Title: Spatio-temporal model and machine learning method reveal process of phenological shift under climate change of North Pacific spiny dogfish

Yuki Kanamori^{1*}, Toshikazu Yano², Hiroshi Okamura³, and Yuta Yagi⁴

¹ Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 25-259 Shimomekurakubo, Samemachi, Hachinohe, Aomori 031-0841, Japan

² National Fisheries University, Japan Fisheries Research and Education Agency, 2-7-1 Nagata-honmachi, Shimonoseki, Yamaguchi 759-6595, Japan

³ Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan

⁴ Niigata Field Station, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 1-5939-22, Suido-cho, Niigata-city, Niigata, Japan

* Corresponding author

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

Abstract

Climate change has disrupted natural phenological patterns, including migration. Despite extensive studies of phenological shifts in migration by climate change and driving factors of migration, a few issues remain unresolved. In particular, little is known about the complex effects of driving factors on migration with interactions and nonlinearity, and partitioning of the effects of factors into spatial, temporal, and spatio-temporal effects. The Pacific spiny dogfish *Squalus suckleyi* (hereafter “spiny dogfish”) is a coastal elasmobranchii that migrates southward for parturition and northward for feeding in the western North Pacific. Here, to elucidate the migration patterns as well as the driving factors under climate change, we first examined long-term changes in the timing and geographic location of migration by applying a spatio-temporal model to ca. 5-decade time series data for the presence/absence of spiny dogfish in the western North Pacific. We then evaluated the spatial, temporal, and spatio-temporal effects of driving factors (sea surface temperature [SST], depth, productivity, and magnetic fields) on seasonal occurrence patterns using a machine learning model. We found that the migration area did not change over ca. 5 decades, whereas the migration timing advanced by a month after 2000. The spatial effects of magnetic fields and depth were consistently large and the spatial and spatio-temporal effects of SST increased in the migration season, even though temporal effect of SST was always weak. These results suggest that the migration area of spiny dogfish was stable over time because their spatial distribution was determined by geographic features, whereas the migration timing advanced by tracking a suitable SST location which increased steeply after 2000. Therefore, temperature as well as other factors influence migration simultaneously under climate change and underline the importance of paying attention biotic/abiotic factors including temperature and process-based understanding to predict future impacts of climate change on phenological shifts.

Keywords

barrier model; gradient boosting; global warming; interpretable machine learning; xAI; apex predator; long-term ecological data; catch statistics

1 Introduction

Climate change has substantially affected organisms worldwide (e.g., Walther et al. 2002, Hoegh-Guldberg and Bruno 2010, Walther 2010, Pecl et al. 2017). Changes in phenology (i.e., seasonal timing of life-history events, such as migration and reproduction) are thought to be an indicator of the effect of climate change on organisms since temperature, which has changed under climate change, is a predominant factor affecting phenology. Recent meta-analyses have revealed the magnitude of phenological shifts relative to a historical baseline (e.g., Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006, Parmesan 2007, Poloczanska et al. 2013, Asch 2015) and variability in the magnitude and patterns among taxa, ecological traits, and ecosystems (e.g., Edward and Richardson 2004, Burrows et al. 2011, Poloczanska et al. 2016, Brown et al. 2016). However, studies about phenological shifts often have gaps in terms climate change and ecology. Since species are affected by various, complex external factors with complex interactions and nonlinear effects (e.g., Araújo and Guisan 2006, Guisan et al. 2006, Sala et al. 2000, Sugihara et al. 2012, Ye et al. 2015, Ryo et al. 2018, Nakayama et al. 2020), phenological shifts should be related to complex interactions and nonlinear effects; simple statistical methods such as correlation, linear regression, and similarity may lead to erroneous results.

Migration, which is a phenological event, plays a role in population and ecosystem dynamics as well as in ecosystem services such as tourism (e.g., Gallagher and Hammerschlag 2011, Bauer and Hoyer 2014, Teitelbaum and Mueller 2019).

Recent developed tracking technology has provided insight into the drivers of migration. One major driver of migration is ecological factors such as prey (e.g., Mathot et al. 2007, Sherrill-Mix et al. 2008, Milner-Gulland et al. 2011, La Sorte and Graham 2021) and temperature (e.g., Marra et al. 2005, Sherrill-Mix et al. 2008, Kanamori et al. 2019, Archer et al. 2020). This type of factors leads to migration through changes in physiological conditions such as reproduction; migration itself also affects physiological conditions, thereby regulating the timing and location of migration. Another major driver of migration is wayfinding factors such as magnetic fields (e.g., Wiltschko and Wiltschko 1995, 2005, Diebel et al. 2000, Cain et al. 2005, Aderson et al. 2017, Keller et al. 2021) and olfactory cues (e.g., Koch et al. 1969, Bett and Hinch 2015, Bett et al. 2018, Durif et al. 2021), which regulate the route and accuracy of migration. Despite extensive evidence and predictions that these factors relate to migration, some challenging problems remain unresolved. The first problem involves considering the complex effects of driving factors on migration because species generally has been affected by various factors with interactions (e.g., Araújo and Guisan 2006, Guisan et al. 2006, Sala et al. 2000, Ryo et al. 2018) and nonlinearity effects (e.g., Sugihara et al. 2012, Ye et al. 2015, Nakayama et al. 2020, Satterthwaite et al. 2020). The complex descriptions of the relationship between species and migration-driving factors make it difficult to interpret the results of analyses; therefore, a method for easily interpreting the results is needed. The second problem involves partitioning the effects of factors into spatial, temporal, and spatio-temporal effects. For example, we consider a general case in which we use time-series data of a species within a given spatial range and use a generalized linear

model to analyze the relationship between species occurrence and a factor such as temperature. Because the data include both temporal and spatial information, the interpretation of the effect of the factor on species occurrence (i.e., regression coefficient) is vague. In other words, does the factor affect the variation in species occurrence spatially, temporally, or both? Use of this approach can lead to further understanding of migration, including whether species actively seek out specific conditions or merely react to changes in conditions (Schlaff et al. 2014).

Elasmobranchs (sharks, skates, and rays) are apex predators with long-distance migration in marine systems (Heupel et al. 2015). Their migration is thought to play an important role in marine communities and ecosystems by horizontally and temporally connecting habitats and transferring energy via the trophic cascade (e.g., Dulvy et al. 2000, Heithaus et al. 2008, Polovina et al. 2009, Heithaus et al. 2012, Hummerschlag et al. 2019). Although this migration also underpins their populations through gaining energy, they have been threatened with extinction (Worm et al. 2013, Dulvy et al. 2014) due to overfishing (e.g., Dulvy et al. 2021, Pacoureau et al. 2021) and climate change (e.g., Chin et al. 2010, Niella et al. 2021, Hammerschlag et al. 2022). Hence, it is necessary to elucidate the spatio-temporal changes in their migration patterns and driving factors for the development of effective conservation and management strategies. Many studies have shown that ecological factors, such as temperature and prey as well as other drivers (e.g., salinity, pH, and tide), trigger the migration (e.g., Ackerman et al. 2000, Torres et al. 2006, Carlisle and Starr 2009, Ortega et al. 2009, Ubeda et al. 2009, Niella et al. 2021). In addition, elasmobranchs are known as species who use magnetic field when migration. Indeed, they perceive

69 magnetic fields (e.g., Kalmijin 1982, Meyer et al. 2005, Mora et al. 2014, Anderson et
70 al. 2017, Newton and Kajiura 2020) and a shark showed that the ability to perceive
71 magnetic fields is used for navigation (Keller et al. 2021).

72 The North Pacific spiny dogfish *Squalus suckleyi* (hereafter “spiny dogfish”) is
73 a demersal and coastal shark, which had less attention in the previous studies of
74 migration of sharks. They widely distribute in the North Pacific, from the Bering Sea
75 to the coast of Japan and from the Gulf of Alaska to California (Orlov et al. 2012). In
76 the western North Pacific, they migrate southward from October to December for
77 parturition, after which the adults and their offspring migrate northward around April
78 for feeding (Kojima 1958; Fig. 1). It is possible that they migrate by following
79 changes in water temperature (Kojima 1958, Ebert 2003). Their preferred water
80 temperature is 6°C to 10°C in the western North Pacific (Yano et al. 2017). A
81 previous study suggested that they may be opportunistic feeders with no specific
82 target prey (Mecklenburg et al. 2018), while another study indicated that their
83 distribution may be related to the presence of potential prey, including sardine,
84 walleye pollock, and squid (Yano et al. 2017). They are a commercially important
85 target species in Japan, the United States, and Canada (Orlov et al. 2012). In Japan,
86 they have been caught in the Sea of Japan and in the western North Pacific. Their
87 stock assessment has been conducted by two abundance indices (catch per unit effort)
88 from the bottom trawl fisheries data in the western North Pacific and the bottom
89 longline data in the Tsugaru Strait (Fig. 1).

90 Here, to elucidate the phenological shift in migration and its processes under
91 climate change, we first examined the long-term changes in timing and geographic

location of migration by applying a spatio-temporal model to ca. 5-decade time series data for the presence/absence of spiny dogfish in the western North Pacific. To understand the processes of the change in migration, we then evaluated the spatial, temporal, and spatio-temporal effects of driving factors (productivity, sea surface temperature [SST], and depth, and magnetic fields) on seasonal occurrence of spiny dogfish using a machine learning model and an interpretable machine learning technique.

2 Materials and Methods

2.1 Data sets

2.1.1 Occurrence data for spiny dogfish

Daily catch statistics for bottom trawl fisheries from 1972 to 2019, except for the fishery closures season (July and August), was used. The spatial resolution was $10'$ latitude $\times$ $10'$ longitude horizontal square in the area from 138°E to 142°E and 37°N to 42°N . We defined the area west of 140.5°E as SJ (Sea of Japan) and the area east of 140.5°E as NP (North Pacific) (Fig. 1).

The daily catch statistics included date, geographic location (longitude and latitude), fishing effort (number of tows), catch weight in each fish category including spiny dogfish, and so on. Even though the data had geographic location, the location was not all fishing points in a day but only one location in a day; fishermen recorded the total catch weight in each fish category and geographic location of the most

113 caught fish category every day. Accordingly, there is the possibility that record of
114 catch weight of spiny dogfish was low or high in a point where spiny dogfish inhabits
115 or doesn't inhabit. Therefore, to estimate the monthly distribution in each year, we
116 transformed the catch weight of spiny dogfish into a binary variable
117 (presence/absence) taking a value of 1 when catch weight > 0 and 0 otherwise.

118 Spiny dogfish was assigned to the category elasmobranchs in SJ from 1972 to
119 2019 and in NP from 1972 to 1993; therefore, the catch weight may include the catch
120 weight of other elasmobranchs. However, we have not simultaneously caught both
121 spiny dogfish and other elasmobranchs at the same sites during bottom trawl surveys
122 in SJ for stock assessments (personal observation). Moreover, Yano et al. (2022)
123 showed evidence that data for elasmobranchs in SJ and NP mostly reflect the catch
124 weight of spiny dogfish.

125 **2.1.2 Data collection for candidate driving factors**

126 Data for three ecological factors (productivity, SST, and depth) and one wayfinding
127 factor (magnetic fields) were collected.

128

129 **Productivity.** Productivity was defined as the total catch weight of all fish
130 categories other than spiny dogfish in a month divided by the total efforts in a month
131 using the daily catch statistics. We assumed that as the total catch weight increases,
132 the abundance of prey that spiny dogfish can use increases. The productivity data
133 were aggregated over two spatial resolutions (0.5° latitude and 1.5° latitude) owing to
134 uncertainty regarding how spatial scale affects the occurrence of spiny dogfish.

135

136 **SST.** The mean global daily SST since 1982 with 25' latitude $\times$ 25' longitude
 137 horizontal square resolution in the study area archived as MGDSST by the Japan
 138 Meteorological Agency (<https://ds.data.jma.go.jp/gmd/goos/data/database.html>)
 139 was collected. The monthly mean SST exhibited positive trends, and the trends
 140 increased after 2000 from September to June (Fig. S1).

141 We calculated both the monthly mean SST and monthly coefficient of
 142 variation (CV) in each year and each data point of MGDSST data since climate
 143 change generally increases both the mean and variability of temperatures. Then, both
 144 the mean and CV of SST were given for the nearest predicted points with spiny
 145 dogfish occurrence using a spatio-temporal model (see 2.2.1 for details) because the
 146 points of MGDSST data and the predicted points were distinct. The mean, minimum,
 147 and maximum distances between the points of MGDSST data points and the
 148 predicted points were ca. 5.8 km, 0.9 km, and 11 km, respectively. The mean and CV
 149 of SST before 1981 were not available because MGDSST was recorded from 1982.

150

151 **Depth.** The depth data in the study area were collected from the Japan
 152 Oceanographic Data Center (<https://ds.data.jma.go.jp/gmd/goos/data/database.html>).
 153

154 In the study area, the depth averagely changes with longitude. For the area
 155 within $\pm 5'$ latitude from a predicted point, depth data for less than 1 km were
 156 obtained. After that, mean depth and coefficient of variation (CV) which means
 157 drastic changes in depth around predicted points (i.e., submarine topography) were

158 calculated. Only three predicted points did not have the depth data within 1 km and
159 $\pm 5'$ latitude; for these three predicted points, depth data within 3 km were obtained.

160

161 **Magnetic fields.** Yearly values of three parameters (declination, inclination, and
162 total intensity; these three parameters are a combination showing magnetic fields)
163 were calculated in each predicted point using the gufm1 and IGRF models developed
164 by the National Oceanic and Atmospheric Administration
165 (<https://www.ngdc.noaa.gov/geomag/>).

166 2.2 Data analyses

167 2.2.1 Estimation of spatio-temporal variation in occurrence

168 To estimate spatio-temporal variation in the monthly occurrence of spiny dogfish, we
169 used the barrier model (Bakka et al. 2019) which is a state-of-the-art spatio-temporal
170 model. This model accounts for spatio-temporal changes in fishing location, which
171 likely cause estimation biases (Thorson et al. 2017a). Additionally, this model
172 accounts for spatial autocorrelation in the physical barrier, which is necessary because
173 the study area contained some islands with complex coastline (Bi et al. 2020). The
174 occurrence rate p_i for each sample i was approximated using a logit-linked linear
175 predictor as follows:

$$\text{logit } p_{s_i, t_i} = \beta(t_i) + u(s_i)$$

176 where $\beta(t_i)$ is the effect of time t defined as a year-month combination (i.e., January
177 1972 is $t = 1$, February 1972 is $t = 2$, ..., December 2020 is $t = 480$), which was

178 estimated as a first-order random walk due to the lack of data for the fishery closures
179 season (July and August). $u(s_i)$ is the spatial random effect for location s in Gaussian
180 random field with a Matérn covariance function through stochastic partial differential
181 equations (SPDE). Although the full conditional distribution at the site in
182 two-dimensional space has the expectation using small set of neighbors' under the
183 Matérn model through SPDE, the paths that crossed the physical barrier (e.g., land
184 and coastal line) are eliminated in the barrier model by adding the idea of
185 Simultaneous Autoregressive model into Matérn model through SPDE. Thus, $u(s)$,
186 which is a spatial random effect in the barrier model, is a solution to the following
187 SPDE using the finite element method:

$$u(s) - \nabla \cdot \frac{r^2}{8} \nabla u(s) = r \sqrt{\frac{\pi}{2}} \sigma_u \mathbf{W}(s), \quad \text{for } s \in \Omega_n$$

188

$$u(s) - \nabla \cdot \frac{r_b^2}{8} \nabla u(s) = r_b \sqrt{\frac{\pi}{2}} \sigma_u \mathbf{W}(s), \quad \text{for } s \in \Omega_b$$

189 where $u(s)$, $s \in \Omega \subseteq \mathbb{R}^2$ is the Gaussian random field, r and σ_u are constants,
190 $\nabla = (\frac{\partial}{\partial x}, \frac{\partial}{\partial y})$, and $\mathbf{W}(s)$ denotes spatial white noise. Ω_n is the normal area, Ω_b is
191 land, and their disjoint union gives the whole study area Ω . For further details, see
192 Bakka et al. (2019).

193 As described above, geographic locations included uncertainties because only
194 one geographic location was not recorded in a day for each fishermen (see details for
195 *2.1.1 Occurrence data for spiny dogfish*). If covariates were included in this model,
196 occurrence rates would be estimated based on inaccurate relationships between the

197 occurrence pattern and covariates. Thus, we did not include any covariates in this
198 model.

199 Parameters in the model were estimated by integrated nested Laplace
200 approximation algorithm (Rue et al. 2009) using the R-INLA package (Bakka et al.
201 2018) in R 3.6.3 (R Development Core Team 2021). Then, we predicted the
202 occurrence rates $\hat{p}(s, t)$ in the study areas. Hereafter, we call the points with predicted
203 occurrence rates as “predicted points.” The distances between the predicted points
204 were ca. 10 km.

205 2.2.2 Migration patterns

206 **Geographic location.** To evaluate long-term changes in the geographic location of
207 migration, we used two measurements. First, the mean spatial distribution of spiny
208 dogfish in each month was used to find the average migration patterns over 5 decades
209 because it was difficult to find the patterns from the extensive number of maps of
210 predicted occurrence rates. The unimodality in each predicted point and month was
211 checked by Silverman ’ s test which was conducted using the package *silvermantest* in
212 R. The raw maps using the predicted occurrence rates $\hat{p}(s, t)$ are shown in the
213 Appendix (Figs. S2-7).

214 Second, we used the inter-annual patterns of the center of gravity (COG) in
215 each month using the predicted occurrence rate for each predicted point $\hat{p}(s, t)$. The
216 latitudinal and longitudinal COG at time t , $\text{COG}_{\text{Lat.}}(t)$ and $\text{COG}_{\text{Lon.}}(t)$ were
217 estimated as:

$$\overline{\text{COG}_{\text{Lat.}}(t)} = \frac{\sum_{s=1}^{n_s} \hat{p}(s, t) \times \text{Latitude}(s)}{\sum_{s=1}^{n_s} \hat{p}(s, t)}$$

218

$$\overline{\text{COG}_{\text{Lon.}}(t)} = \frac{\sum_{s=1}^{n_s} \hat{d}(s, t) \times \text{Longitude}(s)}{\sum_{s=1}^{n_s} \hat{d}(s, t)}$$

219 where Latitude(s) and Longitude(s) are the latitude and longitude of location s . We
220 estimated COGs in both SJ and NP because the study area was separated by land
221 and a single COG was not appropriate. The changes in COGs were small in both of
222 SJ and NP, thus the line graphs using the values of COGs are shown (Fig. S8).

223 **Timing.** To examine the long-term changes in the timing of migration of spiny
224 dogfish, the peak of migration in each year was estimated in both JS and NP. We first
225 calculated the monthly mean occurrence rates in both SJ and NP using estimated
226 occurrence rates $\hat{p}(s, t)$ to obtain the migration patterns in each year (Figs. S9). We
227 then defined the mode of the migration patterns as the peak of migration. Here, the
228 “year” was defined as September of year t to June of $t + 1$ because spiny dogfish
229 begins to migrate southward in autumn and data were not available for July and
230 August due to fishery closures season.

231 In some cases, unimodality was not supported by Silverman ’ s test, especially
232 for migration patterns in NP. For example, a histogram of $\hat{p}$ in September 1972 in NP
233 was not unimodal, with high estimated occurrence rates around the Shimokita,
234 indicating that the mean value is not representative for analyses of migration patterns
235 in each year. Therefore, we also obtained the migration patterns in each year using
236 the mode and median for sensitivity analyses (Figs. S10-11). Then, we defined the
237 mode of the migration patterns in each year as the timing of migration (Figs. S12-13),
238 similar to the analysis using mean values. The results for long-term changes in the

239 timing of migration were consistent, although there were slight differences between
240 results obtained using different metrics, particularly between the mean and the mode
241 (Figs. S12-13).

242 **2.2.3 Evaluating the spatial, temporal, and spatio-temporal effects of** 243 **driving factors**

244 To model the relationship between the estimated occurrence rate of spiny dogfish and
245 driving factors, we used the gradient boosting method which is based on machine
246 learning algorithm (e.g., De'ath 2009, Hastie et al. 2009, Maloney et al. 2012,
247 McLaren et al. 2018, Shiferaw et al. 2019). The method sequentially generates large
248 numbers of weak learners and finally combines them. This combination of weak
249 learners can describe nonlinearity between a response variable and covariates as well
250 as complex interactions among covariates.

251 Firstly, we checked correlations among covariances in each month. The
252 variables related to the magnetic fields (declination, inclination, and total intensity)
253 were consistently correlated with each other. Although this presents an issue when
254 interpreting the model, we did not eliminate any magnetic fields variables; instead, we
255 resolved the issue by the interpretation method described in the last paragraph in this
256 section. Strong correlations among other driving factors were not detected. Then,
257 after data for each month were divided into training data (70%) and test data (30%),
258 we tuned seven hyperparameters (nrounds, max_depth, eta, gamma, colsample_bytree,
259 min_child_weight, and subsample) and trained the models by ten-fold cross-validation
260 using the training data. This tuning was conducted using the packages *caret* (Kuhn

261 2008, Kuhn 2020) in R. The hyperparameters were obtained by five grid searches and
 262 the optimal models (i.e., high performance models) were chosen based on the root
 263 mean squared error (RMSE). All of the driving factors were scaled and standardized.
 264 This analysis was conducted with both high-resolution and low-resolution
 265 productivity data. We determined the best model based on the RMSE when using the
 266 test data. The model using the productivity with low-resolution was selected as the
 267 best model in all months; accordingly, the results using productivity with
 268 low-resolution are presented.

269 To demonstrate that the gradient boosting model had a higher predictive value
 270 than that of a linear model, we also analyzed the relationship between the estimated
 271 occurrence rate and driving factors for each month using the training data by a linear
 272 model which included the terms of all driving factors, pairwise second-order
 273 interactions, squared mean SST and mean depth. We then compared between RMSE
 274 of gradient boosting and the linear model when using the test data.

275 To evaluate the spatial, temporal, and spatio-temporal effects of driving
 276 factors on migration, we used grouped permutation feature importance (GPFI). GPFI
 277 measures the change in prediction errors between the best model and when permuting
 278 a “single set of covariates.” A greater increase in the prediction error is interpreted as
 279 more important covariate for the prediction (Molnar 2020). The original idea of this
 280 method is to calculate the importances of each covariate by permuting correlated
 281 covariates as a single set since like a linear model, the calculated importance when
 282 permuting a single covariate which correlated other covariances is unstable and
 283 difficult to interpret. We applied this method and calculated the RMSE as the

prediction error when permuting within spatial, temporal, spatio-temporal for each covariate. We then calculated the L_2 norm between the RMSE from the best model and the RMSE from the permutations to evaluate the spatial, temporal, and spatio-temporal effects of driving factors. For example, we consider data for 10 sites and 10 years for a species and a factor (e.g., temperature). The L_2 norm between the RMSE from permuting a factor in a fixed site (e.g., site 1) and the RMSE from the best model indicates the importance of the temporal effect of the covariate because the factor data are permuted among years. This permutation was conducted 100 times in each month, and covariates related to magnetic fields (declination, inclination, and total intensity) were treated as a single set due to the observed correlations. We can grasp the macroscopic patterns from figures that summarize the results for all months (Figs. S14-18).

296

3 Results

3.1 Long-term changes in migration patterns

The spatial distribution of spiny dogfish clearly changed seasonally (Figs. 2 and S2-7). Although the mean occurrence rates were low in the whole study area from September to December, spiny dogfish occurred on the north side of the Shimokita Peninsula. In January and February, the mean occurrence rates increased significantly around the Shimokita Peninsula and increased on the north side of SJ and along the coastline of NP. From March to May, the mean occurrence rates in SJ and NP decreased

gradually, although the occurrence rates on the north side of the Shimokita Peninsula remained slightly elevated. In June, the mean occurrence rates were somewhat high only on the north side of the Shimokita Peninsula.

COG did not change in any month during the ca. 5-decade period (Fig. 3). The longitudes of COG in SJ and PO did not change in any month. There were greater fluctuations in latitudes of COG in SJ and NP than in longitudes (Fig. S8). Although the latitude tended to decrease from 1972 to around 2015, the magnitude of change was quite small.

The timing of migration advanced in both SJ and NP (Fig. 4). Before 2000, migration was observed mainly in February, compared with January after 2000. Consistent results were obtained when using the mode and median of estimated occurrence rates (Figs. S12-13).

3.2 Spatial, temporal, and spatio-temporal effects of driving factors on migration

All gradient boosting models had always higher predictability comparing with the linear models, although the linear models were slightly complex due to including interactions among variables and square terms for nonlinearity (Tables S1-2).

The effects of driving factors, particularly SST and productivity, changed seasonally (Fig. 5). The spatial effects of magnetic fields and depth and the spatio-temporal effect of magnetic fields were always large (shown in a pink boxplots). Following those factors, the spatial, temporal, and spatio-temporal effects of productivity, the spatial effects of CV of depth, and the spatial and spatio-temporal

effects of SST also tended to be large (the yellow box plots). The spatial and spatio-temporal effects of SST tended to increase in February and then decrease in April, whereas the effects of productivity tended to decrease in February and then increase in April.

The factors with weak effects were consistent across months (Fig. 5). The temporal effect of magnetic fields was always weak, although the spatial and spatio-temporal effects of these factors were always large. Similarly, the temporal effect of SST was always weak, although the spatial and spatio-temporal effects of SST changed seasonally. Effects of the CV of SST were consistently weak.

4 Discussion

The migration timing of spiny dogfish advanced by a month after 2000 (Fig. 4), whereas the geographic locations of migration have not changed over 5 decades (Figs. 2-3). Seasonal changes in driving factors involved changes mainly in the importance of SST; spatial and spatio-temporal effects of SST tended to increase in February (when spiny dogfish migrate southward) and decrease in April (when the species migrates northward), although temporal effects of SST were always weak (Fig. 5). These results provide two key insights. (i) The advanced timing of migration in spiny dogfish is likely related to SST. (ii) Migration is not directly driven by SST (i.e., it is not merely a reaction to changes in specific conditions) but reflects tracking of areas with the preferred SST (i.e., actively seeking specific conditions), as evidenced by the weak

temporal effect of SST and elevated spatial and spatio-temporal effects of SST during southward migration. In the study area, the mean SST increased, particularly after 2000 (Fig. S1). Therefore, our results imply that spiny dogfish actively seek preferential SST during the peak period of migration for parturition; increases in SST associated with global warming have resulted in a shift to earlier migration in the species.

Marine species are more sensitive to climate change compared with species on land (e.g., Sunday et al. 2012, Pinsky et al. 2019), and disruptions in their natural phenology and distribution have been reported (e.g., Parmesan and Yohe 2003, Edward and Richardson 2004, Perry et al. 2005, Pinsky et al. 2013, Poloczanska et al. 2013, Asch 2015, Brown et al. 2016, Kanamori et al. 2019). Distributional shifts are thought to occur by tracking climate velocity (the rate and direction of the isotherms shifts through space) (e.g., Burrows et al. 2011, Pinsky et al. 2013, Sunday et al. 2015) whereas phenological shifts, which are relatively less reports than distributional shifts in marine systems, are thought to occur by earlier warming (e.g., Edward and Richardson 2004, Asch 2015). Despite warming in the present study area, a distributional shift and an effect of temporal changes in SST were not detected. Alternatively, our results indicated that spiny dogfish seek their suitable SST location where SST has increased, especially after 2000, resulting in advancing their migration timing. These findings provide new evidence that phenological and distributional shifts have occurred by the combination of the way that previous studies assumed, suggesting the necessity to simultaneously evaluate phenological and distributional shifts and to understand processes of those shifts for inferences in the future.

371 The spatial effects of magnetic fields, depth, and CV of depth (i.e., submarine
372 topography) and spatio-temporal effect of magnetic fields were always large (Fig. 5).
373 Accordingly, spiny dogfish had a strong preference for geographic features and
374 therefore the migration area remained stable over 5 decades (Figs. 2-3). However, we
375 need to have a concern for the effects of productivity (especially spatio-temporal effect
376 of productivity), which showed consistently large effects following the effects of
377 magnetic fields, depth, and submarine topography. This is because that the
378 productivity in marine systems is influenced by various factors, such as climate change
379 (e.g., Barange et al. 2014, Free et al. 2019) and overfishing (e.g., Link and Watson
380 2019), leading to that changes in productivity will alter the migration of spiny dogfish.

381 **Utility of the spatio-temporal model and machine learning**

382 Machine learning methods have various advantages that the models can include
383 nonlinearity and complex interactions among covariates as well as high predictability.
384 In contrast, the models require large datasets which are often difficult to obtain in
385 ecology and conservation fields. We overcame this disadvantage by predicting
386 occurrence rates in many locations using a spatio-temporal model. Our approach not
387 only increased the data used for machine learning models but also removed noise
388 associated with data collection. Spatio-temporal models are a well-known method for
389 standardization, that is, removing various kinds of noise (e.g., spatio-temporal
390 changes in survey points and survey effort), effects of target fishing, environmental
391 factors, and species misidentification (e.g., Thorson and Barnett 2017, Thorson et al.
392 2017a,b, Thorson 2019, Kanamori et al. 2019, 2021). Thus, the combination of

393 spatio-temporal models and machine learning algorithms can contribute to research
394 on the relationships between species and external factors.

395 Understanding the spatio-temporal patterns of species occurrence and its
396 process is a major goal in ecology and conservation (Piel et al. 2017). Machine
397 learning methods have used to inference species distribution and relating
398 environmental factors because of their high predictability (e.g., Hastie et al. 2009,
399 Maloney et al. 2012, McLaren et al. 2018, Ryo et al. 2018, Shiferaw et al. 2019), and
400 the interpretable methods of machine learning have developed as well (e.g., Molnar
401 2020, Ryo et al. 2020). However, although interpretable methods can provide the
402 importance of factors for species distribution, it was difficult to more deeply
403 understand how those factors affect species distribution because the data frequently
404 include spatial and temporal aspects and we did not know how those factors are
405 important (i.e., do those factors affect the spatial, temporal, or spatio-temporal
406 patterns of species distribution?). In this study, we challenged to evaluate the spatial,
407 temporal, and spatio-temporal effects of driving factors on migration by an
408 interpretable machine learning method, resulting in we inferred the process driving
409 long-term change in seasonal migration of spiny dogfish; migration area tends not to
410 change by the spatial effects of geographic features (magnetic fields and depth) but
411 migration timing has advances by seeking their suitable SST location (i.e., spatial
412 effect) where SST has increased. This partitioning method provided more simple
413 interpretation than coefficients of linear model with many interactions (e.g., our linear
414 model for comparing with gradient boosting) but more detailed information than
415 importance of previous interpretable methods. Therefore, this partitioning method

can help to infer the process underlying the spatio-temporal variations of species.

Future directions

Although phenological shifts associated with global warming have been reported in marine organisms (e.g., Edward and Recharson 2004, Asch 2015, Kanamori et al. 2019), little is known about phenological shifts of apex predators (c.f., bluefin tunas Dufour et al. 2010, tiger shark Hammerschlag et al. 2022). Previous studies have revealed the disruption of communities and ecosystems after decreases in the abundance of sharks (e.g., Dulvy et al. 2000, Heithaus et al. 2008, Polovina et al. 2009, Heithaus et al. 2012, Hammerschlag et al. 2019). In addition, the migration of apex predators contributes to marine ecosystems by horizontally and temporally connecting habitats and trophic levels (e.g., Dulvy et al. 2000, Heithaus et al. 2008, Polovina et al. 2009, Heithaus et al. 2012, Hammerschlag et al. 2019). Thus, studies of the effects of phenological shifts of apex predators on communities and ecosystems under climate change are required.

Information about population ranges and movement patterns between populations is necessary for management (Frisk et al. 2014, Crossin et al. 2017). We found areas of high species occurrence not only in NP but also in SJ, and these were connected through the Tsugaru Straits (Figs. 2 and S2-7). These results suggest that spiny dogfish can be considered a single population. Stock assessments of spiny dogfish in Japan have been conducted separately in a part of NP and in the Tsugaru Straits (Fig. 1); therefore, individuals in SJ have not been included. Thus, it is necessary to determine how the spatial range influences current stock assessment

438 results, including comparisons of results obtained when treating the species as a single
439 population around Japan, which should improve the stock assessment and
440 management of spiny dogfish.

441 The occurrence rate of spiny dogfish increased everywhere within the study
442 area from January to February, and then decreased gradually in the whole the study
443 area even though the occurrences rate of spiny dogfish were moderately high levels on
444 the north side of the Shimokita Peninsula (Figs. 2 and S2-7). These results suggest
445 that some individuals use this area seasonally and others stay in the area year-round.
446 In sharks, movements and habitats generally differ between sexes and life stages;
447 females migrate from adult habitats, including migration from the mating site to
448 parturition site, and juveniles stay in the juvenile habitat (Chapman et al. 2015). In
449 spiny dogfish, they are thought to migrate southward for parturition (Kojima 1958)
450 and to migrate northward for feeding (Yusa and Ishida 1956), although Ukawa (1955)
451 hypothesized that small individuals stay throughout the year. Yano et al. (2017)
452 recently showed that male individuals tended to be caught more frequently than
453 female individuals on the north side of Shimokita Peninsula from 2007 to 2011, and
454 male individuals were identified as mature based on the length-maturity relationship
455 (Yamamoto and Kibesaki 1950). Therefore, individuals who migrate seasonally and
456 use this area year-round may be mainly females and residents may be males. Given
457 that sharks have long generation times and a low intrinsic population rate due to slow
458 growth, late maturation, and low young production, population recovery after
459 depletion is difficult (Dulvy et al. 2017, Pacoureau et al. 2021). In addition, sharks
460 are thought to return their natal site, because there are observations that they often

collapse by fishing at local geographic scales and it is difficult to recover population quickly by immigration (Chapman et al. 2015). Indeed, we found that strong preference for geographic features. Thus, both collecting individual-level data (e.g., sex, body size, and maturity) and developing management strategies, such as not only how much we can catch in a year but also when and where we can fish in a year, are necessary for sustainable fishing of spiny dogfish.

Conclusion

This study revealed that the geographic location of migration of spiny dogfish has not changed over ca. 5 decades, whereas the timing of migration has advanced by a month after 2000 in the western North Pacific. The spatial and spatio-temporal effects of magnetic fields and depth were consistently large and the spatial and spatio-temporal effects of SST increased in the timing of migration, even though temporal effect of SST was consistently low. These results reveal that the migration area of spiny dogfish has been stable because it is determined by geographic features, whereas the migration timing has advanced. This advancing of migration timing was not a direct response to temporal changes in SST but a consequence of tracking a suitable SST location where SST increased steeply after 2000. Therefore, not only temperature but also other many factors influence migration simultaneously under climate change, underlining the importance of paying attention biotic/abiotic factors including temperature and process-based understanding to predict future impacts of climate change on phenological shifts.

483

484 **Acknowledgments**

485 We appreciate Ms. Akane Yoshikawa, Fisheries Resources Institute, Japan Fisheries
486 Research and Education Agency for organizing the fisheries statistics in the Sea of
487 Japan. This research was financially supported by Japanese Ministry of Agriculture,
488 Forestry and Fisheries, and Japan Sea National Fisheries Institute.

489

490 **Authorship**

491 YK conceived of the research idea. TY and YY organized the catch statistics. YK
492 and HO designed statistical analyses, and YK wrote programs and performed the
493 analyses. YK also wrote the manuscript with input from all co-authors' comments.

494

495 **Conflict of interest**

496 The authors declare there is no conflict of interest.

497

498

499

500 **Literature cited**

501 Ackerman JT, Kondratieff MC, Matern SA, Cech JJJ (2000) Tidal influence on
502 spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay,
503 California. *Environ Biol Fishes* 58:33-43

Anderson JM, Clegg TM, Vras LVMVQ, Holland KN (2017) Insight into shark
magnetic field perception from empirical observations. *Sci Rep* 7:11042

Arajo MB, Anderson RP, Barbosa AM, Beale CM, Dormann CF et al. (2019)
Standards for distribution models in biodiversity assessments. *Sci Adv* 5:
eaat4858

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in
the California Current eco- system. *Proc Natl Acad Sci USA* 112:E4065-E4074

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in
the California Current eco- system. *Proc Natl Acad Sci USA* 112:E4065 – E4074

Bakka H, Vanhatalo J, Illian JB, Simpson D, Rue H (2019) Non-stationary Gaussian
models with physical barriers. *Spatial Statistics* 29:268-288

Bakka H, Rue H, Fuglstad G-A, Riebler A, Bolin D et al. (2018) Spatial modelling
with R-INLA: A review. *Computational Statistics* 10:e1443

Barange M, Coetzee JC, Twatwa NM (2005) Strategies of space occupation by
anchovy and sardine in the southern Benfuela: the role of stock size and
intra-species competition. *ICES J Mar Sci* 62:645-654

Bauer S, Hoyer J (2014) Migratory animals couple biodiversity and ecosystem
functioning worldwide. *Science* 344:1242552

Bett NN, Hinch SG, Kaukinen KH, Li S, Miller KM (2018) Olfactory gene expression
in migrating adult sockeye salmon *Oncorhynchus nerka*. *J Fish Biol*
92:2029-2038

Bett NN, Hinch SG (2015) Olfactory navigation during spawning migrations: a review
and introduction of the Hierarchical Navigation Hypothesis. *Biol Rev* 91:728-759

527 Bi R, Jiao Y, Bakka H, Browder JA (2020) Long-term climate ocean oscillations
528 inform seabird by catch from pelagic logline fishery. ICES J Mar Sci 77:668-679

529 Cain SD, Boles LC, Wang JH, Lohmann KJ (2005) Magnetic orientation and
530 navigation in marine turtles, lobsters, and molluscs: concepts and conundrums.
531 Integr Comp Biol 45:539-546

532 Carlisle AB, Starr RM (2009) Habitat use, residency, and sea- sonal distribution of
533 female leopard sharks *Triakis semi- fasciata* in Elkhorn Slough, California. Mar
534 Ecol Prog Ser 380:213-228

535 Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for
536 climate change: analysing the vulnerability of sharks and rays on
537 Australia's Great Barrier Reef. Glob Change Biol 16:1936-1953

538 Crossin GT, Cooke SJ, Goldbogen JA, Phillips RA (2014) Tracking fitness in marine
539 vertebrates: current knowledge and opportunities for future research. Mar Ecol
540 Prog Ser 496:1-17

541 Diebel CE, Proksch R, Green CR, Neilson P, Walker MM (2000) Magnetite defines a
542 vertebrate magnetoreceptor. Nature 406: 299-302

543 Dulvy et al. 2021 current biol

544 Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM et al. (2014) Extinction
545 risk and conservation of the world ' s sharks and rays. eLife 3:e00590

546 Dulvy NK, Metcalfe JD, Glanville J, Pawson MG, Reynolds JD (2000) Fishery
547 stability, local extinctions, and shifts in community structure in skates. Conserv
548 Biol 14:283-293

549 Durif CM, Stockhausen HH, Skiftesvik AB, Cresci A, Nyqvist D, Browman HI (2021)

550 A unifying hypothesis for the spawning migrations of temperate anguillid eels.
551 Fish Fish 0:1-18

552 Ebert DA (2003) Sharks, rays and chimaeras of California. California Natural History
553 Guides No. 71. University of California Press. 284p

554 Edwards M, Richardson A (2004) Impacts of climate change on marine pelagic
555 phenology and trophic mismatch. Nature 430:881-884

556 Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019)
557 Impacts of historical warming on marine fisheries production. Science
558 363:979-983

559 Frisk MG, Jordaan A, Miller TJ (2014) Moving beyond the current paradigm in
560 marine population connectivity: Are adults the missing link? Fish Fish
561 15:242-54

562 Gallagher AJ, Hammerschlag N (2011) Global shark currency: the distribution,
563 frequency, and economic value of shark ecotourism. Curr Issues Tour 14:797-812

564 Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC et al. (2006) Making better
565 biogeographical predictions of species ' distributions. J Appl Ecol 43:386-392

566 Hammerschlag N, McDonnell LH, Rider MJ, Street GM, Hazen EL et al. (2022)
567 Ocean warming alters the distributional range, migratory timing, and spatial
568 protections of an apex predator, the tiger shark (*Galeocerdo cuvier*). Glob
569 Change Biol 00:1-16

570 Hammerschlag N, Schmitz OJ, Flecker AS, Lafferty KD, Sih A et al. (2019)
571 Ecosystem function and services of aquatic predators in the Anthropocene.
572 Trends Ecol Evol 34:369-383

573 Hastie T, Tibshirani R, Friedman J (2009) The Elements of Statistical Learning:
574 Data Mining, Inference, and Prediction, 2nd edn. Springer, New York

575 Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact
576 top-predator populations: a synthesis of 15 years of research in a seagrass
577 ecosystem. *Mar Freshw Res* 63:1039-1050

578 Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences
579 of marine top predator declines. *Trends Ecol Evol* 23:202-210

580 Heupel M, Simpfendorfer C, Espinoza M, Smoothey A, Tobin A, Peddemors V (2015)
581 Conservation challenges of sharks with continental scale migrations. *Front Mar*
582 *Sci* 2:1-7

583 Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's
584 marine ecosystems. *Science* 328:1523-1528

585 Kalmijn AJ (1982) Electric and magnetic field detection in elasmobranch fishes.
586 *Science* 218:916-918

587 Kanamori Y, Nishijima S, Okamura H, Yukimi R, Watai M, Takasuka A (2021)
588 Spatio-temporal model reduces species misidentification bias of spawning eggs in
589 stock assessment of spotted mackerel in the western North Pacific. *Fish Res*
590 236:105825

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

594 Keller BA, Putman NF, Grubbs RD, Portnoy DS, Murphy TP (2021) Map-like use of
595 Earth's magnetic field in sharks. *Current Biol* 31:1-6

596 Koch AL, Carr A, Ehrenfeld DW (1969) The problem of open sea navigation: the
597 migration of the green turtle to Ascension Island. *J Theor Biol* 22:163-179

598 Kojima I (1958) North Pacific spiny dog fish. *Tsushima Danryu Kaihatsu Chosa*
599 *Hokokusho* 4:34-44 (In Japanese)

600 Kuhn M (2020) caret: Classification and Regression Training.
601 <https://CRAN.R-project.org/package=caret>

602 Kuhn M (2008) Building predictive models in R using the caret package. *J Statistical*
603 *Software* 28:1-26

604 La Sorte FA, Graham CH (2021) Phenological synchronization of seasonal bird
605 migration with vegetation greenness across dietary builds. *J Anim Ecol*
606 90:343-355

607 Link JS, Watson RA (2019) Global ecosystem overfishing: Clear delineation within
608 real limits to production.

609 Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on
610 the timing and rate of spring bird migration. *Oecologia* 142:307-315

611 Mathot KJ, Smith BD, Elner RW (2007) Latitudinal clines in food distribution
612 correlate with differential migration in the western sandpiper. *Ecology*
613 88:781-791

614 McLarenJD, Buler JJ, Schreckengost T, Smolinsky JA, Boone M et al. (2018)
615 Artificial light at night confounds broad-scale habitat use by migrating birds.
616 *Ecol Lett* 21:356-364

617 Mecklenburg CW, Lynghammar A, Johannesen E, Byrkjedal I, Christiansen JS et al.
618 (2018) Marine fishes of the Arctic Region. Volume I. Conservation of Arctic

619 Flora and Fauna, Akureyri, Iceland 28:1-454

620 Meyer CG, Holland KN, Papastamatiou YP (2005) Sharks can detect changes in the
621 geomagnetic field. J R Soc Interface 2:129-130

622 Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) Animal Migration: A Synthesis.
623 Oxford University Press, Oxford

624 Molnar C (2020) Interpretable machine learning: A guide for making black box models
625 explainable. Lulu. com. <https://christophm.github.io/interpretable-ml-book/>

626 Nakayama SI, Fukuda H, Nakatsuka S (2020) Model-free time series analysis detected
627 the contributions of middle-age spawner biomass and the environment on Pacific
628 bluefin tuna recruitment. ICES J Mar Sci 77:1480-1491

629 Newton KC, Kajiura SM (2020) The yellow stingray (*Urobatis jamaicensis*) can use
630 magnetic field polarity to orient in space and solve a maze. Mar Biol 167:36

631 Niella Y, Butcher P, Holmes B, Barnett A, Harcourt R (2021) Forecasting
632 intraspecific changes in distribution of a wide-ranging marine predator under
633 climate change. Oecologia 1-14

634 Orlov AM, Savinykh VF, Kulish EF, Pelenev DV (2012) New data on the distribution
635 and size composition of the North Pacific spiny dogfish *Squalus Suckleyi*
636 (Girard, 1854). Scientia Marina 76:111-122

637 Ortega LA, Heupel MR, Van Beynen P, Motta PJ (2009) Movement patterns and
638 water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a
639 Florida estuary. Environ Biol Fishes 84:361-373

640 Pacoureau N, Rigby CL, Kyne PM, Sherley RB, Winker H et al. (2021) Half a
641 century of global decline in oceanic sharks and rays. Nature 589:567-571

642 Pecl GT, Araújo BA, Bell JD, Blanchard J, Bonebrake TC et al. (2017) Biodiversity
643 redistribution under climate change: Impacts on ecosystems and human
644 well-being. *Science* 355:1389

645 Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species
646 ranges: Scaling from organisms to communities. *Ann Rev Mar Science*
647 12:153-179

648 Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track
649 local climate velocities. *Science* 341:1239-1242

650 Pinsky ML, Fogarty M (2012) Lagged social-ecological responses to climate and range
651 shifts in fisheries. *Climate Change* 115:883-891

652 Polovina JJ, Abecassis M, Howell EA, Woodworth P (2009) Increases in the relative
653 abundance of mid-trophic level fishes concurrent with declines in apex predators
654 in the subtropical North Pacific, 1996-2006. *Fish Bull* 107:523-531

655 R Development Core Team (2020) R: a language and environment for statistical
656 computing. R Foundation for Statistical Computing, Vienna

657 Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent
658 Gaussian models by using integrated nested Laplace approximations. *J R*
659 *Statist Soc B* 71:319-392

660 Ryo M, Angelov B, Mommola S, Kass JM, Benito BM, Hartig F (2020) Explainable
661 artificial intelligence enhances the ecological interpretability of black-box species
662 distribution models. *Ecography* 44:199-205

663 Ryo M, Harvey E, Robinson CT, Altermatt F (2018) Nonlinear higher order abiotic
664 interactions explain riverine biodiversity. *J Biogeogr* 45:628-639

665 Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J et al. (2000) Global
666 biodiversity scenarios for the year 2100. *Science* 287:1770-1774

667 Satterthwaite WH, Andrews KS, Burke BJ, Gosselin JL, Greene CM et al. (2020)
668 Ecological thresholds in forecast performance for key United States West Coast
669 Chinook salmon stocks. *ICES J Mar Sci* 77:1503-1515

670 Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors
671 on shark and ray movement, behaviour and habitat use: a review. *Rev Fish*
672 *Biol Fisheries* 24:1089-1103

673 Sherrill-Mix SA, James MC, Myers RA (2008) Migration cues and timing in
674 leatherback sea turtles. *Behav Ecol* 19:231-236

675 Shiferaw H, Bewket W, Eckert S (2019) Performances of machine learning algorithms
676 for mapping fractional cover of an invasive plant species in a dryland ecosystem.
677 *Ecol Evol* 9:2562-2574

678 Sugihara G, May R, Ye H, Hsieh C, Deyle E, Fogarty M, Munch S (2012) Detecting
679 causality in complex ecosystems. *Science* 338:496-500

680 Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill N, et al. (2015) Species traits and
681 climate velocity explain geographic range shifts in an ocean-warming hotspot.
682 *Ecol Lett* 18:944-953

683 Teitelbaum CS, Mueller T (2019) Beyond migration: Causes and consequences of
684 nomadic animal movements. *TREE* 34:569-581

685 Thackeray SJ, Jones ID, Maberly SC (2008) Long-term change in the phenology of
686 spring phytoplankton: species-specific responses to nutrient enrichment and cli-
687 mate change. *J Ecol* 96:523 – 535

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

691 Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and
692 distribution shifts using single- and multispecies models of fishes and biogenic
693 habitat. *ICES J Mar Sci* 74:1311-1321

694 Thorson JT, Fonner R, Haltuch MA, Ono K, Winker H (2017a) Accounting for
695 spatio- temporal variation and fisher targeting when estimating abundance from
696 multi- species fishery data. *Can J Fish Aquat Sci* 74:1794-1807

697 Thorson JT, Ianelli JN, Kotwicki S (2017b) The relative influence of temperature and
698 size-structure on fish distribution shifts: a case-study on walleye pollock in the
699 Bering Sea. *Fish Fish* 18:1073-1084

700 Thorson JT, Fonner R, Haltuch MA, Ono K, Winker H (2016) Accounting for
701 spatio-temporal variation and fisher targeting when estimating abundance from
702 multispecies fishery data. *Canadian J Fish Aquat Scien* 74:1794-1807

703 Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the
704 distribution and abundance of sharks in Florida Bay, USA. *Hydrobiologia*
705 569:449-455

706 Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads,
707 *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. *Environ*
708 *Biol Fishes* 84:293-303

709 Walther GR (2010) Community and ecosystem responses to recent climate change.
710 *Proc R Soc B* 365:2019-2024

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. *Nature* 416:389-395

Wiltschko W, Wiltschko R (2005) Magnetic orientation and magnetoreception in birds and other animals. *J Comp Physiol A* 191:675-693

Wiltschko R, Wiltschko W (1995) Magnetic orientation in animals. Berlin, Germany: Springer

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman DD, et al. (2013) Global catches, exploitation rates, and rebuilding options for sharks. *Mar Policy* 40:194-204

Yamamoto T, Kibesaki O (1950) Studies on the spiny dog fish *Squalus suckleyi*. (I) on the development and maturity of the genital glands with growth. *Nippon Suisan Gakkaishi* 15:531-538 (in Japanese with English abstract)

Yano T, Hattori T, Shibata Y, Tanaka S (2022) Over 120 years of landing trends in Japan, for the commercially exploited shark species, *Squalus suckleyi*. *Fish Res* 249:106257

Yano T, Ohshimo S, Kanaiwa M, Hattori T, Fukuwaka M et al. (2017a) Spatial distribution analysis of the North Pacific spiny dogfish, *Squalus suckleyi*, in the North Pacific using generalized additive models. *Fish Oceanogr* 26:668-679

Yano T, Hattori T, Tamukai T, Ohshimo S (2017b) Body-length frequency and spatial segregation of the North Pacific spiny dogfish *Squalus suckleyi* in Tsugaru Strait, northern Japan. *Fish Sci* 83:917-928

Ye H, Beamish RJ, Glaser SM, Grant SCH, Hsieh CH et al. (2015) Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling.

734

E1569-E1576

Captions

Fig. 1 Study area. North Pacific spiny dogfish *Squalus suckleyi* starts migrating southward from October to December for parturition and then migrates northward around April. In this study, the Sea of Japan (SJ) and the North Pacific (NP) were defined as the areas west and east of 140.5°E, respectively. Stock assessment in Japan has been conducted using bottom longline data from the Tsugaru Strait and bottom trawl data within the dashed area

Fig. 2 Mean spatial distribution of spiny dogfish from September to June, as estimated using the model

Fig. 3 Long-term changes in the center of gravity (COG) from September to June

Fig. 4 Long-term changes in the timing of migration of spiny dogfish in the Sea of Japan (SJ) and in the western North Pacific (NP). Here, each year started from September to June because spiny dogfish start to migrate in autumn

Fig. 5 Spatial, temporal, and spatio-temporal effects of driving factors from September to June estimated from GPFI. Boxplots show the medians and the 25% and 75% quantiles. Whiskers indicate the data points within $\times 1.5$ of the quartiles and gray circles represent outliers. Large L_2 norm indicates more important factors for predicting the estimated occurrence rates of spiny dogfish. Letters after the slash (/) on the y-axis indicate spatial (s), temporal (t), and spatio-temporal (st) effects. *Dep*, *Mag*, *Prod*, and *SST* are depth, magnetic fields, productivity, and monthly mean SST, respectively. *Dep_cv* and *SST_cv*

756 are the coefficient of variation of depth around the estimated points (i.e.,
757 submarine topography) and monthly coefficient of variation of SST (i.e.,
758 monthly variability of SST), respectively. A detailed description of parameters
759 is provided in *2.1.2 Data collection for candidate driving factors*

Fig. 1:

Fig. 2:

Fig. 3:

Fig. 4:

Fig. 5: