatio–temporal model
48 incorporating chub mackerel egg density as a catchability covariate.

49

50 **2 Materials and Methods**

51 **2.1 Data sets**

52 **2.1.1 Survey and data**

53 The egg density data with 30′ latitude \times 30′ longitude horizontal square resolution in the
54 areas from 122°E to 150°E and 24°N to 43°N was used. The egg density data set was
55 derived from monthly egg surveys off the Pacific coast of Japan from January to June,
56 2005–2019 (Takasuka et al., 2008a, 2019). The aim of the surveys was to monitor the egg
57 abundance of major small pelagic fish species, including chub mackerel and spotted
58 mackerel, so that the spatial area and survey month of the data largely covered the major
59 spawning grounds and spawning season. While some sampling locations were fixed, others
60 varied for various reasons (e.g., environmental conditions). Accordingly, the survey design
61 changed slightly each year (Kanamori et al., 2019). Although the sampling efforts were
62 approximately consistent year-round, the efforts tended to be more intensive during early
63 spring; effort was highest in February and decreased gradually thereafter (Takasuka et al.,
64 2008b).

65 The egg surveys were conducted by 18 prefectural experimental stations or fisheries
66 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 a 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 100 randomly selected individuals was assumed to be the same for the whole sample. Additionally, the number of eggs per unit area in the water column (number m^{-2}) for each sampling tow was calculated by flow-meter revolutions, flow-meter revolutions per meter tow in the calibration, wire length (m), opening mouth area of the net (m^{-2}), and wire angle. Then, the arithmetic average of the number of eggs was obtained with $30'$ latitude \times $30'$ longitude horizontal square resolution. The mean proportion of the total number of eggs of spotted mackerel against the total number of eggs of *Scomber* was less than 20 % from 2005 to 2019. Therefore, the effect of the misidentification error that we considered was from chub

90 mackerel on spotted mackerel (i.e., we assumed that the effect of the misidentification error
91 from spotted mackerel on chub mackerel was small.) More detailed descriptions of the
92 surveys and data set are provided in previous studies of the reproductive biology of small
93 pelagic fish species (e.g., Takasuka et al. 2008a,b, 2017, 2019).

94 **2.2 Data analyses**

95 **2.2.1 Indices of egg density**

96 In this study, we used the three indices of egg density of spotted mackerel; nominal, chub–,
97 and chub+. The nominal index was the arithmetic mean of egg density for each year. The
98 chub– index was the estimated egg density by considering sampling effects (i.e.,
99 spatio–temporal changes in survey design). The chub+ index was the estimated egg density
100 by considering sampling effects and the effect of egg density of chub mackerel on the
101 catchability of egg density of spotted mackerel. The process for estimating chub– and the
102 chub+ is described in the following section.

103 **2.2.2 Estimation of the indices of egg density**

104 To estimate the chub– and the chub+ indices of egg density by considering sampling effects
105 (i.e., spatio–temporal changes in survey design) as well as the effect of the egg density of
106 chub mackerel on the catchability of egg density of spotted mackerel, we used the
107 multivariate vector autoregressive spatio-temporal (VAST) model (Thorson and Barnett,
108 2017), which accounts for spatio-temporal changes in survey design, survey effort, and
109 observation rates and can accurately estimate relative local densities at high resolution by
110 standardizing sampling designs (Thorson and 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 and Barnett, 2017):

$$\begin{aligned}\text{logit } p_i &= \beta_p(t_i) + \omega_p(s_i) + \varepsilon_p(s_i, t_i) + \eta_p(v_i) + \lambda_p Q(i) \\ \log d_i &= \beta_d(t_i) + \omega_d(s_i) + \varepsilon_d(s_i, t_i) + \eta_d(v_i) + \lambda_d Q(i)\end{aligned}\tag{1}$$

where $\beta(t_i)$ is the intercept for year t , and $\omega(s_i)$ and $\varepsilon(s_i, t_i)$ are the spatial and spatio-temporal random effects for year t and location s , respectively. $\eta(v_i)$ is the overdispersion random effect of factor v_i , which is the interaction of year and month. λ is the effect of the catchability covariate $Q(i)$:

$$Q(i) = \log(d_{chub}(s_i) + 0.1).$$

That is, this term considers the effect of species misidentification between chub mackerel and spotted mackerel; as mentioned earlier, we suspected overestimation of egg density of spotted mackerel because the difference in egg diameter has become ambiguous according to increase in egg density of chub mackerel and the distributions of egg diameters between species have overlapped (Yukami et al., 2019). The constant 0.1 was added because $\log 0$ (i.e., no chub mackerel eggs) is undefined, and the same result was obtained when using 1 in place of 0.1.

The probability density function of $\omega(\cdot)$ is a multivariate normal distribution

128 $\text{MVN}(0, \mathbf{R})$, where the variance–covariance matrix \mathbf{R} is a Matérn correlation function. The
 129 probability density function of $\varepsilon(s_i, t_i)$ is

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

130 Here, we set $\rho_\varepsilon = 0$ under the assumption that the year was independent. Therefore, the
 131 probability density function of $\eta(v_i)$ is $\eta(v_i) \sim \text{N}(0, 1)$.

132 For computational reasons, the spatio-temporal variation $\varepsilon_p(s_i, t_i)$ was approximated
 133 as being piecewise constant at a fine spatial scale. We used a k-means algorithm to identify
 134 200 locations (termed “knots”) to minimize the total distance between the location of
 135 sampling data (Thorson et al., 2015) using R-INLA software (Lindgren, 2012). The number
 136 of knots was increased to the greatest extent possible, and similar results were obtained for
 137 low knots (= 100; Akaike information criterion [AIC] = 6773.01) and high knots (= 200;
 138 AIC = 6676.25).

139 Parameters in the VAST model were estimated using the VAST package (Thorson et
 140 al., 2015, 2016a) in R 3.6.1 (R Development Core Team, 2019). Bias-correction for random
 141 effects (Thorson and Kristensen, 2016) was applied when estimating the derived parameters.
 142 We evaluated the model diagnostics plots and confirmed that there were no serious problems
 143 with the model. The relative egg density in year t at location s , $\hat{d}(s, t)$ and the index of egg
 144 density in year t , $\hat{D}(t)$, were estimated using the predicted values for random effects as
 145 follows (Thorson et al., 2017):

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

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

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

where $a(s)$ is the area of location s . It is noteworthy that the effect of the catchability covariate $\lambda Q(i)$ in the above equation (1) is removed in the calculation of densities. This means that the abundance index can be derived from the model by removing the bias from the contamination of spotted mackerel eggs with chub mackerel eggs.

2.2.3 Estimation of stock abundance

To examine the validity of the three indices (i.e., nominal index, chub- index, and chub+ index), we estimated the three measurements of stock abundance (total number of individuals, total stock biomass, and SSB) from 1995 to 2018 using a tuned virtual population analysis (VPA). This model is an age-based cohort analysis for estimating the historical abundance and fishing mortality rates from catch-at-age data and has been applied to spotted mackerel in Japan (Yukami et al., 2019). In addition to the three indices of egg density, we used catch-at-age, weight-at-age (not constant over time), maturity-at-age (constant over time) for four age categories (1 to 3, and 4+), the natural mortality coefficient, and a recruitment index following stock assessment in Japan (Yukami et al., 2019). The fishing mortality coefficients other than the terminal age in the terminal year were estimated under the assumption that the selectivity in the latest year was equal to the average

selectivity of the prior 5 years (Ichinokawa and Okamura, 2014; Mori and Hiyama, 2014). We confirmed that this assumption did not change our results when using the average selectivity of the prior 3 years 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:

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

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^2 is the variance in fitting the abundance estimate to the index, and y_k is the first year of index k .

2.2.4 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 estimation of stock abundance for 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 the VAST model and considering the effect of the chub mackerel, 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):

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

where B_{y-i} is the value of the year $y - i$ estimate using the full data and B_{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

3.1 Temporal trend in the indices of egg density

When comparing the standardized indices (i.e., chub- and chub+ indices) to the nominal index, the standardized indices reduced temporal fluctuation (Fig. 2). Whereas the nominal index increased substantially in 2018, the standardized indices were reduced to a considerable degree. Moreover, the standardized indices for some years, such as 2008, 2009, and 2012, were increased.

205 The model with the effect of chub mackerel egg density on the catchability of spotted
206 mackerel was more parsimonious than the model without the effect of chub mackerel based
207 on AIC (chub+, AIC = 8250.12; chub–, AIC = 8978.81). The coefficient of the effect of
208 chub mackerel on the catchability of spotted mackerel, λ , indicates a positive effect ($\lambda =$
209 0.17). The estimated index with the effect of chub mackerel effect reached a peak in 2008
210 and decreased gradually thereafter. The value of this index in 2019 was the lowest since
211 2005 (Fig. 2).

212 **3.2 Spatial distribution of the relative egg density**

213 The relative egg density with the effect of chub mackerel was high off the coast of Kyushu,
214 Shikoku, and the Izu Islands (Fig. 3). In addition, the relative egg density was slightly high
215 off the coast of the Tohoku region. These patterns were consistent during the study period.
216 The relative egg density did not clearly increase or decrease in any area during the study
217 period.

218 **3.3 Retrospective analysis**

219 Recent estimated values of stock abundance (i.e., total numbers of individuals, total
220 biomass, and SSB) differed depending on the indices used, whereas the directions of
221 retrospective bias were sometimes consistent depending on the indices used (Fig. 4). In all
222 the three measurements of stock abundance, the recent estimated values were higher when
223 using the nominal and estimated index without the effect of chub mackerel than using the
224 estimated index with the effect of chub mackerel. The directions of retrospective bias were
225 always positive, independent of the indices used.

226 For all the three measurements of stock abundance (i.e., total numbers of individuals,

total biomass, and SSB), retrospective biases clearly improved when using the estimated index with the effect of chub mackerel (Table 1). Values of Mohn's rho, which represents the magnitude and direction of retrospective bias, were similar when using the nominal index and the estimated index without the effect of chub mackerel (Table 1). In contrast, Mohn's rho decreased when using the estimated index with the effect of chub mackerel. 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 spotted mackerel eggs to the egg density of chub mackerel. We found that the model incorporating the effect of the egg density of chub mackerel was better, based on AIC (Fig. 2). In addition, the model showed that the egg density of chub mackerel had a positive effect 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.

Whereas the nominal index increased substantially in 2018, the standardized indices of chub- and chub+ were similarly reduced (Fig. 2). The reduction in both standardized indices, irrespective of whether the effect of the egg density of chub mackerel was incorporated, may be explained by spatio-temporal changes in survey design, survey effort, and observation rate by the VAST model. Indeed, the surveys in 2018 were conducted by chance, at the site with a high egg density of spotted mackerel (Yukami et al., 2019), which

248 was spatially smoothed by considering the spatial correlation using the VAST model.
249 Hence, we think that the nominal index in 2018 included both species identification bias and
250 spatio-temporal bias from the survey.

251 The retrospective biases in all the three measurements of stock abundance were clearly
252 improved when using the estimated index that incorporates the effect of chub mackerel; the
253 magnitude of the retrospective biases decreased by about half compared with those for the
254 other indices (Fig. 4 and Table 1). These results suggest that our new application is effective
255 for reducing the bias in species misidentification and greatly improves stock estimation,
256 especially for pelagic eggs, which have relatively minor differences in shape and size for
257 species identification. The samples are usually fixed with formalin to preserve their
258 morphological characteristics, which makes DNA extraction difficult or impossible due to
259 DNA fragmentation and protein cross-linking (e.g., Goelz et al., 1985; Impraim et al.,
260 1987). Accordingly, samples collected prior to the development of DNA techniques cannot
261 used for DNA analysis. In contrast, our new method requires only the geographic locations
262 and “prior-” information, such as the species name (which can be based on morphological
263 characteristics), to use various data types, such as survey data for eggs and larvae collected
264 in the ICES area. Thus, our method should be of great benefit in fisheries science.

265 Our results can play an important role in the actual management of spotted mackerel.
266 The stock status and management of this species have received substantial attention in Japan
267 because this species is one of the nine TAC (total allowable catch) species, whose catches
268 are strictly managed according to output control. In fact, a new harvest control rule based on
269 maximum sustainable yield (MSY) was implemented in 2020 (Yukami et al. 2020). The
270 stock abundance of spotted mackerel has been decreasing in recent years, and positive

271 retrospective bias caused overestimates of abundance in the terminal year in a previous stock
272 assessment using an unstandardized index of spawning eggs (Yukami et al. 2019). This
273 indicates that the allowable biological catch (ABC) was also overestimated, and this may
274 have led to overfishing. The stock assessments with the nominal and chub- indices would
275 estimate, respectively, 140 and 105 thousand tons as ABC in 2020, whilst that with the
276 chub+ index would derive 38 thousand tons as ABC in 2020. The present study found that
277 the retrospective bias was considerably reduced in the stock assessment with the chub+
278 index and this approach would therefore contribute to the derivation of an adequate ABC.
279 Although the current status is overfishing and overfished (Yukami et al. 2020), it is expected
280 that the Pacific stock of spotted mackerel will show a recovery to a level that produces the
281 MSY by using our assessment method and the new Harvest Control Rules.

282 Although detailed information on spawning grounds is necessary for understanding
283 fluctuations in recruitment as well as for providing a basis for stock management, prior data
284 for spotted mackerel has not been reliable. For example, some studies have reported that the
285 area around the Izu Islands may not be a suitable spawning ground for spotted mackerel
286 because few eggs have been observed (Yukami et al. 2019). In contrast, it is possible that the
287 spotted mackerel spawns around the Izu Islands because the estimated hatch day and the
288 spatial distribution of spotted mackerel at the Kuroshio–Oyashio transition area were similar
289 to those of chub mackerel, which spawns around mainly the Izu Islands (Takahashi et al.,
290 2010). The present study showed that the relative egg density, which was estimated using
291 the better model, was equally high off the coast of Kyushu, Shikoku, and the Izu Islands
292 (Fig. 3), providing direct evidence that the area around the Izu Islands are also a major
293 spawning ground of spotted mackerel. It is possible that spotted mackerel spawn in the area

294 around the Izu Islands because they are not sensitive to rising water temperatures and they
295 are generally distributed farther south than chub mackerel (Mitani et al., 2002). Indeed,
296 although both spotted mackerel and chub mackerel spawn at the same time around the Izu
297 Islands (Tanoue et al., 1960; Hanai and Meguro, 1997), the reproductive phenology of chub
298 mackerel has changed due to rising sea surface temperatures associated with climate change;
299 since 2000, chub mackerel migrate to their feeding ground earlier and spawn farther
300 northward (Kanamori et al., 2019).

301 Understanding migration patterns is necessary for conducting stock assessments
302 (Crossin et al., 2017). It has been assumed that the spawning grounds of spotted mackerel
303 change with age; individuals migrate from around the Izu Islands to the Kuroshio–Oyashio
304 transition area to feed before spawning at 2 years of age (Nishida et al., 2000; Kawabata et
305 al. 2008). Adults that have spawned gradually migrate westward, using the spawning
306 grounds off the coast of Kyushu and Shikoku (Hanai, 1999; Nishida et al., 2006). Although
307 the number of recruits were particularly high in 2004 and 2009 (Yukami et al., 2019), we did
308 not find evidence for an increase in the relative egg density around the Izu Islands in 2006
309 and in 2011 or the other spawning grounds after 2007 and 2012 (Fig. 3). One explanation
310 for this is that the migration range of spotted mackerel is narrower than we assumed.

311 Previous studies have reported that spotted mackerel remains around the Izu Islands and off
312 the coast of Shikoku (Hanai, 1999; Nishida et al., 2006). Another explanation is that part of
313 a strong year may remain in another area due to the expansion of the spatial distribution
314 resulting from an increase number in recruitments. For example, Kawabata et al. (2008)
315 reported that the 2004 year class migrated for feeding and overwintering until at least 3
316 years old over the Emperor Seamounts (around 165 – 170°E and 30 – 55°N). Testing these

317 hypotheses will be the subject of future research and should improve our understanding of
318 the migratory patterns of the spotted mackerel, which in turn should improve stock
319 assessment and management.

320

321 **Conclusion**

322 This study showed that indices of egg density of spotted mackerel, which were standardized
323 using a spatio-temporal model, reduced temporal fluctuation. In particular, the standardized
324 indices in 2018 were reduced to a considerable degree compared with the nominal index.

325 The model incorporating the effect of chub mackerel egg density on the catchability of
326 spotted mackerel (i.e., the model incorporating species misidentification bias) was the better
327 model according to the AIC. In addition, the retrospective bias decreased by about half when
328 using the egg density index from the better model. These results suggest that incorporating
329 species misidentification bias is an essential process for improving stock assessment.

330

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334

335 **Literature cited**

336 Crossin, G.T., Cooke, S.J., Goldbogen, J.A., Phillips, R.A. 2014. Tracking fitness in marine
337 vertebrates: current knowledge and opportunities for future research. *Mar. Ecol. Prog.*
338 *Ser.* 496:1-17.

339 Elphick, C.S. 2008. How you count counts: the importance of methods research in applied
 340 ecology. *J. Appl. Ecol.* 45:1313-1320.

341 Garcia-Vazquez, E., Machado-Schiaffino, G., Campo ,D., Juanes, F. 2012. Species
 342 misidentification in mixed hake fisheries may lead to overexploitation and population
 343 bottlenecks. *Fish. Res.* 114:52-55.

344 Goelz, S.E., Hamilton, S.R., Vogelstein, B. 1985. Purification of DNA from formaldehyde
 345 fixed and paraffin embedded human tissue. *Biochem. Biophys. Res. Commun.*
 346 130:118 - 126.

347 Hashimoto, M., Nishijima, S., Yukami, R., Watanabe, C., Kamimura, Y., Furuichi, S.,
 348 Ichinokawa, M., Okamura, H. 2019. Spatiotemporal dynamics of the Pacific chub
 349 mackerel revealed by standardized abundance indices. *Fish. Res.* 219:105315.

350 Hashimoto, M., Okamura, H., Ichinokawa, M., Hiramatsu, K., Yamakawa, T. 2018. Impacts
 351 of the nonlinear relationship between abundance and its index in a tuned virtual
 352 population analysis. *Fish. Sci.* 84:335-347.

353 Hurtado-Ferro, F., Szuwalski, C.S., Valero. J.L., Andderson. S.C., Cunningham, C.J.,
 354 Johnson, K.F., Licandeo, R.L., McGilliard, C.R., Monnahan, C.C., Muradian, M.L.,
 355 Ono, K., Vert-Pre, K.A., Whitten, A.R., Punt, A.E. 2015. Looking in the review
 356 mirror: bias and retrospective patterns in integrated, age-structured stock assessment
 357 models. *ICES J. Mar. Sci.* 72:99-110.

358 Ichinokawa, M., Okamura, H. 2014. Review of stock evaluation methods using VPA for
 359 fishery stocks in Japan: implementation with R. *Bull. Jpn. Soc. Fish. Oceanogr.*
 360 78:104-113 (in Japanese with English abstract).

361 Impraim, C.C., Saiki. R.K., Erlich, H.A., Teplitz, R.L. 1987. Analysis of DNA extracted

362 from formalin-fixed, paraffin-embedded tissues by enzymatic amplification and
 363 hybridization with sequence-specific oligonucleotides. *Biochem. Biophys. Res.*
 364 *Commun.* 142:710 - 716.

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

368 Ko, H.L., Wang, Y.T., Chiu, T.S., Lee, M.A., Leu, M.Y., Chang, K.Z. et al. 2013. Evaluating
 369 the accuracy of morphological identification of larval fishes by applying DNA
 370 barcoding. *PLoS ONE* 8:e53451.

371 Lindgren, F. 2012. Continuous domain spatial models in R-INLA. *ISBA Bull.* 19:14-20.

372 MacKenzie, D.I., Nichols, J.D., Lanchman, G.B., Droege, S., Royle, J.A., Langtimm, C.A.
 373 2002. Estimating site occupancy rates when detection probabilities are less than one.
 374 *Ecology* 83:2248-2255.

375 Marko, P.B., Lee, S.C., Rice, A.M., Gramling, J.M., Fitzhenry, T.M., McAlister, J.S.,
 376 Harper, G.R., Moran, A.L. 2004. Mislabelling of a depleted reef fish. *Nature*
 377 430:309-310.

378 Matarese, A.C., Spies, I.B., Busby, M.S., Orr, J.W. 2011. Early larvae of *Zesticelus*
 379 *profundorum* (family Cottidae) identified using DNA barcoding. *Ichthyol. Res.* 58:
 380 170-174.

381 Mohn, R. 1999. The retrospective problem in sequential population analysis: an
 382 investigation using cod fishery and simulated data. *ICES J. Mar. Sci.* 56:473-488.

383 Mori, K., Hiyama, Y. 2014. Stock assessment and management for walleye pollock in
 384 Japan. *Fish. Sci.* 80:161-172.

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

388 Okamura, H., Yamashita, Y., Ichinokawa, M. 2017. Ridge virtual population analysis to
 389 reduce the instability of fishing mortalities in the terminal year. ICES J. Mar. Sci.
 390 74:2427-2436.

391 R Development Core Team, 2019. R: a language and envi- ronment for statistical
 392 computing. R Foundation for Sta- tistical Computing, Vienna.

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

398 Takasuka, A., Kubota, Hm., Oozeki, Y. 2008a. Spawning overlap of anchovy and sardine in
 399 the western North Pacific. Mar. Ecol. Prog. Ser. 366:231-244.

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

403 Takasuka, A., Tadokoro, K., Okazaki, Y., Ichikawa, T., Sugisaki, H., Kuroda, H., Oozeki, Y.
 404 2017. In situ filtering rate vari- ability in egg and larval surveys off the Pacific coast of
 405 Japan: Do plankton nets clog or over-filter in the sea? Deep-Sea Res. I 120:132 —
 406 137.

407 Takasuka, A., Yoneda, M., Oozeki, Y. 2019. Density depend- ence in total egg production

per spawner for marine fish. *Fish. Fish.* 20:125 – 137.

Thorson, J.T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. *Fish. Res.* 210:143-161.

Thorson, J.T., Barnett, L.A.K. 2017. Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES J. Mar. Sci.* 74:1311 – 1321.

Thorson, J.T., Kristensen, K. 2016. Implementing a generic method for bias correction in statistical models using random effects, with spatial and population dynamics examples. *Fish. Res.* 175: 66 - 74.

Thorson, J.T., Shelton, A.O., Ward, E.J., Skaug, H.J. 2015. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. *ICES J. Mar. Sci.* 72:1297 – 1310.

Victor, B.C., Hanner, R., Shivji, M., Hyde, J., Caldow, C. 2009. Identification of the larval and juvenile stages of the cubera snapper, *Lutignus cyanopterus*, using DNA barcoding. *Zootaxa* 2215:24-36.

Watanabe, C., Hanai, T., Meguro, K., Ogino, R., Kubota, Y., Kimura, R. 1999. Spawning biomass estimates of chub mackerel *Scomber japonicus* of Pacific subpopulation off central Japan by a daily egg production method. *Nippon Suisan Gakkaishi* 65: 695-702 (in Japanese with English abstract).

Watanabe, C., Nishida, H. 2002. Development of assessment techniques for pelagic fish stocks: applications of daily egg production method and pelagic trawl in the northwestern Pacific Ocean. *Fish. Sci.* 68:97-100.

- 431 Watanabe, C., Yatsu, A. 2006. Long-term changes in maturity at age of chub mackerel
432 (*Scomber japonicus*) in relation to population declines in the waters off northeastern
433 Japan. Fish. Res. 78:323-332.
- 434 Watanabe, T., 1970. Morphology and ecology of early stages of life in Japanese common
435 mackerel, *Scomber japonicus* HOUTTUYN, with special reference to fluctuation of
436 population. Bull. Tokai Reg. Fish. Res. Lab. 62:1-283 (in Japanese with English
437 abstract).
- 438 Williams, B.K., Nichols, J.D., Conroy, M.J. 2002. Analysis and management of animal
439 population. Academic Press, New York.
- 440 Yukami, R., Isu, S., Watanabe, C., Kamimura, Y., Furuichi, S. 2019. Stock assessment and
441 evaluation for the Pacific stock of spotted mackerel (fiscal year 2018). In: Marine
442 fisheries stock assessment and evaluation for Japanese waters (2018/ 2019). Fisheries
443 Agency and Fisheries Research Agency of Japan, Yokohama, Kanagawa, p 248 –
444 278 (in Japanese).
- 445 Yukami, R., Isu, S., Kamimura, Y., Furuichi, S., Watanabe, R., Kanamori, Y. 2020. Stock
446 assessment and evaluation for the Pacific stock of spotted mackerel (fiscal year 2019).
447 In: Marine fisheries stock assessment and evaluation for Japanese waters (2019/
448 2020). Fisheries Agency and Fisheries Research Agency of Japan, Yokohama,
449 Kanagawa (in Japanese).

Captions

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 trends in indices of egg density. The gray line represents the scaled nominal index, the blue line represents the estimated index without the effect of chub mackerel, and the red line represents the estimated index with the effect of chub mackerel. Vertical bars are 95% confidence intervals of the estimated indices.

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

Fig. 4 Retrospective patterns of total numbers of individuals, total biomass, and spawning stock biomass (SSB). Color differences denote differences in sequentially removing data for the five most recent years (blue, light blue, green, orange, and red indicate removal of data for years 1 to 5 years, respectively) from the full data set (gray).