1 **Title:**

2 Stronger density-dependent growth of Japanese sardine with lower food availability:
3 Comparison of growth and zooplankton biomass between a historical and current stock-
4 increase period in the western North Pacific

5
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18
19 **Abstract**

20 Density dependence is a fundamental concept for fish population dynamics. Although
21 density-dependent growth and maturity among older juveniles and adults is important
22 for regulating fish population size and for fisheries management, the mechanism of
23 density dependence for marine fishes remains unclear. Here, we examined changes in

24 Japanese sardine growth with increasing abundance beginning in the 2010s and how the
 25 current pattern of density-dependent growth differs from that of a previous stock-
 26 increase period from the 1970s to early 1980s. During the current period of increasing
 27 abundance, mean standard length has already dropped to the lowest level yet observed
 28 and growth has declined more sharply with increased abundance than in the 1970s and
 29 1980s. Mesozooplankton biomass in July in the summer feeding grounds was also lower
 30 during the current period. Therefore, our results suggest that summer food availability in
 31 the western North Pacific controls the strength of density-dependent growth. A lower
 32 carrying capacity for Japanese sardine could account for the stronger density
 33 dependence of growth observed in the 2010s; this indicates that future Japanese sardine
 34 abundance might not increase as much as in the 1980s unless food availability improves.

35

36 **Keywords:** *Sardinops melanostictus*, density dependence, otolith, age determination,
 37 Oyashio

38

39 **1. Introduction**

40 Density dependence plays a key role in population dynamics. Changes in mortality,
 41 growth, maturity, and habitat selection during population fluctuations have been
 42 observed in many fishes (e.g., Lorenzen and Enberg, 2002; Rose et al., 2001;
 43 Zimmermann et al., 2018). When constructing population dynamics models for fisheries
 44 management, it is common to consider density dependence in early life stages (e.g., for
 45 egg production or for the period between hatching to recruitment) as a stock–
 46 recruitment relationship (Beverton and Holt, 1957; Ricker, 1954). On the other hand,
 47 density dependence in the late juvenile and adult stages (e.g., on growth and maturation)
 48 is rarely considered in these models because the process is currently not fully
 49 understood (Andersen et al., 2017). Density-dependent growth and maturity in later life
 50 stages could have important implications for fish population regulation (Lorenzen and
 51 Enberg, 2002) and for calculating reference points for management (Van Gemert and
 52 Andersen, 2018). Therefore, there is an urgent need to clarify the underlying processes
 53 to improve the implementation of effective management schemes.

54 For lake- and stream-dwelling fishes such as salmonids, the theoretical framework
 55 for the density dependence of growth and mortality (i.e., decreases in growth or
 56 increases in mortality with increasing population density) has been examined in detail
 57 through field and laboratory experiments as well as field observations (e.g., Matte et al.,
 58 2020a, 2020b). These studies have demonstrated the importance of food availability in
 59 the process of density dependence (Amundsen et al., 2007; Jenkins et al., 1999; Post et
 60 al., 1999), and of the application of both density-dependent and independent factors to
 61 growth models (Matthias et al., 2018). However, for marine fishes, the frameworks and

62 processes of density dependence have not yet been fully examined (Andersen et al.,
63 2017), despite the many studies that have reported negative density dependence in
64 growth (e.g., Rueda et al., 2015; Zimmermann et al., 2018). Examining how the density-
65 dependent growth of marine fishes is altered by environmental conditions (i.e., food
66 availability) could prove useful for understanding the processes underlying population
67 fluctuations and effective management schemes.

68 The Japanese sardine *Sardinops melanostictus* Temminck & Schlegel, 1844,
69 supports one of the largest fisheries of small pelagic fishes in the western North Pacific,
70 and its abundance has fluctuated repeatedly on a multidecadal scale (Furuichi et al.,
71 2020a; Kuwae et al., 2017). These fluctuations are particularly evident in the history of
72 the Pacific stock of Japanese sardine over the past 50 years. The stock initially increased
73 in the early 1970s (Wada and Jacobson, 1998) and maintained high recruitment into the
74 1980s (Fig. 1), with total biomass over 13×10^6 t (Furuichi et al., 2020a), until the stock
75 collapsed due to recruitment failure after 1988 (Watanabe et al., 1995). Abundance
76 remained at low levels until 2010, after which the stock has steadily recovered. This
77 recent trend toward increasing abundance is likely to be similar to that in the 1970s
78 based on estimates reported in a stock assessment (Furuichi et al., 2020a; Fig. 1) and in
79 a previous study (Wada and Jacobson, 1998).

80 Growth patterns of Japanese sardine are clearly affected by intra-specific density
81 dependence (Kawabata et al., 2011; Kim et al., 2006; Morimoto, 2003; Ohshimo et al.,
82 2009). Growth and maturity-at-age of the Pacific stock decreased in the late 1970s to
83 early 1980s, when abundance was increasing, but increased in the 1990s, when
84 abundance was in decline (Kawabata et al., 2011; Morimoto, 2003). For the most recent

85 period of increasing abundance (i.e., after 2010), although recent studies have reported
86 annual changes in larval and juvenile growth (Furuichi et al., 2020b; Niino et al., 2021),
87 late-juvenile and adult growth patterns remain unexamined. This information is urgently
88 needed to inform management strategies and forecasts of future abundance for this stock.

89 As mentioned above, although the commercial importance and growth variability of
90 Japanese sardine have interested many researchers, the annual periodicity of otolith
91 increments has not been confirmed in this species, meaning that scales are the only
92 available method for aging individuals (e.g., Nakai, 1962). This method has been used
93 successfully as a basis for stock assessment (Furuichi et al., 2020a) as well as in several
94 studies of late-juvenile and adult growth (Kawabata et al., 2011; Kim et al., 2006;
95 Morimoto, 2003; Wada and Jacobson, 1998). However, scale-based aging can be
96 somewhat unreliable as scales can easily detach from the body and be replaced by
97 regenerated scales. Generally, mean otolith ages tend to be slightly more precise
98 (Campana, 2001), and otolith-based age determination is the dominant method for other
99 sardines (Fletcher and Blight, 1996; ICES, 2019; Yaremko, 1996). Therefore, there is an
100 urgent need to confirm the annual periodicity of otolith increment formation in Japanese
101 sardine.

102 In the present study, we aim to understand the processes underlying the density
103 dependence of growth in the Pacific stock of late-juvenile and adult Japanese sardine,
104 with a particular focus on food availability. To do so, we relied partly on datasets of
105 changes in Japanese sardine growth from 1976 to the early 1980s (Wada and Kashiwai,
106 1991a, 1991b) and of zooplankton biomass since the 1970s in Oyashio waters in
107 summer (Odate, 1994; Tadokoro et al., 2005), which is when Japanese sardine undergo

108 northward feeding migrations (Nakai, 1962; Yatsu, 2019). First, we investigated
109 changes in growth during the period of increasing abundance since 2011 by confirming
110 the annual periodicity of otolith-ring formation. Then, we compared Japanese sardine
111 growth and summer zooplankton biomass during the period of stock increase in the
112 2010s (hereafter, “the current period of increase”) against the period of increase from
113 the 1970s to early 1980s (hereafter, “the previous period of increase”) with the
114 assumption that summer food availability affects the strength of density dependence.
115 Finally, we briefly discuss the implications of our results for the future trajectory of the
116 Pacific stock of Japanese sardine.

117

118 **2. Material and methods**

119 **2.1. Fish sampling**

120 Japanese sardine samples were selected from commercial catches landed at Hachinohe
121 port (40°5'N, 141°6'E) by purse seine fisheries and from among individuals collected
122 during scientific surveys. All samples were caught from 36–48°N and 141–172°E in the
123 western North Pacific from 2011 to 2020 (Fig. 2). Scientific surveys were conducted by
124 using a surface–midwater trawl net (NST-99, Nichimo Co., Ltd.; opening dimensions:
125 30 m × 30 m; cod-end mesh size: 17.5 mm) towed once at each station (15–60 min at
126 3.0–5.0 kn at 0–30-m depth) from aboard the training vessel (T/V) *Hokuho Maru*.
127 Samples were frozen at –20 °C on board for subsequent measurement and otolith
128 analysis. Standard length (SL) was measured to the nearest 0.1 mm by using digital
129 calipers in the laboratory.

130

131 **2.2. Age determination from sagittal otoliths**

132 We randomly selected 5–50 individuals from each sampling day or station. Sagittal
133 otoliths were extracted from each fish and washed with fresh water. The external faces
134 of sagittae were observed on a glass petri dish filled with 99% ethanol against a black
135 background under a stereo microscope (SZX16, Olympus Corp., Tokyo, Japan) with
136 reflected illumination units, and photographs were captured by using a digital camera
137 (DP27, Olympus Corp., Tokyo, Japan). We evaluated our otolith-based age
138 determination by using edge analysis, a commonly used validation method, in which we
139 recorded whether an opaque or translucent zone appears on the outer margin of an
140 otolith during every month or season (Campana, 2001). The annual periodicity of otolith
141 increment formation was confirmed (see results), and therefore each sample was aged
142 by counting the number of translucent zones on the posterior side of the otolith; the
143 annulus for a single year consisted of one opaque zone and one translucent zone. The
144 hatch date was assumed to be 1 January for the purposes of age determination in this
145 study. A previous report recommended the use of a reference radius to aid the
146 identification of the first annual ring for sardines (ICES, 2019). Therefore, we measured
147 the radius from the nucleus to the first translucent zone on the posterior side of the
148 otolith (r_l) to the nearest 1 μm for several selected samples of each age.

149

150 **2.3. Growth estimation**

151 Changes in growth of Japanese sardine during the previous period of increase (i.e., for
152 the 1976 to 1982 year-classes [YCs] except for the 1979 YC), have been previously
153 estimated by using the von Bertalanffy growth formula (VBGF) (Wada and Kashiwai,

154 1991a, 1991b). Therefore, we fit a VBGF to data for the 2011 to 2018 YCs to compare
155 growth rates between the previous and current periods of increase. The VBGF was fitted
156 separately to length-at-age data for each year-class to estimate cohort-specific growth
157 parameters:

$$158 \quad L_t = L_{\text{inf}} \{1 - \exp[-K(t - t_0)]\} \quad (1)$$

160
161 where L_t , L_{inf} , K , and t_0 are SL at age t , asymptotic SL, growth coefficient, and
162 hypothetical age at zero SL, respectively. Non-linear least-squares regression was used
163 to estimate these parameters. Wada and Kashiwai (1991b) estimated VBGFs for samples
164 collected from July to October and assumed a hatch month of September; hence, we
165 modified the t_0 of VBGFs obtained in their study by assuming a hatch month of January
166 to better compare growth rates between the two periods.

167 The VBGF parameters for the previous period of increase were based on scale-based
168 age determination. Because we used otolith-based age determination for the current
169 period of increase, we evaluated the possible effects of the different choices of aging
170 character by roughly comparing VBGFs estimated by otolith and scale data from the
171 2013 and 2018 YCs. Scale-based length-at-age was evaluated with a monthly age–
172 length key (ALK) estimated from individuals caught on the Pacific side of northern
173 Japan, which was the same as the ALK used for a previous stock assessment (Furuichi
174 et al., 2020a). Since the ALK used 5-mm length intervals, the minimum SL was set to
175 2.5 mm. Scale-based VBGF parameters were estimated in the same way as for the
176 otolith-based VBGF.

177

178 **2.4 Examination of density dependence in growth**

179 To examine the density-dependent growth of Japanese sardine, Kawabata et al. (2011)
 180 examined the relationship between body length at age estimated from a VBGF (L_t) and
 181 N_c , an index of the abundance that a given year-class experienced. In this study, we
 182 adopted the same index to examine density-dependent growth. Conceptually, N_c is the
 183 cumulative sum of Japanese sardine abundances over the period from when a given
 184 year-class is born to when it reaches the age $t - 1$, or in equation form: $\sum_{i=t-1}^{t-1} N_i$, where
 185 N_i is the total population abundance in year i . The age range of samples previously used
 186 to estimate VBGF parameters during the previous period of increase was 1–4 (Wada and
 187 Kashiwai, 1991b); therefore, the range of t used in our study was 2–4 .

188

189 **2.5. Annual changes in zooplankton biomass in the Oyashio area**

190 Oyashio waters provide the summer feeding ground for small pelagic fishes in the
 191 western North Pacific (Yatsu, 2019), and the zooplankton biomass in these feeding
 192 grounds is known to affect the population dynamics of these fishes (Odate, 1994;
 193 Tadokoro et al., 2005; Yatsu, 2019). Annual changes in mean zooplankton biomass in
 194 June and July in the Oyashio area from 1971 to the 1980s have been reported in
 195 previous studies (Odate, 1994; Tadokoro et al., 2005). In these studies, Oyashio waters
 196 were defined as the area where temperature at 100-m depth was less than 5 °C (Kawai,
 197 1972), and mean monthly mesozooplankton biomass collected by plankton nets was
 198 calculated within this area. In June, the eastern margin of this area was bounded by the

199 longitude 145°E from 35–37°N, and by the longitude 146°E from 38–43°N (Fig. 2). In
 200 July, the eastern margin was bounded by the longitude 155°E from 36–45°N. The area
 201 in July of water depth <500 m was excluded from this analysis. Although in these
 202 previous analyses mean mesozooplankton biomass was calculated without the use of a
 203 flow meter, a recent study of filtering-rate variability for vertical plankton tows has
 204 suggested that data lacking flow-meter information are still suitable for large-scale
 205 comparisons such as annual comparisons of zooplankton biomass (Takasuka et al.,
 206 2017). Therefore, we used these analysis results to compare mesozooplankton
 207 biomasses between the current and previous period of increase. For the current period of
 208 increase, mesozooplankton was collected in NORPAC and modified-NORPAC nets
 209 towed vertically from a depth of 150 m during the years 2011–2019. Both net types had
 210 the same mouth diameter (45 cm) and mesh size (0.335 mm), but were of different
 211 lengths and shapes. We did not correct for the difference in the nets because they have
 212 been reported to have the same sampling efficiency (Kotani, 1994).

213 We estimated mean monthly mesozooplankton biomass (g/m^2) by calculating
 214 biomass per 150 m of depth within the defined areas to compare against the previous
 215 studies (Fig. 2). Biomass data for June were drawn from Odate (1994) and data for July
 216 were extracted from figures published in Tadokoro et al. (2005) by using
 217 WebPlotDigitizer v. 4.5 (Rohatgi, 2021).

218

219 **2.6. Statistical analysis**

220 Mean r_l by age was compared by using Tukey's honestly significant difference (HSD)
 221 test. Relationships between L_t and N_c were analyzed by using general linear models to

222 examine the density dependence of growth. We hypothesized that the strength of density
223 dependence would differ between the previous and current periods of increase.
224 Therefore, the effects of *period* (a categorical variable) and the interaction of N_c and
225 *period* ($N_c \times \text{period}$) were also examined in the model. We used L_t as the response
226 variable, and N_c , *period*, and $N_c \times \text{period}$ as explanatory variables. The significance of
227 explanatory variables was examined by a likelihood-ratio test.

228 All statistical tests were performed in R v. 3.6.3 (R Core Team, 2020). VBGF
229 parameters were estimated by using the package FSA (Ogle et al., 2020), and
230 likelihood-ratio tests were conducted by using the packager car (Fox and Weisberg,
231 2019).

232

233 **3. Results**

234 A total of 1642 Japanese sardine of SL 82–245 mm were used for otolith analysis. The
235 proportion of otoliths with an opaque zone on the outer margin of the posterior side was
236 higher from May to September in all age classes (Fig. S1). Opaque and translucent
237 zones were clearly visible, and ages were determined for all individuals (Fig. S2). The
238 maximum estimated age was 7 years (SLs 225 and 230 mm) (Table 1). r_l values were
239 measured for 348 samples. Mean r_l values for ages 0 to 4+ were 980.7 μm , 1079.7 μm ,
240 1082.5 μm , 1088.8 μm , and 1106.5 μm , respectively, and the mean r_l for age 0 was
241 significantly lower than that for the other ages ($p < 0.001$) (Fig. S3).

242 VBGF parameters were estimated for the 2011–2018 YCs from 1491 samples (Table
243 1). L_{inf} ranged from 201.0 (2016 YC) to 235.9 (2012 YC), K from 0.47 (2018 YC) to
244 0.89 (2015 YC), and t_0 from -1.20 (2018 YC) to -0.20 (2011 YC) (Table 1). The

245 estimated VBGFs of the most recent eight YCs showed lower growth in later cohorts
246 (Fig. 3 and Table S1). Comparisons between the previous and current periods of
247 increase indicated similar growth for the 1980–1982, 2017, and 2018 YCs (Fig. 3).

248 The VBGFs estimated from otolith data showed roughly similar growth patterns to
249 those estimated from scale data. However, the confidence intervals for the otolith data
250 were wider (Table S1 and Fig. S4).

251 The general linear model and likelihood-ratio tests for growth and abundance in age 2
252 to age 4 sardine showed that N_c and $N_c \times Period$ were significant variables (Table 2).
253 The predicted relationships between L_t and N_c had higher slopes during the current
254 period of increase than during the previous period, indicating that the density
255 dependence of growth has become stronger in recent years (Fig. 4 and Table 2).

256 Mean monthly mesozooplankton biomass from 1971–1985 ranged from 12.2 to 65.7
257 g/m² in June and from 3.1 to 70.7 g/m² in July (Fig. 5). Mean biomass declined from
258 1971 to the 1980s, likely due to a combination of climatic changes and the increase in
259 Japanese sardine abundance after 1980 (Tadokoro et al., 2005). From 2011–2019, mean
260 mesozooplankton biomass ranged from 27.3 to 57.8 g/m² in June of each year and from
261 11.1 to 30.6 g/m² in July of each year. In June, mean mesozooplankton biomass for
262 1971–1979 (43.0 g/m²) was similar to that for 2011–2019 (40.7 g/m²). In July, mean
263 monthly mesozooplankton biomass for 1971–1979 (18.7 g/m²) was less than that for
264 2011–2019 (39.3 g/m²) and similar to that in the early 1980s, when Japanese sardine
265 abundance was more than four-fold higher than currently.

266

267 4. Discussion

Our results show a negative relationship between length at ages 2–4 and the cumulative sum of abundance, which indicates that growth rates have a negative density dependence. Additionally, the strength of this density dependence appears to differ between the previous and current period of increase (Fig. 4). Although there have been several reports of negatively density-dependent growth among the Clupeidae, such as in the genera *Clupea* (Brunel and Dickey-Collas, 2010), *Sardinops* (Dorval et al., 2015; Kawabata et al., 2011; Ohshimo et al., 2009), and *Sardina* (Véron et al., 2020), these previous studies did not examine changes in the strength of density dependence over time. A study on Northeast Arctic cod (*Gadus morhua*) did suggest that the density dependence of growth changed across several decades in response to environmental factors such as water temperature, prey availability, and the status of the North Atlantic Oscillation, but the effects of these factors were not fully explored (Eikeset et al., 2016).

Food availability is one of the most important factors affecting the density dependence of growth (Amundsen et al., 2007; Jenkins et al., 1999; Kamimura et al., 2021). Our results show that mean mesozooplankton biomass in the Oyashio area in June was roughly equivalent in the 1970s (average, 43.0 g/m²) and 2010s (40.7 g/m²), but mean biomass in July was considerably lower in the 2010s (18.7 g/m²) than in the 1970s (39.3 g/m²) (Fig. 5). This suggests that lower food availability in summer feeding grounds during and after July has caused stronger density-dependent growth through increases in intra-specific competition during the current period of increase.

Japanese sardine feed on both zooplankton and phytoplankton (Yatsu, 2019), but feed more intensively on zooplankton in summer (Kawasaki, 1984). This is also consistent with the importance of mesozooplankton biomass during and after July in the Oyashio

291 area for Japanese sardine growth. Changes in the spatial distribution of Japanese sardine
292 could also affect the strength of density dependence by changing food availability and
293 the energetic cost of feeding. Indeed, as Japanese sardine populations increase, the
294 expansion of feeding grounds to offshore waters might affect the strength of density-
295 dependent growth (Wada and Kashiwai, 1991b). Similarly, temporal changes in the
296 density dependence of body condition in sprat (*Sprattus sprattus*) in the Baltic Proper
297 have been suggested to have been triggered by spatial changes in habitat in response to
298 predation pressure (Casini et al., 2014). Future studies of changes in the spatial
299 distribution of Japanese sardine could provide further insight into this possible
300 mechanism.

301 Both bottom-up and top-down effects are thought to impact annual changes in
302 zooplankton biomass in the western North Pacific (Chiba et al., 2004, 2006; Odate,
303 1994; Tadokoro et al., 2005). In fact, reduced chlorophyll-*a* concentrations following
304 the 1976/1977 climatic regime shift and the flourishing of Japanese sardine have been
305 suggested as possible factors behind the decrease in summer mesozooplankton biomass
306 in the 1980s (Tadokoro et al., 2005). During the current period of increase, although
307 Japanese sardine abundance has been similar to or lower than that reported for the
308 previous period of increase (Fig. 1) (Wada and Jacobson, 1998), mean mesozooplankton
309 biomass in July has remained lower than during the previous period. This likely reflects
310 the importance of bottom-up processes in limiting mesozooplankton biomass during
311 recent years. SSTs from July to September in the western North Pacific have increased
312 since 2010, and are currently 1–2 °C higher than in the 1980s (Kuroda et al., 2020). This
313 temperature increase is a possible factor in the recent decline of mesozooplankton

314 biomass.

315 Temporal changes in the abundance of chub mackerel (*Scomber japonicus*), an
316 abundant and planktivorous small pelagic fish in the western North Pacific (Nakatsuka
317 et al., 2010; Taga and Yamashita, 2018; Yatsu, 2019), provide further evidence of the
318 importance of bottom-up processes during the current period. Mackerel abundances
319 ranged between 18×10^9 to 25×10^9 individuals from 1970 to 1978, and then decreased
320 to 8×10^9 individuals in 1982 (Yukami et al., 2020). Since 2011, abundances have
321 increased, and remained at similar levels during the years 2013 to 2017 (23×10^9 to 28
322 $\times 10^9$ individuals) as those reached in the 1970s. In fact, abundances in 2018 (46×10^9
323 individuals) and 2019 (35×10^9 individuals) were the highest ever recorded. Although
324 this might be expected to exert a negative top-down effect on mesozooplankton biomass,
325 in reality there has been no clear relationship between mesozooplankton biomass and
326 chub mackerel abundance since 2011 (Fig. 5). Follow-up studies on possible bottom-up
327 effects and on intra- and inter-specific competition based on dietary analysis would help
328 clarify changes in food availability for planktivorous fishes in this area.

329 Estimated growth trajectories for the 2017 and 2018 YCs were similar to those for the
330 1980 to 1982 YCs (i.e., the lowest-growth YCs since 1976) (Fig. 3), even though total
331 Japanese sardine abundance and biomass since 2018 were only about one-third to one-
332 fifth of that in the 1980s (Fig. 1). This suggests that the abundance of small pelagic
333 fishes is already approaching the carrying capacity of the North Pacific. Observations of
334 decreased chub-mackerel growth and body condition in the western North Pacific since
335 2013 also support this contention (Kamimura et al., 2021). Previous analyses have
336 indicated that population increases of Japanese sardine have been stunted by low growth

337 since the 1980 YC (Wada and Kashiwai, 1991b); therefore, sardine abundance might not
338 increase as much in the near future as it did in the 1980s unless food availability
339 improves.

340 Our results show that the strength of density dependence of growth differed across
341 the study period. Although previous studies have examined the density dependence of
342 Japanese sardine growth and egg production by using long-term multi-decadal datasets
343 (e.g. Kawabata et al., 2011; Takasuka et al., 2019), such studies implicitly assumed that
344 the strength of density dependence is time invariant. It is important when examining the
345 relationship between biological characteristics and population abundance for the
346 purpose of applying them to fisheries management and future forecasts to allow for
347 temporal changes in these relationships, as has been indicated by previous reports of
348 likely changes in the growth–recruitment relationship of this species over time (Furuichi
349 et al., 2020b).

350 Our study is the first to assess the annual periodicity of otolith increments in
351 Japanese sardine, and is also the first to successfully carry out otolith-based age
352 determination and growth estimation in this species. Otolith increments were clearly
353 distinguishable by the surface reading method (Fig. S2) and proved as useful for age
354 determination in this species as has been the case for other sardines (Fletcher and Blight,
355 1996; ICES, 2019; Yaremko, 1996). The mean r_l of age 1+ individuals ranged from
356 1079 to 1108 μm , which is similar to mean r_l for *Sardina pilchardus* (about 1.1 mm;
357 ICES, 2019). This result can be used to guide the identification of the first annual ring in
358 Japanese sardine.

359 The mean r_l of age-1+ fish was about 100 μm larger than that of age-0 fish; in other

words, the mean length of age-1+ fish when the first translucent zone was formed was about 10 mm longer than that of age-0 fish as calculated from the relationship between otolith radius and body length in juvenile Japanese sardine (Ohshimo et al., 1997). This suggests that larger Japanese sardine were more likely to survive their first year of life. This is consistent with previous reports that, in addition to larval survival, cumulative mortality between the egg stage and age 1 is important for recruitment success (Watanabe et al., 1995).

Otolith- and scale-based VBGFs showed similar growth trajectories, although the otolith-based VBGFs had wider confidence intervals simply due to the smaller sample size of length-at-age measurements (Fig. S4 and Table S1). This suggests that there is little difference among mean ages as determined by otolith and scale examination, and that the differences between the methods did not meaningfully affect our results. Further work is still needed to assess the precision and accuracy of age determination in this species from otolith- and scale-based methods.

5. Conclusions

Our study clarified changes in the recent growth of late-juvenile and adult Japanese sardine, and is the first to confirm the annual periodicity of otolith ring formation in this species. Otolith analysis is a powerful tool for understanding experienced environments and for reproducing migration histories of individual sardine (Sakamoto et al., 2017, 2019); therefore, our results should provide a strong basis for such research in the future. Our growth analyses showed that growth decreased with increasing abundance, and that density dependence in the current period of increase is likely to be stronger than in the

383 past. Mean mesozooplankton biomass in the Oyashio area in July was also reduced in
384 recent years as compared to the previous period of increase. Therefore, we suggest that
385 the stronger density dependence in recent years is caused by lower food availability, and
386 that zooplankton biomass during and after July in the Oyashio area is an important
387 determinant of the strength of density dependence. The implied lower carrying capacity
388 in the western North Pacific may indicate that Japanese sardine abundance will not
389 increase to past levels. Similar considerations of environmental conditions could be
390 useful for determining reference points for this stock, forecasting future stock status,
391 and for constructing population dynamics models of this species.

392

393 **CRedit authorship contribution statement**

394 Yasuhiro Kamimura: Conceptualization, Data curation, Methodology, Formal analysis,
395 Investigation, Writing – Original Draft. Kazuaki Tadokoro: Data curation, Investigation,
396 Resources, Writing – Review & Editing. Sho Furuichi: Data curation, Investigation,
397 Resources, and Writing – Review & Editing. Ryuji Yukami: Data curation, Investigation,
398 and Writing – Review & Editing.

399

400 **Declaration of Competing Interest**

401 The authors declare that they have no known competing financial interests or personal
402 relationships that could have appeared to influence the work reported in this paper.

403

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410

411 **Appendix A. Supplementary data**

412 Supplementary material related to this article can be found in the online version.

413

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602

603 **Figure captions**

604 Fig. 1. Abundances (10^9 individuals) of the Pacific stock of Japanese sardine estimated

605 by Furuichi et al. (2020a).

606

607 Fig. 2. Sampling locations of (a) Japanese sardine, (b) zooplankton in June, and (c)

608 zooplankton in July. Shading indicates the areas defined by Odate (1994) and Tadokoro

609 et al. (2005).

610

611 Fig. 3. Comparison of von Bertalanffy growth formulas of Japanese sardine among 14

612 year-classes. Formulas from 1976 to 1978 and 1980 to 1982 are based on parameters

613 modified from Wada and Kashiwai (1991a, 1991b).

614

615 Fig. 4. Relationship between the cumulative sum of Japanese sardine abundance and
616 estimated standard length using von Bertalanffy growth formulas at ages (a) 2, (b) 3,
617 and (c) 4. Circles and lines indicate observed values and predicted linear functions from
618 the general linear model, respectively. Shaded areas show 95% confidence intervals.

619

620 Fig. 5. Annual changes in mean mesozooplankton biomass in the areas defined by Odate
621 (1994) and Tadokoro et al. (2005) during (a) June and (b) July. Vertical bars indicate
622 standard errors. June data from 1971 to 1985 are from Odate (1994), and July data are
623 from Tadokoro et al. (2005).

Table 1. Standard length (SL) and age (t) ranges, number of individuals (n), and estimated parameters (95% confidence interval [CI]) of von Bertalanffy growth formulas, asymptotic SL (L_{inf}), growth coefficient (K), and hypothetical age at zero SL (t_0), by year-class from the present study and modified from Wada & Kashiwai (1991a, 1991b).

Source	Year class	n	SL range (mm)	t range (years)	L_{inf} (95% CI)	K (95% CI)	t_0 (95% CI)
This study	2011	89	101–234	0.8–6.5	223.5 (217.0, 229.9)	0.72 (0.60, 0.84)	−0.20 (−0.35, −0.04)
	2012	117	106–245	0.7–7.3	235.9 (230.1, 241.7)	0.67 (0.60, 0.75)	−0.30 (−0.40, −0.20)
	2013	256	123–235	0.7–6.3	224.4 (217.7, 231.1)	0.81 (0.65, 0.97)	−0.39 (−0.65, −0.14)
	2014	272	130–234	0.7–5.8	228.3 (220.8, 235.7)	0.56 (0.47, 0.64)	−0.84 (−1.06, −0.63)
	2015	199	116–232	0.8–5.9	206.8 (202.3, 211.4)	0.89 (0.72, 1.05)	−0.41 (−0.63, −0.19)
	2016	112	114–219	0.6–4.9	201.0 (193.5, 208.5)	0.75 (0.54, 0.96)	−0.78 (−1.16, −0.40)
	2017	179	83–214	0.4–3.9	205.8 (185.5, 226.1)	0.48 (0.29, 0.67)	−1.18 (−1.67, −0.69)
	2018	269	100–198	0.4–2.9	203.5 (185.4, 221.7)	0.47 (0.32, 0.63)	−1.20 (−1.58, −0.81)
Wada & Kashiwai (1991a, 1991b)	1976	-	-	1–4	225.0	0.53	−1.11
	1977	-	-	1–4	225.4	0.52	−0.94
	1978	-	-	1–4	212.4	0.65	−0.88
	1980	-	-	1–4	204.7	0.37	−1.84
	1981	-	-	1–4	211.5	0.32	−2.50
	1982	-	-	1–4	206.5	0.46	−1.40

627 Table 2. Results of a linear model with likelihood-ratio tests for growth of Japanese sardine. N_c , cumulative sum of Japanese sardine
628 abundance; *Period*, the previous or current period of increase.

Age (<i>t</i>)	Likelihood-ratio test			Selected model		
	Variable	χ^2 value	<i>P</i> value	Parameter	Estimate	SE
2	N_c	16.40	<0.001	Intercept	191.413	3.173
	<i>Period</i>	0.05	0.820	N_c	−0.039	0.006
	$N_c \times \textit{Period}$	10.61	0.001	$N_c \times \textit{Period}$	−0.121	0.028
3	N_c	22.90	<0.001	Intercept	214.617	3.503
	<i>Period</i>	0.22	0.640	N_c	−0.032	0.004
	$N_c \times \textit{Period}$	10.98	<0.001	$N_c \times \textit{Period}$	−0.092	0.022
4	N_c	21.24	<0.001	Intercept	227.255	4.198
	<i>Period</i>	0.05	0.817	N_c	−0.024	0.003
	$N_c \times \textit{Period}$	5.97	0.015	$N_c \times \textit{Period}$	−0.068	0.012

629 Figure 1

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631 Figure 2

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637 Figure 5

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