1 **Title:**

2 Intra- and inter-specific density dependence of body condition, growth, and habitat
3 temperature in chub mackerel (*Scomber japonicus*)

4

5 **Authors:**

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7

8 **Abstract**

9 The density dependence of growth and body condition have important impacts on fish
10 population dynamics and fisheries management. Although population density is known
11 to affect the temperature of the habitat selected, how this affects the density dependence
12 of growth and body condition remains unclear. Here, we investigated annual changes in
13 body condition, habitat temperature, and cohort-specific growth of chub mackerel
14 (*Scomber japonicus*) in the western North Pacific and examined quarterly changes in the
15 density dependence of body condition. We hypothesized that chub mackerel body
16 condition is affected both directly (e.g., through competition for food) and indirectly
17 (through changes in habitat temperature) by the abundance of both conspecifics (i.e.,
18 chub mackerel) and heterospecifics (the Japanese sardine *Sardinops melanostictus*).
19 Indeed, chub mackerel body condition, habitat temperature, and growth all decreased
20 with increasing conspecific and heterospecific abundance. Mean annual growth rates in
21 chub mackerel were positively correlated with body condition. The best model showed
22 that conspecific and/or heterospecific abundance had strong negative effects on chub
23 mackerel body condition in all seasons, and influenced habitat temperature in some

24 seasons. By contrast, temperature effects on body condition were weak. Therefore,
25 direct effects likely have more impact than indirect effects on density-dependent body
26 condition and growth.

27

28 **Keywords:** population density, condition factor, growth, temperature, chub mackerel,
29 Japanese sardine

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41 **Introduction**

42 Density-dependent processes are fundamental to fish population dynamics (Rose *et al.*,
 43 2001; Andersen *et al.*, 2017). Growth, survival, movement, and reproduction are all
 44 affected by population density, and can contribute to a decrease or increase in
 45 population growth rate at high or low densities (Rose *et al.*, 2001). In general,
 46 density-dependent mortality is a dominant factor in fish population dynamics in the
 47 early juvenile stage, and density-dependent growth becomes dominant in the late
 48 juvenile and adult stages (Lorenzen and Enberg, 2002; Lorenzen, 2008; Van Gemert and
 49 Andersen, 2018; Zimmermann *et al.*, 2018). Although the density dependence of
 50 recruitment is a stronger regulator of fish population size, the density dependence of
 51 growth affects productivity and catch composition and may be particularly important for
 52 fisheries management (Zimmermann *et al.*, 2018). In addition, rapid changes in fish
 53 population density and the subsequent drastic changes in growth and maturation often
 54 complicate stock assessment and fisheries forecasting (Eero *et al.*, 2015). There is an
 55 urgent need to understand the density dependence of growth to inform effective
 56 management decisions.

57 As with growth, body condition is often used as a proxy of individual fitness, as it
 58 reflects the size of individual energy reserves. Many studies have sought to identify
 59 determinants of body condition, such as conspecific and heterospecific density,
 60 temperature, prey availability, and fishing impacts, as a way to understand fish
 61 population dynamics (Rueda *et al.*, 2015; Brosset *et al.*, 2017). It is widely accepted that
 62 fish body condition can affect growth, reproductive potential, and survival (Blackwell *et*
 63 *al.*, 2000; Lloret *et al.*, 2002) and is an important data point for stock assessment and

64 fisheries management (Blackwell *et al.*, 2000; Dahl *et al.*, 2019).

65 Temperature is one of the most important abiotic factors for fish growth and body
66 condition (Houde, 1989; Rueda *et al.*, 2015). Many studies have considered temperature
67 to be a density-independent factor when examining its effects on growth and body
68 condition (Brunel and Dickey-Collas, 2010; Casini *et al.*, 2011, 2016; Brosset *et al.*,
69 2015; Cormon *et al.*, 2016). However, because the temperature of habitats selected by
70 fish can vary with population density (Swain and Kramer, 1995), population density can
71 indirectly affect growth and body condition through changes in habitat temperature. In
72 addition, this indirect effect can vary with season. Comprehensive analyses of the effect
73 of density-dependent changes in habitat temperature on growth and body condition, and
74 how these effects change over the seasons, are required to properly understand the
75 process of density dependence.

76 Chub mackerel (*Scomber japonicus*) is widely distributed across the North Pacific
77 and is one of the most productive and economically important fisheries resources in the
78 world, with annual catches reaching ca. 1.5 million metric tons (FAO, 2020). However,
79 the abundance of the Pacific stock of chub mackerel declined in the 1990s and early
80 2000s (Yukami *et al.*, 2020a). Since 2013, when a strong year class occurred, its
81 abundance has dramatically increased (Table 1). Although previous studies reported
82 changes in factors such as growth and maturity during the period of population decline
83 (Watanabe and Yatsu, 2004, 2006), limited information is available for the period of
84 population increase, especially for recent years. In addition, although much attention has
85 been paid to the impact of environmental and endogenous factors (e.g., temperature,
86 food availability, and age/size) on chub mackerel growth in the larval and early juvenile

87 stages (Hunter and Kimbrell, 1980; Sassa and Tsukamoto, 2010; Kamimura *et al.*, 2015;
88 Higuchi *et al.*, 2019; Kaneko *et al.*, 2019; Taga *et al.*, 2019; Nakamura *et al.*, 2020),
89 comparatively little research has been conducted on later growth stages (Parrish and
90 Mallicoate, 1995; Watanabe and Yatsu, 2004; Yatsu *et al.*, 2019).

91 Chub mackerel mainly spawns in the waters around the Izu islands and the Boso
92 peninsula, Japan (Figure 1a) from March to June (Watanabe and Yatsu, 2006; Kanamori
93 *et al.*, 2019). Larvae and early juveniles are transported offshore from April to
94 September by the Kuroshio and Kuroshio extension to a large region in the western
95 North Pacific stretching from the Kuroshio–Oyashio transition region to the Oyashio
96 region, after which juveniles begin to migrate to the coastal waters of northern Japan
97 (Watanabe and Nishida, 2002; Takahashi *et al.*, 2014; Kamimura *et al.*, 2015). Age-1+
98 mackerel typically migrate northward along the Japanese coast from July to September
99 and southward from October to December (Watanabe, 1970; Usami, 1973).

100 Japanese sardine (*Sardinops melanostictus*) is also an important fishery resource in
101 Japan, and the size of the Pacific stock has been increasing over the past ten years
102 (Table 1). Seasonal changes in its distribution are similar to those of chub mackerel
103 (Watanabe and Nishida, 2002; Yatsu *et al.*, 2005; Yatsu, 2019). The major prey items of
104 juveniles and adults, such as Copepoda, Eupausiidae, Decapoda, and Amphipoda
105 (Yamashita, 1955; Nakai, 1962; Kawasaki, 1984; Yamamoto and Katayama, 2012),
106 overlap with those of late-juvenile and adult chub mackerel (Sato *et al.*, 1975;
107 Nakatsuka *et al.*, 2010; Taga and Yamashita, 2018). Therefore, Japanese sardine is a
108 potential competitor of chub mackerel (Kishida and Matsuda, 1993; Yatsu *et al.*, 2005),
109 and a previous study has indicated that Japanese sardine density has a negative effect on

110 chub mackerel recruitment (Kishida and Matsuda, 1993). However, the mechanisms of
111 inter-specific density dependence of chub mackerel growth and body condition remain
112 unknown.

113 The principal aim of this study was to clarify the density dependence of growth and
114 body condition of late-juvenile and adult chub mackerel in the Pacific by considering
115 the direct (e.g., through competition for food) and indirect (i.e., through changes in
116 habitat temperature) effects of conspecific and heterospecific density. In addition, we
117 also aimed to identify seasonal changes in density dependence and the drivers of
118 fluctuations in body condition. First, individual size-at-age, relative condition factor,
119 and habitat temperature were estimated to analyze the relationship between mean annual
120 growth rate and mean body condition on a quarterly basis. Second, we used structural
121 equation models (SEMs) to examine the effects of chub mackerel and Japanese sardine
122 abundance, environmental conditions (i.e., the location of the Oyashio Current and the
123 locations of sample capture), and an endogenous factor (age) on body condition and
124 habitat temperature by quarter.

125

126 **Materials and methods**

127 **Fish sampling and laboratory procedures**

128 A total of 18,302 chub mackerel landed in fishing ports on the Pacific coast of northern
129 Japan between 2006 and 2019 were used for the study (Figure 1b). Fishing gear
130 included purse seines, dipnets, setnets, and vertical long lines. Most of the samples
131 (12,379 individuals, or 68%) were captured by purse seine fisheries. Fork length (FL)
132 was measured to the nearest 1 mm by using digital calipers. Total weight (TW), gonad

weight (GW), and stomach content weight (SCW) were measured to the nearest 0.1 g by using digital scales. Sex was determined by direct gonad observation.

Ages were determined by counting annual rings on scales (Kondo and Kuroda, 1966) or sectioned sagittal otoliths (Kawashima *et al.*, 2017) under electronic microscopes. Previous studies have used gonad observation of mature fish and otolith microstructure analysis of juveniles to reveal that spawning mainly occurs in April (Watanabe, 2010; Kamimura *et al.*, 2015). Therefore, we assumed that the hatch date was in April and calculated ages as $t = A + m/12$, where A is age (in years) estimated from scale and otolith observations, and m is the number of months between the catch month and the preceding April.

Growth analysis

A total of 15,415 fish in the 2006 to 2016 year classes were used for growth analysis. (Table 2). The von Bertalanffy (VB) equation was fitted separately to the FL-at-age data for each year class to estimate cohort-specific growth parameters:

$$L_t = L_{\text{inf}} \{1 - \exp[-K(t - t_0)]\} \quad (1)$$

where L_t , L_{inf} , K , and t_0 are FL at age t , asymptotic FL, growth coefficient, and hypothetical age at zero FL, respectively. Non-linear least-squares regression was used to estimate these parameters. Initial values were estimated by using the Ford–Walford plot. Sex-specific models were calculated for each year class, and VB growth formulae were compared between males and females within each year class by using the F test.

156 Annual growth rates in length (G_L) for ages 1–5 were calculated as follows:

157

$$158 \quad G_L = L_{A+1} - L_A \quad (2)$$

159

160 where L_{A+1} is the FL of chub mackerel at age $A + 1$, and L_A is the age A estimated by the

161 VB growth formula for each year class.

162

163 **Body condition**

164 Relative condition factor (K_n ; Le cren, 1951; Froese, 2006) was computed to examine

165 individual fish condition by using 8429 age-1+ chub mackerel from the 2006–2016 year

166 classes (caught from 2007 to 2018 in 510 hauls) whose catch locations were recorded.

167

$$168 \quad K_n = W/W_{\text{pred}} \quad (3)$$

169

170 where W is body weight (excluding GW and SCW) and W_{pred} is the predicted W from a

171 weight–length relationship of the form:

172

$$173 \quad W_{\text{pred}} = aL^b \quad (4)$$

174

175 where L is FL, a is the allometric coefficient between weight and length, and b is the

176 exponent of that relationship. We estimated these parameters by using non-linear

177 least-squares regression.

178

179 **Abundance indices of the Pacific stock of chub mackerel and Japanese sardine**

180 Abundances of the Pacific stock of chub mackerel and Japanese sardine were estimated
181 by virtual population analysis from the 1970s to 2018 (Furuichi *et al.*, 2020; Yukami *et*
182 *al.*, 2020a). We used these estimates as abundance indices for this study. As mentioned
183 above, the distributions of age-0 chub mackerel and Japanese sardine are different from
184 those of older individuals; hence, the age-1+ abundances were used as the abundance
185 indices. Age-1+ chub mackerel abundances (N_m) ranged from 8.5×10^9 (2007) to 141.2
186 $\times 10^9$ individuals (2017), and Japanese sardine abundances (N_s) ranged from 5.2×10^9
187 (2008) to 313.6×10^9 individuals (2018; Table 1). N_m increased dramatically in 2014
188 and reached about 140×10^9 individuals. N_s gradually increased after 2011 and
189 stabilized at about 300×10^9 individuals after 2016.

190

191 **Confirmation of overlapping distributions of chub mackerel and Japanese sardine** 192 **by comparing catch locations**

193 To confirm the distributional overlap of chub mackerel and Japanese sardine in recent
194 years, we compared mackerel (chub and spotted mackerel, *S. australasicus*, were
195 combined) and Japanese sardine catch locations by season by using catch reports of
196 purse seine fisheries made by the Japan Fisheries Agency from 2010 to 2017.

197

198 **Habitat temperature**

199 Seasonal changes in the vertical distribution of chub mackerel were reported in previous
200 studies (Usami, 1973; Sato, 1974). Hence, we examined mean monthly habitat depths
201 based on 266 school-depth records from fishing vessel logbooks recorded by the North

202 Pacific district purse seine fishery for 2008–2019. Mean monthly school depths showed
203 that mackerel habitat was deeper in winter (November to February) than in summer
204 (May to August; Figure 2).

205 We used the temperatures at which chub mackerel had been caught (TC) as a proxy
206 for habitat temperature in this study. Temperature data were obtained from reanalysis
207 data of the Regional Ocean Modelling System (ROMS) developed by the Japan
208 Fisheries and Education Agency (FRA) for fisheries science (FRA-ROMS; Kuroda *et*
209 *al.*, 2017). Temperatures were estimated by using fishing locations and dates recorded in
210 the logbooks. FRA-ROMS provides averaged daily temperatures at 1/10-degree scale at
211 depths of 0, 10, 30, 50, 75, 100, and 200 m in the Kuroshio–Oyashio region. Therefore,
212 we extracted temperatures for the depths provided by FRA-ROMS that were closest to
213 the mean monthly school depths estimated above (i.e., 75 m in January and February;
214 50 m in March, November, and December; 30 m in April, September, and October; and
215 10 m in May, June, July, and August) (Figure 2).

216

217 **The First Oyashio Intrusion**

218 The Oyashio Current is a western boundary current of western subpolar gyre in the
219 North Pacific (Qiu, 2001) that transports cold, low-salinity subarctic water together with
220 chemical and organic matter along the Kuril, Hokkaido, and Honshu (the main island in
221 the Japanese archipelago) islands (Figure 1a). The southward current on the continental
222 slope along the east coast of Honshu is referred to as the First Oyashio Intrusion (FOI),
223 and plays an important role in the supply of nutrients and copepods to the region
224 (Shimizu *et al.*, 2009; Kuroda *et al.*, 2017). Therefore, the FOI could potentially impact

the growth and body condition of fisheries species. In this study, the southernmost position of the FOI (the SFOI) was determined from FRA-ROMS reanalysis data by using a procedure described in previous studies (Murakami, 1994; Kuroda *et al.*, 2017). We defined the SFOI as the point at which the southward convex locations of the 5-°C isotherm at a depth of 100 m (as calculated from approximately 10-d means) was the closest to the coast of Honshu. SFOIs were averaged for each month during 2006–2018.

231

232 **Statistical analysis**

The piecewise SEM (Lefcheck, 2016) was used to investigate the effects of biotic and abiotic factors on the body condition of age-1+ chub mackerel. Classical SEMs assume that all observations are independent and that all variables are normally distributed. By contrast, in the piecewise SEM, the path diagram is translated to a set of linear equations and parameters are calculated by solving each equation separately; hence, the piecewise SEM can include random effects and distributions of various shapes (Lefcheck, 2016). We developed an *a priori* SEM (Figure S1) by using previous studies to parameterize the relationships between fish condition factor (K_n), chub mackerel abundance (N_m), Japanese sardine abundance (N_s), age (A), the southernmost position of the FOI (SFOI), habitat temperature (TC), catch latitude (Lat), and catch longitude (Lon) (Parrish and Mallicoate, 1995; Watanabe and Yatsu, 2004). We hypothesized that these causal variables affect body condition indirectly through TC, as well as directly. Because monthly mackerel condition factor and temperature are most closely correlated at short lag times (i.e., a lag of 0 or 1 month) (Parrish and Mallicoate, 1995), TC was used as a causal variable for K_n in this study. Piecewise SEMs were constructed for each

248 quarter starting in April, with the quarters defined as follows: Q1, April to June; Q2,
249 July to September; Q3, October to December; and Q4, January to March. We assumed
250 Q1 as the spawning season, Q2 as the season for the northward feeding migration, Q3 as
251 the season for the southward migration, and Q4 as the pre-spawning season, based on
252 previous studies of seasonal distribution (Watanabe, 1970; Usami, 1973) and
253 reproductive surveys of chub mackerel (Watanabe and Yatsu, 2006). The goodness-of-fit
254 of each model was evaluated using Shipley's d-separation test (Shipley, 2000, 2009) ,
255 which tests the assumption that all variables are conditionally independent, and we
256 considered the final SEM consistent with the data if Fisher's C statistic was $p > 0.05$.
257 The model with the lowest Bayesian information criterion (BIC) was considered the
258 final model; BIC is appropriate for confirmatory analyses and for finding the correct
259 model (Aho *et al.*, 2014). Standardized path coefficient estimates were calculated for
260 each path model.

261 To construct the piecewise SEM, the K_n model and TC model were separately fitted
262 with individual regressions by using linear mixed models (LMMs). For the K_n model,
263 K_n was used as a response variable; N_m , N_s , TC, A , SFOI, Lat, and Lon were used as
264 explanatory variables; and sex (male, female, and unidentified) and haul ID (a
265 categorical variable) were included as random variables. For the TC models, TC was
266 used as a response variable; N_m , N_s , A_t , SFOI, Lat, and Lon were used as explanatory
267 variables; and sex was included as a random variable. The multicollinearity of models
268 was checked by calculating a variance inflation factor for each explanatory variable.
269 Collinearity was assessed with a cut-off value of 5 (James *et al.*, 2013); as a result, N_s
270 and Lon were eliminated from the models in Q1 and Lon was eliminated in Q4.

271 To examine whether chub mackerel body condition was related to G_L , relationships
272 between mean K_n in each quarter and G_L -at-age were analyzed by using LMMs. We
273 used G_L for ages 1–5 as a response variable and mean K_n by age as explanatory
274 variables with age as a random intercept. A likelihood-ratio test was conducted to
275 examine the significance of K_n in this analysis.

276 All statistical tests were performed in R v. 3.6.3 (R Core Team, 2020). VB
277 parameters were estimated by using the package *FSA* (Ogle *et al.*, 2020). Piecewise
278 SEMs were constructed with the package *piecewiseSEM* (Lefcheck, 2016), and LMMs
279 were analyzed with the package *lme4* (Bates *et al.*, 2015).

280

281 **Results**

282 Chub mackerel was caught mainly from January to June in the waters offshore of the
283 central Japanese archipelago between 34°N and 39°N (Figure 1b). During summer (July
284 to September), catch locations were mainly in northern waters between 37°N and 43°N,
285 and after October, they moved southward. The catch locations of mackerels (i.e., chub
286 and spotted mackerel) and Japanese sardine in purse seine fisheries followed similar
287 seasonal patterns and overlapped from 2010 to 2017 (Figure S2). We used catch data on
288 chub mackerel (Yukami *et al.*, 2020a) and spotted mackerel (Yukami *et al.*, 2020b) to
289 calculate the percentage of chub mackerel in the total mackerel catch in the Pacific
290 stock. The percentages for each study year were 2010, 40.4%; 2011, 36.1%; 2012,
291 47.8%; 2013, 67.0%; 2014, 71.6%; 2015, 84.5%; 2016, 90.7%; and 2017, 93.6%. We
292 estimated that most of the catches from 2010 to 2017 were in fact chub mackerel.

293 The mean monthly SFOI changed seasonally, with high latitudes in

October–January followed by a rapid transition to low latitudes (Figure 3). The highest (farthest north) SFOI was observed in December 2015 (42°4'N), and the lowest (farthest south) in March 2017 (37°4'N).

The FLs of individuals used in the VB growth formulae ranged from 121 to 470 mm, and ages ranged from 0.2 to 11.1 years. VB growth formulae were fitted to each year class by sex. We found significant differences between male and female formulae in the 2008, 2009, and 2013 year classes (Figure S3 and Table S1). However, differences by sex in these year classes were small after age 1; therefore, we combined data from males, females, and individuals of unidentified sex to establish VB growth formulae for each year class.

Estimates of L_{inf} , K , and t_0 ranged from 339.9 (for the 2016 year class) to 440.5 (the 2006 year class), from 0.25 (for the 2015 year class) to 0.55 (the 2012 year class), and from –2.88 (for the 2011 year class) to –1.26 (the 2007 year class), respectively (Table 2). G_L ranges were 29.6–51.2 at age 1, 20.8–33.3 at age 2, 13.4–25.6 at age 3, 7.7–19.6 at age 4, and 4.4–15.1 at age 5 (Table S2). The estimated FLs were especially high for the 2007–2011 year classes and low for the 2013–2016 year classes, with the 2012 year class showing intermediate growth (Figure 4 and Table S2). The G_L s of 2012 year class were lower after age 2 than the other year classes (Table S2).

The weight–length relationship was estimated as $W = 1.09 \times 10^{-6} L^{3.41}$. Values of K_n followed a generally downward trend in recent years and were lower in Q1 among older individuals and higher in Q3 and Q4 (Figure 5a and Tables S3 and S4). TC also declined over time and was higher among older individuals in Q1 and Q4. (Figure 5b and Tables S3 and S4). The mean TC in Q1 was relatively high (around 20 °C) until 2013, and fell

317 to around 16 °C after 2014. Similarly, the mean TC in Q3 was around 20 °C until 2012,
318 after which it fell to around 16 °C. The mean TC in Q4 dropped from around 17 °C to
319 14 °C beginning in 2014. The mean TC in Q2 ranged from 15 to 22 °C and there was no
320 clear trend.

321 G_L was significantly correlated with mean K_n in each quarter (Q1: $\chi^2 = 34.6$, $p <$
322 0.001 ; Q2: $\chi^2 = 7.23$, $p = 0.007$; Q3: $\chi^2 = 6.50$, $p = 0.011$; Q4: $\chi^2 = 4.83$, $p = 0.028$). Our
323 model showed that G_L increased with higher K_n for ages 1–5 in all quarters (Figure 6
324 and Table 3).

325 The final SEM for each quarter was selected based on BIC (Table S5), and provided
326 good fit to the data (Q1: Fisher's $C = 4.21$, $p = 0.38$; Q2: Fisher's $C = 1.07$, $p = 0.98$; Q3:
327 Fisher's $C = 5.39$, $p = 0.25$; and Q4: Fisher's $C = 6.14$, $p = 0.19$). In these SEMs, biotic
328 and abiotic effects on mackerel K_n and TC varied by quarter (Figure 7 and Table S6).
329 Homogeneity tests of residuals for the best models showed that the residuals
330 approximately follow a normal distribution, meaning that the assumption of
331 homogeneous variances was met (Figures S4 and S5).

332 N_m had strong negative direct effects on K_n in Q1, Q2, and Q3, and N_s had strong
333 negative direct effects in Q2 and Q4 (Figure 7 and Table S6). A had direct positive
334 effects on K_n in Q3 and Q4, but had a negative direct effect in Q1. SFOI had a negative
335 direct effect on K_n in Q3 and a positive direct effect in Q1 and Q4. Lat had positive
336 direct effects on K_n in Q2 and Q3. TC had a negative effect on K_n in Q2 and Q3 and a
337 positive effect in Q1 and Q4, but its effects were non-significant in Q1 and Q2.

338 N_m had positive effects on TC in Q2 and Q4 and negative effects in Q1 and Q3. N_s
339 had positive effects on TC in Q3 and a negative effect in Q4 (Figure 7 and Table S6).

340 The indirect effects of N_m on K_n via TC were negative in Q1 ($-0.41 \times 0.05 = -0.02$) and
 341 Q2 ($0.15 \times -0.05 = -0.01$) and positive in Q3 ($-0.37 \times -0.12 = 0.04$) and Q4 ($0.14 \times$
 342 $0.22 = 0.03$). The indirect effects of N_s were negative in Q3 ($0.11 \times -0.12 = -0.01$) and
 343 Q4 ($-0.38 \times 0.22 = -0.08$). A had positive effects on TC in Q1 and Q4 and negative
 344 effects in Q2 and Q3, and had positive indirect effects on K_n via TC in Q3 ($-0.11 \times$
 345 $-0.12 = 0.01$) and Q4 ($0.15 \times 0.22 = 0.03$). The effects of SFOI on K_n differed among
 346 quarters, but had positive indirect effects on K_n via TC in Q3 ($-0.38 \times -0.12 = 0.05$) and
 347 Q4 ($0.29 \times 0.22 = 0.06$). Although the direct and indirect effects of SFOI on K_n in Q3
 348 were in opposite directions, the direct effects of SFOI were of greater magnitude than
 349 the indirect effects. Lat and Lon had negative effects on TC in all quarters.

350

351 Discussion

352 Over the past decade, chub mackerel body condition and growth have declined with
 353 increasing chub mackerel and Japanese sardine abundance in the western North Pacific
 354 (Figures 4 and 5a). This has likely been caused by the negative intra- and inter-specific
 355 density dependence of chub mackerel body condition. Positive relationships between
 356 body condition and mean annual growth rate in terms of length in fish aged 1–5 (Figure
 357 6) suggest that body condition affects growth, and growth is affected by similar
 358 mechanisms as body condition. Previous studies on chub mackerel in the western North
 359 Pacific have underlined the importance of intra-specific density-dependent changes in
 360 growth, maturity, and egg production (Watanabe and Yatsu, 2004, 2006; Takasuka *et al.*,
 361 2020). Our results show that chub mackerel body condition is as strongly affected by
 362 Japanese sardine abundance as by chub mackerel abundance. Therefore, we suggest that

the inter-specific density dependence of body condition and growth are important factors for understanding chub mackerel population dynamics. Moreover, our data indicate that the carrying capacity of the western North Pacific for small pelagic fishes may have been reached within the last ten years.

In general, higher population densities cause lower food consumption and higher metabolic cost due to an increase in foraging effort, resulting in slower fish growth (Biro *et al.*, 2003; Amundsen *et al.*, 2007). In the case of chub mackerel, this appears to apply not only to the population density of chub mackerel itself but also to that of Japanese sardine. Chub mackerel and Japanese sardine are known to overlap in their feeding habits; additionally, in the present study, we show that the distribution of chub mackerel likely overlapped with that of Japanese sardine from 2010 to 2017 (Figure S2). Therefore, the decline in chub mackerel body condition associated with an increase in the density of conspecifics and heterospecifics was possibly mediated by changes in food consumption rate and/or metabolic cost. A previous study in Norwegian waters showed that the length- and weight-at-age of adult Atlantic mackerel (*Scomber scombrus*) decreases with increasing mackerel and Atlantic herring (*Clupea harengus*) density, suggesting that intra- and inter-specific food competition in summer feeding grounds is responsible for growth regulation (Olafsdottir *et al.*, 2016). In our study, our piecewise SEM analyses confirmed that both intra- and inter-specific density dependence negatively affected mackerel body condition in the northward feeding migration season (Figure 7 and Table S6), when chub mackerel and other small pelagic fishes generally converge on the same subarctic summer feeding grounds in the western North Pacific (Yatsu, 2019). Seasonal changes in the negative effects of chub mackerel

386 and Japanese sardine abundance on body condition, as estimated by our models, might
387 indicate the timing of the occurrence of intra- and inter-specific competition. If the
388 competition is over food resources, as is suggested in our study, future work that
389 directly compares seasonal changes in the diets of chub mackerel and Japanese sardine
390 could provide further insight into the possible mechanisms.

391 High body condition was associated with low temperatures during the southern
392 migration and high temperatures in the pre-spawning season (Figure 7 and Table S6).
393 Temperature likely affects fish metabolism directly as well as indirectly through the
394 regulation of food resources (Lloret *et al.*, 2014), and the relationship between
395 temperature and body condition is specific to species, seasons, and ecosystems. For
396 example, one study reported a negative relationship between water temperature and
397 chub mackerel body condition in the eastern North Pacific (Parrish and Mallicoate,
398 1995), and suggested that higher temperatures, which reflected a reduction in the flow
399 of the California Current, likely caused a decrease in food availability. In contrast,
400 temperature was positively related to the body condition of sprat (*Sprattus sprattus*), a
401 thermophilic species in the Baltic Proper (Casini *et al.*, 2011). In our study area, because
402 complex ocean structures are formed by the collision of the cold Oyashio and warm
403 Kuroshio currents, there is a great deal of seasonal variability in productivity and fish
404 food availability (Yasuda, 2003; Kobari *et al.*, 2004, 2008; Yatsu *et al.*, 2013; Itoh *et al.*,
405 2015), and the relationship between body condition and temperature may have differed
406 among seasons.

407 Our results suggest that chub mackerel habitat temperatures were affected by intra-
408 and inter-specific density dependence during the spawning, southward migration, and

pre-spawning seasons in recent years. During the southward migration and pre-spawning seasons, Japanese sardine abundance had negative indirect effects (i.e., through habitat temperature) on chub mackerel body condition. This suggests that inter-specific competition displaced chub mackerel into habitats of different temperature, resulting in a decline in body condition. However, temperature effects on body condition are relatively small, and judging from the standardized path coefficients of the final models, these indirect effects likely had little impact compared to direct effects. This is consistent with previous studies that found that food availability is the main factor behind the density dependence of growth and body condition (Biro *et al.*, 2003; Amundsen *et al.*, 2007).

One source of uncertainty in our estimates of chub mackerel habitat temperature is our use of the assumption that monthly distribution depth does not change spatiotemporally. In reality, habitat depths can change in response to population fluctuation and environmental variability (Nye *et al.*, 2009). However, we believe that our estimates are reliable. The most frequent habitat of chub mackerel schools and the annual experienced temperatures of chub mackerel in the western North Pacific have been estimated to be about 15–20 °C (Usami, 1973) and 14.4–18.7 °C (Guo *et al.*, 2021), respectively. These temperatures are consistent with our estimates, which provides confidence in our calculations.

The location of the Oyashio Current is also likely to be an important determinant of chub mackerel body condition. Our SEMs showed a positive effect of latitude on body condition and a negative effect of latitude and longitude on habitat temperature (Figure 7 and Table S6). These results are consistent with the strong influence of the Oyashio

432 Current in the northern and eastern waters off northern Japan, and the fact that this
433 current provides an influx of cold water and abundant prey for small pelagic fishes. In
434 addition, our piecewise SEM analysis during the southward migration season showed a
435 strong negative direct effect of SFOI on body condition (Figure 7 and Table S6),
436 meaning that chub mackerel body condition improved with decreasing FOI latitude
437 during the southward migration season. This is a testament to the importance of the FOI
438 as a rich source of nutrients for chub mackerel. The FOI transports a large amount of
439 carbon (in the form of large grazing copepods) from the Oyashio region to the Oyashio-
440 Kuroshio transition region, and this southward transport is estimated to be an important
441 source of organic carbon in this region (Shimizu *et al.*, 2009). It is unclear why the
442 relationships between SFOI, body condition, and temperature during the southward
443 migration season are diametrically opposed to those of the pre-spawning season. One
444 possible factor is the influence of the Kuroshio Current, because almost all samples in
445 the pre-spawning season were caught in waters that are strongly affected by the
446 Kuroshio Current (i.e., <37°N). Future work should examine the effects of the Kuroshio
447 Current on chub mackerel body condition, growth, habitat temperature, and food
448 availability.

449 Age was also an important endogenous factor for chub mackerel body condition.
450 We identified positive direct and indirect effects of age on body condition during the
451 southward migration and pre-spawning seasons (Figure 7 and Table S6). This suggests
452 that older individuals might distribute in temperatures that are closer to optimum,
453 allowing them to allocate more energy to the accumulation of body energy stores. By
454 contrast, age had a negative direct effect on body condition during the spawning season

(Figure 7 and Table S6); this likely reflects the energetic cost of reproduction. Increasing reproductive investment in older, bigger fish (which are more likely to have reached maturity) could explain this decline in body condition.

Previous studies have suggested that the mean growth rate of a given cohort negatively correlates with the population density of the cohort and of the cohort from the preceding year. In chub mackerel, there was negative correlation between size at age 0 (about six months after hatching) and year-class strength (Watanabe and Yatsu, 2004). In Atlantic mackerel, mean length at ages 0–2 negatively correlated with the population density of the cohort and of the cohort from the preceding year (Jansen and Burns, 2015). In our study, the strongest year class of chub mackerel occurred in 2013, and relatively high recruitment continued until 2018 (Table 1). Age-1+ abundance jumped up in 2014 (4.8 times the abundance in 2013) and subsequently remained high, with the 2013 year class accounting for 90% of chub mackerel abundance in 2014 and 57% in 2015 (Table 1). Our results also indicate slower growth of the 2013–2016 year classes after age 0, which is consistent with a previous study (Watanabe and Yatsu, 2004). In addition, growth trajectories and growth-at-age of the 2012 year class indicated slower growth after age 2 (Figure 4 and Table S2). This suggests that growth stagnation of a cohort can be caused by the strength of a subsequent year class, not just by that of the same or previous year.

High growth rates caused early maturation in chub mackerel during the period of declining abundance from 1970 to 2007 (Watanabe and Yatsu, 2006; Watanabe, 2010). Therefore, it is likely that the slow-growing 2013–2016 year classes experienced delayed maturity. Even though high recruitment events occurred several times in the

1990s, recovery of this stock has been prevented due to the overfishing of immature fish (Kawai *et al.*, 2002). To properly maintain and manage this resource, it will be necessary to conserve immature fish and investigate length- and age-at-maturity during the recent phase of increasing stocks.

Conclusion

Our results show that chub mackerel body condition and growth declined during recent years. These declines were likely caused by the intra- and inter-specific density dependence of these factors. This suggests that intra- and inter-specific competition is a key determinant of chub mackerel body condition and growth variability, and that food availability and carrying capacity for small pelagic fishes in the western North Pacific are approaching their limit. The water temperatures inhabited by chub mackerel were influenced by intra- and inter-specific density dependence, and this likely affected body condition and growth. In other words, our data suggest that the population densities of conspecifics and heterospecifics partly affected chub mackerel body condition and growth through changes in habitat temperature (i.e., indirectly). However, these indirect effects were weaker than the direct effects. This is consistent with previous studies that have identified food availability as the main factor affecting the density dependence of growth and body condition (Biro *et al.*, 2003; Amundsen *et al.*, 2007). Our results will be useful for future stock assessment and management. Further studies of diet and food availability could help clarify the causes of seasonal changes in the intra- and inter-specific density dependence of body condition identified in the present study, and the collection of more data on reproductive traits could help improve our understanding

501 of the plasticity of maturity in chub mackerel.

502

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506

507 **Supplementary data**

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509

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516 **Author contributions**

517 Yasuhiro Kamimura: Conceptualization, Data curation, Methodology, Formal analysis,
518 Investigation, Writing – Original Draft. Makoto Taga: Conceptualization, Investigation,
519 Resources, Writing – Review & Editing. Ryuji Yukami: Data curation, Investigation,
520 Resources, Writing – Review & Editing. Chikako Watanabe: Investigation, Resources,
521 Writing – Review & Editing. Sho Furuichi: Resources and Writing – Review & Editing.

522

523 **Data availability**

524 The data that support the findings of this study are available from the corresponding
525 author, YK, upon reasonable request.

526

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790
791 **Figure captions**

792 Figure 1. Maps of (a) the oceanographic features of the western North Pacific and (b)
793 the monthly catch locations of chub mackerel used in this study.

794
795 Figure 2. Monthly changes in chub mackerel vertical distribution. The black solid line
796 indicates the mean school depth recorded in logbooks by purse seine fisheries, and the
797 red dashed line indicates the habitat depths used when estimating habitat temperatures
798 with FRA-ROMS. Vertical error bars show standard deviations.

799

800 Figure 3. Monthly changes in the southernmost position of the First Oyashio Intrusion
801 from January 2006 to December 2018.

802

803 Figure 4. Comparison of von Bertalanffy growth formulas for chub mackerel among 11
804 year classes. Grey dots show the raw data, and coloured lines show von Bertalanffy
805 curves fitted to each year class.

806

807 Figure 5. Box plots of (a) chub mackerel relative condition factor (K_n) and (b) the
808 estimated temperatures at which individuals were caught by age and quarter from 2006
809 to 2018.

810

811 Figure 6. Relationships between mean relative condition factor (K_n) and annual
812 growth-at-age (G_L ; mm year⁻¹) by quarter. Lines represent linear functions estimated by
813 using linear mixed models of G_L and K_n .

814

815 Figure 7. Final piecewise structural equation model of chub mackerel condition factor
816 (K_n) by quarter. The variables examined were chub mackerel abundance (N_m), Japanese
817 sardine abundance (N_s), age (A), habitat temperature (TC), southernmost position of the
818 First Oyashio Intrusion (SFOI), catch latitude (Lat), and catch longitude (Lon). Black
819 arrows and red arrows represent positive and negative relationships, respectively. Solid
820 lines indicate significant relationships ($p < 0.05$), and dotted lines indicate
821 non-significant relationships. Standardized path coefficients are shown in black or red
822 text, and the thickness of the paths correspond to the magnitude of these coefficients. R^2

823 values inside the boxes are conditional R^2 .

824

825 Table 1. Abundances (10^9 individuals) of the Pacific stock of chub mackerel and Japanese sardine as estimated by Yukami *et al.* (2020a)
826 and Furuichi *et al.* (2020).
827

Species	Year	Age						
		0	1	2	3	4	5+	1+
Chub mackerel	2006	0.418	0.412	0.949	0.049	0.015	0.004	1.429
	2007	1.636	0.275	0.226	0.328	0.013	0.005	0.846
	2008	0.566	0.749	0.141	0.095	0.091	0.008	1.083
	2009	1.769	0.330	0.277	0.056	0.027	0.021	0.711
	2010	1.266	1.043	0.193	0.081	0.018	0.008	1.344
	2011	1.161	0.783	0.566	0.085	0.024	0.005	1.464
	2012	3.097	0.755	0.453	0.308	0.040	0.012	1.568
	2013	18.632	2.025	0.464	0.230	0.152	0.014	2.884
	2014	5.992	12.247	1.154	0.249	0.091	0.085	13.826
	2015	5.211	3.902	7.544	0.639	0.114	0.088	12.287
	2016	12.958	3.466	2.470	3.910	0.323	0.105	10.274
	2017	8.927	8.604	2.208	1.463	1.682	0.240	14.197
	2018	29.212	5.909	5.653	1.263	0.635	0.657	14.117
Japanese sardine	2006	1.241	1.073	0.114	0.049	0.022	0.005	1.264
	2007	1.420	0.691	0.340	0.041	0.014	0.005	1.091
	2008	2.423	0.338	0.111	0.059	0.011	0.005	0.524

2009	1.304	1.249	0.080	0.045	0.027	0.008	1.409
2010	7.707	0.776	0.329	0.030	0.022	0.017	1.173
2011	5.276	4.995	0.188	0.052	0.009	0.012	5.255
2012	6.567	2.914	1.900	0.063	0.023	0.003	4.903
2013	7.611	3.980	1.452	0.807	0.022	0.013	6.274
2014	20.894	4.832	2.003	0.528	0.345	0.014	7.720
2015	40.075	11.915	2.774	0.947	0.111	0.170	15.916
2016	25.286	23.160	5.708	1.534	0.462	0.100	30.965
2017	27.962	13.646	13.972	2.801	0.746	0.239	31.404
2018	79.451	13.759	8.019	8.218	0.995	0.371	31.362

828

829 Table 2. Fork length (FL) range, age (t) range, and estimated von Bertalanffy parameters
830 (L_{inf} , K , and t_0) by year class for chub mackerel.

831

Year class	n	FL range (mm)	t range (years)	L_{inf}	K	t_0
All	15 415	121–470	0.2–11.1	371.0	0.39	–1.96
2006	525	207–426	0.4–8.1	440.5	0.26	–2.25
2007	1 548	188–460	0.3–9.8	400.4	0.49	–1.26
2008	659	226–434	0.6–11.1	396.0	0.50	–1.38
2009	1 315	212–440	0.8–10.1	400.6	0.44	–1.62
2010	1 351	208–470	0.4–9.3	396.5	0.48	–1.59
2011	830	226–455	0.8–8.3	393.5	0.35	–2.88
2012	1 865	121–457	0.3–7.3	360.2	0.55	–1.41
2013	4 522	160–460	0.5–6.7	356.9	0.32	–2.41
2014	1 533	198–430	0.4–5.7	348.4	0.36	–2.37
2015	647	193–420	0.4–4.7	400.5	0.25	–2.23
2016	620	136–358	0.2–3.7	339.9	0.47	–1.29

832

833 Table 3. Parameter estimates of the models showing the effects of mean relative
834 condition factor (K_n) on growth rate in terms of length (G_L) by quarter for chub
835 mackerel.

836

Quarter	Parameter	Estimate	SE
Q1	Intercept	-91.84	16.06
	K_n	119.32	16.63
Q2	Intercept	-19.35	15.35
	K_n	40.39	14.23
Q3	Intercept	-11.01	13.27
	K_n	29.69	11.09
Q4	Intercept	-9.34	14.32
	K_n	30.08	13.06

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838 Figure 1

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840 Figure 2

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843 Figure 3

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846 Figure 4

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