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Author(s)	Karasawa, Yuka; Ueno, Hiromichi; Tanisugi, Ryo; Dobashi, Ryo; Yoon, Seokjin; Kasai, Akihide; Kiyota, Masashi
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1 **Quantitative estimation of the ecosystem services supporting the growth**
2 **of Japanese chum salmon**

3 Yuka Karasawa^a, Hiromichi Ueno^{a,*}, Ryo Tanisugi^a, Ryo Dobashi^a,

4 Seokjin Yoon^b, Akihide Kasai^a, Masashi Kiyota^c

5 ^aGraduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, 041-8611,

6 Japan

7 ^bNational Institute of Fisheries Science, Gijanghaean-ro, Gijang-eup, Busan 46083, Korea

8 ^cGraduate School of Fisheries and Environmental Sciences, Nagasaki University

9

10 Corresponding author.

11 E-mail address: ueno@fish.hokudai.ac.jp (H. Ueno)

12

13 **Abstract**

14 Chum salmon (*Oncorhynchus keta*) are distributed widely in the subarctic North Pacific.
15 The Japanese stock is maintained by artificial release procedures. Chum salmon,
16 including the Japanese stock, provide important ecosystem services for humans that are
17 related to provisioning, culture and support. These ecosystem services are supported by
18 the supply of prey and habitat that the fish use. We regard the supply of prey and habitat
19 as supporting services for salmon. We developed a procedure to estimate supporting
20 services quantitatively, based on the prey biomass consumed by individual salmon, by
21 coupling a bioenergetics model and a lower trophic level ecosystem model. Using this
22 procedure, we estimated the prey biomass consumed by a cohort of Japanese chum
23 salmon released in a single year. The phytoplankton biomass indirectly consumed by a
24 cohort was also estimated and considered to be the primary production supporting the
25 fish. The Japanese chum salmon cohort was estimated to consume *ca.* $4.2\text{--}4.7 \times 10^9$ kg
26 wet weight of zooplankton, of which more than half is eaten in the Bering Sea. The
27 Japanese chum salmon cohort is supported by an estimated primary production of 2.0--
28 2.2×10^9 kg C, which amounts to 0.17%–0.19% of primary production in the areas and
29 periods through which the fish migrate. We also attempted to calculate the monetary value
30 of supporting services for the growth of Japanese chum salmon.

31

32 **Keywords**

33 Ecosystem services; Japanese chum salmon; Bioenergetics model; Lower trophic level
34 ecosystem model

35 **1. Introduction**

36 The chum salmon (*Oncorhynchus keta*) is one of six congeners occurring in the
37 Pacific Ocean. Over 50% of the chum salmon harvest in the North Pacific from 1974 to
38 2014 was Japanese chum salmon, primarily due to the success of their hatchery program
39 (Murphy et al., 2016). Japanese chum salmon are predominant in the Bering Sea during
40 summer and fall. Although recent studies indicate that small numbers of this species
41 spawn naturally in the rivers of Hokkaido (Morita et al., 2013), the major stock of the
42 Japanese group is maintained largely by artificial hatching and release (Hiroi, 1998;
43 Kaeriyama, 1999; Saito et al., 2015).

44 Japanese chum are released in spring, spend several months near the coast of Japan,
45 then migrate to the Okhotsk Sea, where they remain until late fall (Urawa, 2000; Azumaya
46 and Ishida, 2004) (Fig. 1). The fish then migrate toward the western North Pacific, where
47 they overwinter, then migrate into the Bering Sea by the following summer. In the fall,
48 they move into the Gulf of Alaska in the eastern North Pacific, where they spend one
49 winter. They repeat the migration track between the Bering Sea (summer) and the Gulf
50 of Alaska (winter) 3–4 times, and then return to Japan when approaching maturity in the
51 summer of their fourth to fifth year.

52 Pacific salmon, including the Japanese chum, have played an important role in the
53 lives of people living close to the coasts of the northern North Pacific. These fish
54 reportedly confer three of four categories of the ecosystem services defined by the
55 Millennium Ecosystem Assessment (MEA) (2005) and The Economics of Ecosystems
56 and Biodiversity (TEEB) (2010): provisioning, culture and supporting services for human
57 populations (Bottom et al., 2009). The clearest ecosystem service is provisioning. Pacific
58 salmon are also important as a principal focus of the spiritual and cultural lives of native

59 communities in North America (Bottom et al., 2009), as well as in Hokkaido, Japan
60 (Okada, 2012). Salmon are also a principal food item in the diets of many terrestrial
61 wildlife species (Willson and Halupka, 1995; Merz and Moyle, 2006). They are a source
62 of marine-derived nutrients for coastal lakes and streams (Bilby et al. 1996; Cederholm
63 et al., 1999; Finney et al., 2000), thereby providing additional support services (Bottom
64 et al., 2009).

65 As described above, salmon provide provisioning, culture and supporting services
66 for human populations. However, salmon are themselves also supported by the ecosystem
67 services provided by their habitat, which are called “supporting services” or “habitat
68 services” (TEEB, 2010). The ecosystem providing the reproduction habitat for
69 commercially valuable species provides an important so-called “nursery-service,” which
70 is (economically) valued in its own right (TEEB, 2010). However, it is difficult to
71 evaluate the monetary value of supporting services from the ecosystem when they are not
72 traded on the market. In this case, revealed preference or stated preference approaches
73 are used, but both approaches have limitations (TEEB, 2010). As for salmon, their growth
74 and survival are dependent on the supply of appropriate prey and their habitat in the ocean,
75 which we regard here as supporting services for salmon. However, a means for
76 quantitatively estimating supporting services for salmon in oceans has yet to be developed.

77 As noted above, Japanese chum populations are maintained by artificial release
78 practices. Hence, the commercial fisheries for this species differ from capture fisheries
79 for other species/populations. In capture fisheries, harvesting reduces the predation
80 pressure on prey organisms and may therefore affect ecosystem structure via trophic
81 cascades (Scheffer et al., 2005). Artificially released chum salmon consume low trophic
82 level resources in each migration area; they return to the rivers from which they were

83 released and are harvested there. Thus, artificially released Japanese chum salmon are
84 likely supported by low trophic level components of the ecosystems in the Sea of Okhotsk,
85 the North Pacific and the Bering Sea. Quantitative estimations of the supporting services
86 for the growth and survival of Japanese chum salmon are required for evaluations of the
87 marine ecosystem impacts of the artificial release and harvesting of this species.

88 In this study, we focused on the prey consumption, growth and survival of Japanese
89 chum salmon, and developed a method that quantitatively estimates the supporting
90 services for the growth of Japanese chum salmon using a bioenergetics model coupled
91 with a lower trophic level ecosystem model (NEMURO: North Pacific Ecosystem Model
92 for Understanding Regional Oceanography; Kishi et al., 2007). We estimated the prey
93 biomass consumed by a cohort of Japanese chum salmon, defined as a group of Japanese
94 chum salmon released in a single year. The phytoplankton biomass indirectly consumed
95 by this cohort was also estimated; this was considered to be the primary production
96 supporting the fish. We also attempted to calculate the monetary value of supporting
97 services for the growth of Japanese chum salmon.

98

99

100 **2. Methods**

101 ***2.1. Migration of Japanese chum salmon***

102 It was assumed that 1.8×10^9 Japanese chum salmon fry (corresponding to the
103 average number of artificially released salmon in the period 2001–2015;
104 http://salmon.fra.affrc.go.jp/zousyoku/ok_relret.html) were released in Japan on March 1
105 (Fig. 2). In our analysis, we adopted the 4-box lower trophic level ecosystem model
106 NEMURO (Kishi et al., 2007) to represent the migration habitats of Japanese chum

107 salmon. The boxes were as follows: the Sea of Okhotsk (Stage 1), the western North
108 Pacific (Stage 2), the Bering Sea (Stages 3, 5, 7 and 9) and the Gulf of Alaska (Stages 4,
109 6 and 8), according to Urawa (2000). In our study, the Sea of Okhotsk, which was not
110 included in Kamezawa et al. (2007) or Kishi et al. (2010), was considered a part of the
111 migration route. Japanese chum salmon are supposed to instantly migrate from one box
112 to another as they moved from one migration stage to the next (Fig. 1). We simulated the
113 growth of Japanese chum salmon until the end of Stage 9, immediately before the return
114 to Japan, because the salmon stop feeding during their homing migration (e.g. Tanaka et
115 al., 2000). The number of fish was assumed to decrease according to the survival function
116 proposed by Kishi et al. (2012) (Fig. 2). By coupling a bioenergetics model with the
117 NEMURO model (see 2.2 below) we were able to estimate the prey biomass consumed
118 by individual salmon. We also calculated the prey biomass consumed by a cohort of
119 salmon as the product of the estimated prey biomass consumed per individual and the
120 number of fish (Fig. 2). It is important to note that the prey biomass consumed by a cohort
121 in this study includes the prey biomass consumed by fish that died before the end of stage
122 9.

123

124 **2.2. Bioenergetics model**

125 The bioenergetics model used in this study was developed from the works of
126 Rudstam (1988), Ware (1978), Beauchamp et al. (1989) and Trudel et al. (2004), with
127 later modifications by Kamezawa et al. (2007) and Kishi et al. (2010). The growth of
128 individual Japanese chum salmon was represented by the following expression:

129

130

131
$$\frac{dW}{dt} = [C - (R + SDA + F + E)] \cdot \frac{CAL_z}{CAL_f} \cdot W \quad (1)$$

132

133

134 where W is the wet weight of a fish (g wet weight; g fish) and C represents consumption
 135 (g prey g fish⁻¹ d⁻¹). C is determined by temperature, prey density and the wet weight of
 136 the fish. R represents respiration or losses through metabolism (g prey g fish⁻¹ d⁻¹), SDA
 137 represents the specific dynamic action or losses due to the energetic costs of digesting
 138 food (g prey g fish⁻¹ d⁻¹), F is egestion or losses in feces (g prey g fish⁻¹ d⁻¹), E represents
 139 the excretion or losses of nitrogenous excretory wastes (g prey g fish⁻¹ d⁻¹); and CAL_z
 140 and CAL_f are the caloric equivalents of prey (i.e. zooplankton) (cal g prey⁻¹) and fish (cal
 141 g fish⁻¹), respectively.

142 The growth of Japanese chum salmon is determined primarily by the
 143 consumption rate (C). C is estimated as the proportion of the maximum daily ration of
 144 Pacific salmon at a particular mass and temperature (Beauchamp et al., 1989; Megrey et
 145 al., 2002; Ito et al. 2004):

146

147
$$C = C_{MAX} \cdot \rho \cdot f_c(T) \quad (2)$$

148
$$C_{MAX} = ac \cdot W^{bc} \quad (3)$$

149
$$\rho = \frac{\frac{PD \cdot V_i}{K_i}}{1 + \frac{PD \cdot V_i}{K_i}} \quad (4)$$

150

151 where C_{MAX} is the maximum consumption rate (g prey g fish⁻¹ d⁻¹), ρ (dimensionless) is
 152 the consumption rate without temperature effects (prey dependence function for
 153 consumption), $f_c(T)$ (dimensionless) is a temperature dependence function for

154 consumption that was formulated by Thornton and Lesserm (1978), T is water
155 temperature ($^{\circ}\text{C}$), a_c is the intercept of the mass dependence function for 1.0 g wet weight
156 at the optimum water temperature (set to a constant: 0.303), and b_c is the coefficient of
157 the mass dependence (set to a constant: -0.275) (Beauchamp et al. 1989), PD is the
158 density of prey (g wet weight m^{-3} or g prey m^{-3}), V_i is the vulnerability at stage i
159 (dimensionless), which was set to a constant (1.0), and K_i is the half-saturation constant
160 (g prey m^{-3}), which was set to 0.15 (Kamezawa et al., 2007; Kishi et al., 2010). Both ρ
161 and $f_c(T)$ range from 0 to 1; high values are indicative of better prey and temperature
162 conditions.

163 The formulations for the individual processes followed those used by Kamezawa et al.
164 (2007) and Kishi et al. (2010). The $f_c(T)$ in the Sea of Okhotsk, which we added to the
165 migration route, was set to be equal to that in the Bering Sea in Kamezawa et al. (2007)
166 and Kishi et al. (2010). The seasonal variation in the temperature input to the
167 bioenergetics model is shown in Fig. 3a; the values approximate monthly climatological
168 sea surface temperatures: World Ocean Atlas (2009) (Locarnini et al., 2009) over each
169 migration area (Fig. 1).

170

171 ***2.3. North Pacific Ecosystem Model for Understanding Regional Oceanography*** 172 ***(NEMURO)***

173 The prey density input to our bioenergetics model was estimated by NEMURO
174 (Kishi et al., 2007). The NEMURO model has three categories of zooplankton: small
175 zooplankton (ZS), large zooplankton (ZL) and predatory zooplankton (ZP) (Kishi et al.,
176 2007). Previous studies have assumed that modeled chum salmon prey upon ZP
177 (Kamezawa et al., 2007; Kishi et al., 2010; Yoon et al., 2015; Ueno et al., 2016) because

178 the fish have high prey diversity across a range of zooplankton, e.g. *Themisto* spp.,
 179 pteropods and gelatinous zooplankton (Tadokoro et al., 1996; Kaeriyama et al., 2004; Qin
 180 and Kaeriyama, 2016), and we incorporated this assumption. ZP, a top predator in the
 181 NEMURO model, includes all carnivorous zooplankton (i.e. gelatinous zooplankton,
 182 euphausiids and other large carnivorous species); these were not further resolved in the
 183 model.

184 The NEMURO model describes zooplankton density as the nitrogen concentration
 185 ($\mu\text{mol N L}^{-1}$), and we converted this into wet weight ($\text{g wet weight m}^{-3}$) with the following
 186 multiplicative expression (Megrey et al., 2002):

$$187 \frac{14 \mu\text{g N}}{1 \mu\text{mole N}} \cdot \frac{10^{-6} \text{ g}}{1 \mu\text{g}} \cdot \frac{1 \text{ g } dw}{0.07 \text{ g N } dw} \cdot \frac{1 \text{ g } W}{0.2 \text{ g } dw} \cdot \frac{10^3 \text{ L}}{1 \text{ m}^3} \quad (5)$$

189 where dw is dry weight, and W is wet weight.
 190

191 In contrast to previous studies (Kamezawa et al., 2007; Kishi et al., 2010; Yoon et
 192 al., 2015), the NEMURO model used in the present study considered the reduction in ZP
 193 consumed by salmon released in a single year. To input the consumption by salmon, the
 194 salmon were assumed to be in the 0–20 m depth layer, and the areas of the Sea of Okhotsk,
 195 western North Pacific, Bering Sea and Gulf of Alaska were 1.1×10^{12} , 1.2×10^{12} , $1.9 \times$
 196 10^{12} and $3.9 \times 10^{12} \text{ m}^2$, respectively.

197 The seasonal variation in the temperature input in the NEMURO model was the
 198 same as that in the bioenergetics model (Fig. 3a). The seasonal variation in light intensity
 199 input in the NEMURO model (Fig. 3b) indicated the daily downward solar radiation flux
 200 (NCEP/NCAR Reanalysis 1; Kalnay et al., 1996) from 2001 to 2015 at 50°N , 150°E (Sea

201 of Okhotsk); 50°N, 165°E (western North Pacific); 55°N, 175°W (Bering Sea); and 50°N,
 202 145°W (Gulf of Alaska), assuming the albedo of water is 11% (Talley et al., 2011).

203

204 ***2.4. Estimating primary production that supports Japanese chum salmon***

205 The primary production that supports Japanese chum salmon was estimated from
 206 the small and large phytoplankton (PS and PL, respectively) that were directly or
 207 indirectly consumed by ZP, which were consumed by Japanese chum salmon through
 208 five pathways in the NEMURO, as shown in Fig. 4. Path (1) is from PL directly to ZP,
 209 path (2) is from PL to ZP via ZL, path (3) is from PS to ZP via ZL, path (4) is from PS to
 210 ZP via ZS and ZL, path (5) is from PL to ZP via ZS. For each transfer pathway, the
 211 primary production consumed by Japanese chum salmon was described by the following
 212 expressions:

213

$$214 \quad PP_1 = \frac{\alpha_{ZP} \cdot raZP2Salmon}{P/Q(ZP)} \quad (6)$$

$$215 \quad PP_2 = \frac{\alpha_{ZL} \cdot \beta_{ZP} \cdot raZP2Salmon}{P/Q(ZP) \cdot P/Q(ZL)} \quad (7)$$

$$216 \quad PP_3 = \frac{\beta_{ZL} \cdot \beta_{ZP} \cdot raZP2Salmon}{P/Q(ZP) \cdot P/Q(ZL)} \quad (8)$$

$$217 \quad PP_4 = \frac{\gamma_{ZL} \cdot \beta_{ZP} \cdot raZP2Salmon}{P/Q(ZP) \cdot P/Q(ZL) \cdot P/Q(ZS)} \quad (9)$$

$$218 \quad PP_5 = \frac{\gamma_{ZP} \cdot raZP2Salmon}{P/Q(ZP) \cdot P/Q(ZS)} \quad (10)$$

219

220 where PP_1 , PP_2 , PP_3 , PP_4 and PP_5 are the primary production (g wet weight) consumed
 221 by Japanese chum salmon through transfer pathways 1, 2, 3, 4 and 5, respectively.

222 $GraZP2Salmon$ represents the ZP consumed by Japanese chum salmon (g wet weight).

223 α_{ZP} , β_{ZP} and γ_{ZP} indicate the ratios of prey (PL, ZL and ZS, respectively) consumed by
224 ZP, and α_{ZL} , β_{ZL} and γ_{ZL} indicate the ratios of prey (PL, PS and ZS, respectively) consumed
225 by ZL (see Appendix A for the respective formulations). Averaged values of these ratios
226 in each stage were used to estimate the primary production consumed by Japanese chum
227 salmon. P/Q (ZP), P/Q (ZL) and P/Q (ZS) are the transfer efficiencies for ZP, ZL
228 and ZS (see Appendix A for the formulations).

229 The dimensions of PP_1 to PP_5 calculated with equations (6) through (10) were
230 identical to that of *GraZP2Salmon*, i.e. g wet weight. We converted this dimension to kg
231 C using conversion ratio (5), assuming that the Redfield ratio was applicable.

232

233 ***2.5. Estimating primary production in each migration area using satellite data***

234 Total primary production in each migration area was evaluated using satellite-
235 derived monthly primary production data together with a carbon-based primary
236 production model (Westberry et al., 2008, <http://www.science.oregonstate.edu/ocean.productivity/index.php>), to estimate the ratio
237 of primary production supporting Japanese chum salmon to the total primary production
238 in each migration area. First, we prepared monthly maps of primary production averaged
239 over the period 2012–2017. Using the averaged values, we next calculated the primary
240 production in each migration area (the Sea of Okhotsk, the western North Pacific, the
241 Bering Sea and the Gulf of Alaska) through the integration of primary production in each
242 region and the migration period. In this estimation, the western North Pacific and the Gulf
243 of Alaska were designated as the areas spanning 157°E–178°E and 45°N–52°N, and north
244 of 45°N and east of 170°W, respectively.

246

247

248 3. Results

249 Figure 5a depicts the time series of Japanese chum salmon body weights simulated
250 by the coupling of the bioenergetics and NEMURO models. The individual body mass
251 increased gradually up to *ca.* 3800 g wet weight by the end of Stage 9 (Bering Sea). The
252 weight increase trend was steeper in the Bering Sea than in the Gulf of Alaska, in
253 accordance with previous studies showing that the Bering Sea is the main feeding ground
254 for Japanese chum salmon (e.g. Urawa, 2000). Multiplying the body wet weight (Fig. 5a)
255 by the number of Japanese chum salmon (Fig. 2), we obtained a time series for the fish
256 biomass (Fig. 5b). The biomass gradually increased to *ca.* 2×10^8 kg wet weight through
257 the end of Stage 9.

258 $f_c(T)$ (the temperature dependence function for consumption) was generally 1.0
259 during migration (Fig. 5c), indicating that temperature barely affected prey consumption
260 by Japanese chum salmon in our model configuration. Low $f_c(T)$ values occurred near the
261 time of transfer between areas due to the low temperatures in the Sea of Okhotsk and the
262 Bering Sea. Low $f_c(T)$ values in the middle of Stage 1 were due to high temperatures
263 exceeding 10°C in the Sea of Okhotsk from August to September. ρ (the prey dependence
264 function for consumption) was generally between 0.7 and 0.8, and higher in the Bering
265 Sea than in the Gulf of Alaska, which led to faster growth in the Bering Sea (Fig. 5a).

266 Figure 6a depicts a time series of ZP wet weight consumed by individual Japanese
267 chum salmon per hour. Consumption gradually increased up to *ca.* 4 g wet weight h^{-1} as
268 the body weight of salmon increased through the end of Stage 9, except when (i) $f_c(T)$
269 was low near to the time of area-transfer (Fig. 5c), or (ii) ρ was low in the midpoints of
270 stages 6–9 (Fig. 5d). The time series of ZP wet weight consumed by a cohort of Japanese

271 chum salmon per hour is presented in Fig. 6b (Fig. 6a was multiplied by Fig. 2 to give the
272 plot in Fig 6b). The value also increased gradually up to *ca.* 2×10^5 kg wet weight h^{-1} ,
273 except when $f_c(T)$ and ρ were low.

274 We next integrated the values in Fig. 6a for each migration area, as shown in Table
275 1. Individual Japanese chum salmon consumed 0.8, 2.8, 45.8 and 35.3 kg wet weight of
276 prey in the Sea of Okhotsk, the western North Pacific, the Bering Sea and the Gulf of
277 Alaska, respectively, i.e. 84.7 kg wet weight in total. Thus, individual Japanese chum
278 salmon surviving through the end of Stage 9 consumed more than 20 times their body
279 weight throughout their life spans immediately prior to their return to Japan, when they
280 weighed 3.8 kg. More than half of total prey was consumed in the Bering Sea.

281 A cohort of Japanese chum salmon consumed 1.5×10^8 , 3.2×10^8 , 28.4×10^8 and
282 21.8×10^8 kg prey wet weight in the Sea of Okhotsk, the western North Pacific, the Bering
283 Sea and the Gulf of Alaska, respectively, for a total of 55.0×10^8 kg wet weight (Table
284 1). The numbers of salmon decreased over time (Fig. 2); hence, there was a mismatch in
285 consumption among regions between the calculations based on individual fish and those
286 based on the cohort. We calculated the primary production indirectly consumed by the
287 cohort Japanese chum salmon: 0.8×10^8 kg C, 1.3×10^8 kg C, 15.0×10^8 kg C and $8.5 \times$
288 10^8 kg C in the Sea of Okhotsk, the western North Pacific, the Bering Sea and the Gulf
289 of Alaska, respectively, for a total of 25.6×10^8 kg C.

290 Finally, we compared the primary production supporting the cohort Japanese chum
291 salmon with the integrated primary production in each migration area and period from
292 satellite data. The integrated values from satellite data were 1.2×10^{11} kg C, 0.2×10^{11}
293 kg C, 6.4×10^{11} kg C and 3.7×10^{11} kg C in the Sea of Okhotsk, the western North Pacific,
294 the Bering Sea and the Gulf of Alaska, respectively, for a total 11.4×10^{11} kg carbon.

295 Thus, Japanese chum salmon were supported by 0.06%, 0.55%, 0.22% and 0.23% of the
296 integrated primary production in the Sea of Okhotsk, the western North Pacific, the
297 Bering Sea and the Gulf of Alaska, respectively, and by 0.21% across all regions.

298

299

300 **4. Discussion**

301 Our model estimates showed that a cohort of Japanese chum salmon consumed in
302 total *ca.* 5.5×10^9 kg wet weight of zooplankton during Stages 1–9, and that the cohort
303 indirectly consumed 2.6×10^9 kg C of primary production, which amounted to 0.21% of
304 primary production in the areas and periods through which the salmon migrated. Thus, a
305 cohort of artificially released Japanese chum salmon was supported by 2.6×10^9 kg C of
306 primary production during Stages 1–9. This is the production that supports the human
307 harvest of a cohort. Although we applied the model similarly to previous studies
308 examining the impact of environmental variability on the growth of Japanese chum
309 salmon, including prediction of future scenarios (Kamezawa et al., 2007; Kishi et al.,
310 2010; Yoon et al., 2015), this is the first attempt to estimate the supporting services for
311 these fish.

312 The values estimated in our model were almost the same as those estimated
313 without considering the reduction in ZP by salmon consumption in the NEMURO model.
314 For example, the difference was less than 0.01×10^9 kg (~0.2% of estimated values) for
315 the wet weight of zooplankton consumed by a cohort of Japanese chum salmon. This is
316 consistent with Starovoytov (2007), who reported that the influence of chum salmon on
317 the forage resources in the Bering Sea ecosystem was insignificant, because the chum

318 salmon biomass and consumption of plankton were much smaller than those of Walleye
319 pollock (*Theragra chalcogramma*) based on ship survey data.

320 The wet weight of Japanese chum salmon in our model (indicated by the line in
321 Fig. 5a) was compared with that from ship survey data from summer 2003 (indicated by
322 the dots in Fig. 5a from Urawa et al. 2009). This comparison indicated that our model
323 accurately reproduced the wet weight of salmon at Stage 7, but overestimated the weight
324 at Stages 3 and 5. This suggests that the wet weight of ZP consumed by a salmon cohort
325 (5.5×10^9 kg) and the primary production supporting a cohort (2.6×10^9 kg C) during
326 Stages 1–9 were also overestimated. When the ZP consumption during Stages 1–5 was
327 set to be half of the values in Table 1, considering the observed salmon weight, the total
328 ZP consumption and primary production decreased by 20% to 4.4×10^9 kg and 2.0×10^9
329 kg C, respectively.

330 Starovoytov (2007) indicated that chum salmon in the western Bering Sea
331 consumed 4.2×10^8 and 18.3×10^8 kg wet weight of prey during summer 1995 and 2003,
332 respectively, based on ship survey data. These values are similar to the 28.4×10^8 kg wet
333 weight of ZP consumed by a Japanese salmon cohort in the Bering Sea (Stages 3, 5, 7 and
334 9) yielded in our model (Table 1). Since our estimation included the entire Bering Sea
335 and was limited to Japanese chum salmon, it is difficult to compare the two values.
336 However, the similarity suggests that our model estimates are not so far from the estimates
337 based on survey data.

338 Miyakoshi et al. (2013) reported the age composition of Japanese chum salmon in
339 Hokkaido (northern Japan) from 1983 to 2006. They observed that age-4 (Stage 7 in our
340 model) was the dominant age among Hokkaido chum salmon. The age composition
341 changed interannually, with the percentage of fish returning to Japan at Stages 5 and 7

342 varying from 50% to 75%. Considering this interannual variation, that is, assuming that
343 only 25%–50% of salmon reached Stages 8 and 9 in our model, the total ZP consumption
344 and primary production were estimated to be $4.2\text{--}4.7 \times 10^9$ kg and $2.0\text{--}2.2 \times 10^9$ kg C,
345 respectively, and Japanese chum salmon were estimated to be supported by 0.17%–0.19%
346 of the integrated primary production across all regions.

347 Several attempts have been made to estimate the value of supporting services
348 provided by ecosystems, e.g. the revealed preference and stated preference approaches.
349 However, these methods have some important limitations (TEEB, 2010). The method that
350 we developed in this study (coupling bioenergetics and lower trophic level ecosystems
351 models) enabled estimation of the supporting services for the growth and survival of
352 artificially released fish, i.e. the amount of prey and the primary production directly and
353 indirectly consumed through the life stages of a cohort. Thus, we were able to determine
354 the ecological footprint of the cohort in the ecosystems through which it migrated. This
355 approach is different from previous assessments of the ecosystem impacts of fisheries.
356 Earlier approaches focused on the effects of fishing on marine ecosystems.

357 It is possible to extend our new approach to briefly consider the monetary value
358 of supporting services for the growth of Japanese chum salmon. As an example, we
359 calculated the monetary value of ZP consumed by Japanese chum salmon assuming that
360 the monetary value of ZP is equivalent to that of krill. Krill is an important component of
361 ZP in NEMURO (Kishi et al., 2007), and it is also traded in the Japanese commercial
362 market. We used the average price in the Tokyo Metropolitan Central Wholesale Market
363 for the period 2002–2018 (<http://www.shijou-tokei.metro.tokyo.jp/index.html>), i.e. 476
364 Japanese yen kg^{-1} wet weight. Using the market price of krill, the total value of ZP
365 consumed by Japanese chum salmon was estimated to be $2.0\text{--}2.2 \times 10^{12}$ Japanese yen

366 (0.1 × 10¹², 0.2 × 10¹², 1.0–1.1 × 10¹² and 0.7–0.8 × 10¹² Japanese yen in the Sea of
367 Okhotsk, the western North Pacific, the Bering Sea and the Gulf of Alaska, respectively).
368 These values were estimated considering the interannual variation in age composition (i.e.
369 the percentage of fish returning to Japan at Stages 5 and 7 varied from 50% to 75%). The
370 sum total (18–20 × 10⁹ US dollars based on the exchange rate in 2018) far exceeds the
371 value of the Japanese chum salmon harvest (0.06 × 10¹² Japanese yen or 0.5 × 10⁹ US
372 dollars averaged over the period 2001–2017). Thus, the harvest of *ca.* 0.06 × 10¹²
373 Japanese yen was supported by a shadow cost (prey) of up to 2.0–2.2 × 10¹² Japanese yen.

374 It is important to note that the example discussed in the previous paragraph is
375 based on very simple assumptions, and many issues remain to be solved. For example,
376 krill is not the main prey of chum salmon (Qin and Kaeriyama, 2016), and the market
377 prices of salmon and krill include the cost of harvesting, processing and transportation.
378 Although a detailed evaluation of the monetary value is beyond our scope, we have
379 nevertheless developed a novel approach for the quantitative estimation of ecosystem
380 services that support seafood production. The evaluation framework developed in this
381 study could be combined with future models to help predict the change in ecosystem
382 services under global climate change and other environmental shifts, including changes
383 in migration route/season/period and prey composition.

384

385

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396

397 **Appendix A: Estimating the primary production supporting Japanese chum salmon**

398 Estimates were based on phytoplankton (PS and PL) directly or indirectly
 399 consumed by ZP, which were in turn consumed by Japanese chum salmon through the
 400 five pathways shown in Fig. 4 using expressions (6) to (10). The symbols used in (6) to
 401 (10), i.e. α_{ZP} , β_{ZP} , γ_{ZP} (the ratios of prey [PL, ZL and ZS, respectively] consumed by ZP),
 402 α_{ZL} , β_{ZL} and γ_{ZL} (the ratios of prey [PL, PS and ZS, respectively] consumed by ZL) and
 403 P/Q (ZP), P/Q (ZL) and P/Q (ZS) (transfer efficiencies for ZP, ZL and ZS,
 404 respectively) were written as follows:

405

$$406 \quad \alpha_{ZL} = \frac{GraPL2ZL}{GraPL2ZL + GraPS2ZL + GraZS2ZL} \quad (A1)$$

$$407 \quad \beta_{ZL} = \frac{GraPS2ZL}{GraPL2ZL + GraPS2ZL + GraZS2ZL} \quad (A2)$$

$$408 \quad \gamma_{ZL} = \frac{GraZS2ZL}{GraPL2ZL + GraPS2ZL + GraZS2ZL} \quad (A3)$$

$$409 \quad \alpha_{ZP} = \frac{GraPL2ZP}{GraPL2ZP + GraZL2ZP + GraZS2ZP} \quad (A4)$$

$$410 \quad \beta_{ZP} = \frac{GraZL2ZP}{GraPL2ZP + GraZL2ZP + GraZS2ZP} \quad (A5)$$

$$411 \quad \gamma_{ZP} = \frac{GraZS2ZP}{GraPL2ZP + GraZL2ZP + GraZS2ZP} \quad (A6)$$

412

413 $P/Q (ZP)$

414
$$= \frac{GraPL2ZP + GraZL2ZP + GraZS2ZP - (EgeZP + ExcZP)}{GraPL2ZP + GraZL2ZP + GraZS2ZP} \quad (A7)$$

415
$$P/Q (ZL) = \frac{GraPL2ZL + GraPS2ZL + GraZS2ZL - (EgeZL + ExcZL)}{GraPL2ZL + GraPS2ZL + GraZS2ZL} \quad (A8)$$

416
$$P/Q (ZS) = \frac{GraPS2ZS - (EgeZS + ExcZS)}{GraPS2ZS} \quad (A9)$$

417

418 where *GraPL2ZL*, *GraPS2ZL* and *GraZS2ZL* represent the grazing rates of PL by ZL, PS
419 by ZL, and ZL by ZL (g wet weight day⁻¹), respectively, and *GraPL2ZP*, *GraZL2ZP* and
420 *GraZS2ZP* represent the grazing rates of PL by ZP, ZL by ZP, and ZS by ZP (g wet weight
421 day⁻¹), respectively. *EgeZP*, *EgeZL* and *EgeZS* are the egestion rates of ZP, ZL and ZS (g
422 wet weight day⁻¹), respectively, and *ExcZP*, *ExcZL* and *ExcZS* are the extracellular
423 excretion rates of ZP, ZL and ZS (g wet weight day⁻¹), respectively. These formulations
424 are based on the work of Kishi et al. (2007).

425

426

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- 564

565 **Table Captions**

566 Table 1. Wet weights of predatory zooplankton (ZP) consumed by (i) individual salmon
567 and (ii) a salmon cohort in each geographical region and life stage.

568

569 **Figure Captions**

570 Fig. 1. Japanese chum salmon migration path, duration of stay en route and life stages.

571 Y1, Y2, Y3, Y4 and Y5 indicate Years 1, 2, 3, 4 and 5, respectively.

572 Fig. 2. (a) Number of Japanese chum salmon over time following the release of $1.8 \times$

573 10^9 fry and (b) the daily survival rate of Japanese chum salmon (day^{-1}). OH, Sea of

574 Okhotsk; WNP, western North Pacific; BS, Bering Sea; GA, Gulf of Alaska.

575 Fig. 3. Seasonal variation in (a) sea surface temperature ($^{\circ}\text{C}$) and (b) light intensity (ly

576 min^{-1}) in the Sea of Okhotsk (OH), western North Pacific (WNP), Bering Sea (BS) and

577 the Gulf of Alaska (GA) that were input to the bioenergetics model and NEMURO

578 (North Pacific Ecosystem Model for Understanding Regional Oceanography).

579 Fig. 4. Diagram of the NEMURO model showing transfer paths of organic matter from

580 PL (large phytoplankton) and PS (small phytoplankton) to ZP (predatory zooplankton).

581 Arrow (1) indicates a direct path from PL to ZP, arrow (2) is a pathway from PL to ZP

582 via ZL, arrow (3) is a pathway from PS to ZP via ZL, arrow (4) is a pathway from PS to

583 ZP via ZS and ZL, and arrow (5) is a pathway from PL to ZP via ZS. α_{ZP} , β_{ZP} , γ_{ZP} and

584 α_{ZL} , β_{ZL} , γ_{ZL} are the ratios of prey consumed by ZP and ZL, respectively.

585 Fig. 5. Time series of (a) simulated body weights of Japanese chum salmon (g wet
586 weight), (b) biomass in the ocean (10^8 kg wet weight), (c) $f_c(T)$ (temperature
587 dependence function for consumption), and (d) ρ (prey dependence function for
588 consumption).

589 Fig. 6. Time series of ZP wet weights consumed by (a) individual Japanese chum
590 salmon per hour (g h^{-1}) and (b) a cohort of Japanese chum salmon per hour (10^3 kg h^{-1}).

Table 1. Wet weights of predatory zooplankton (ZP) consumed by (i) individual salmon and (ii) a salmon cohort in each geographical region and stage.

Region	Stage	Wet weight of ZP consumed by individual salmon (kg)	Wet weight of ZP consumed by a salmon cohort (10 ⁸ kg)
Sea of Okhotsk (OH)	1	0.8	1.5
Western North Pacific (WNP)	2	2.8	3.2
Bering Sea (BS)	3	5.5	4.9
	5	10.5	7.0
	7	13.9	8.0
	9	15.9	8.5
	Total	45.8	28.4
Gulf of Alaska (GA)	4	8.1	6.1
	6	12.3	7.6
	8	14.9	8.2
	Total	35.3	21.8
Total		84.7	55.0

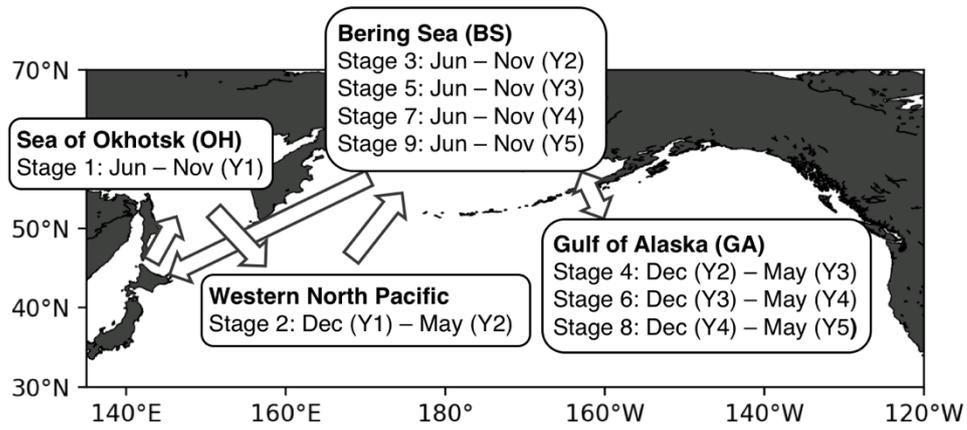


Fig. 1. Japanese chum salmon migration path, duration of stay en route, and life stages.

Y1, Y2, Y3, Y4 and Y5 indicate Years 1, 2, 3, 4 and 5, respectively.

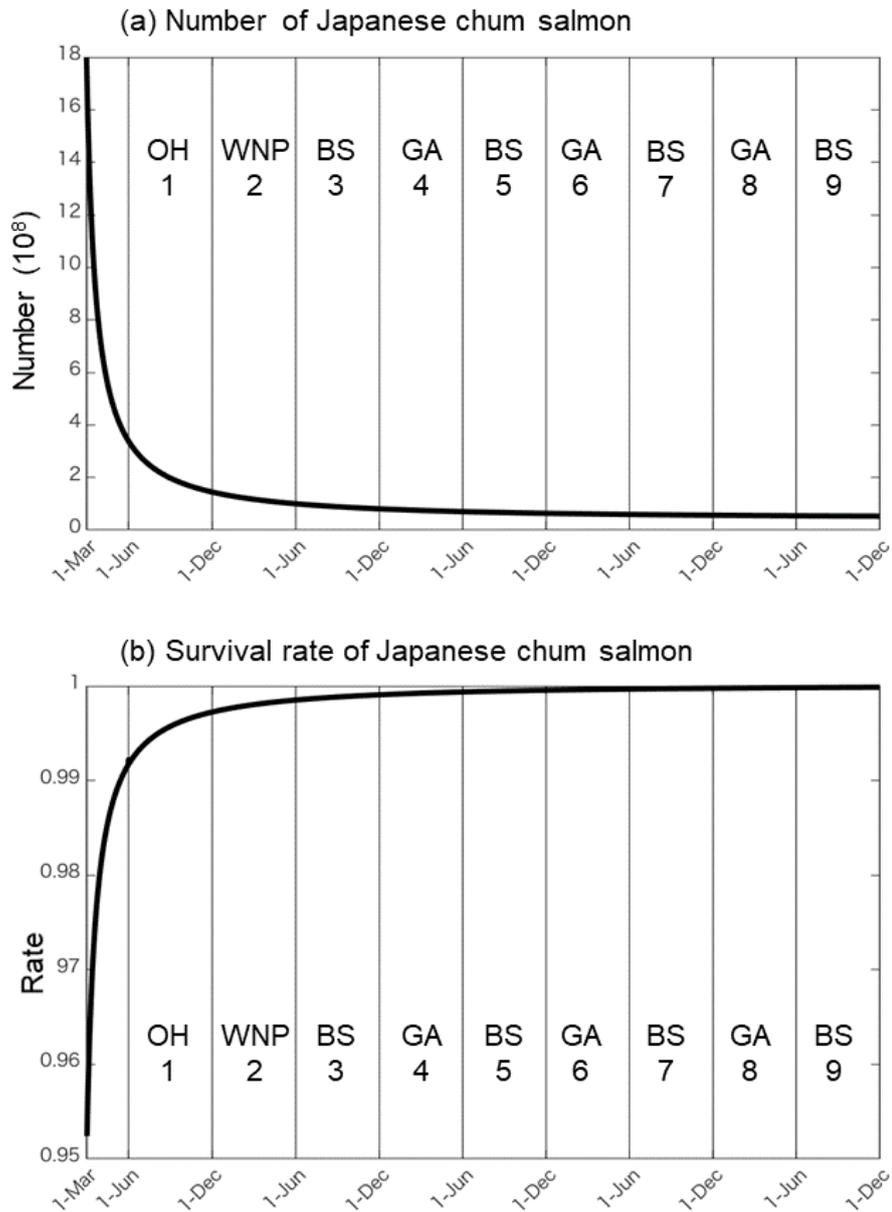


Fig. 2. (a) Number of Japanese chum salmon over time following the release of 1.8×10^9 fry and (b) the daily survival rate of Japanese chum salmon (day^{-1}). OH, Sea of Okhotsk; WNP, western North Pacific; BS, Bering Sea; GA, Gulf of Alaska.

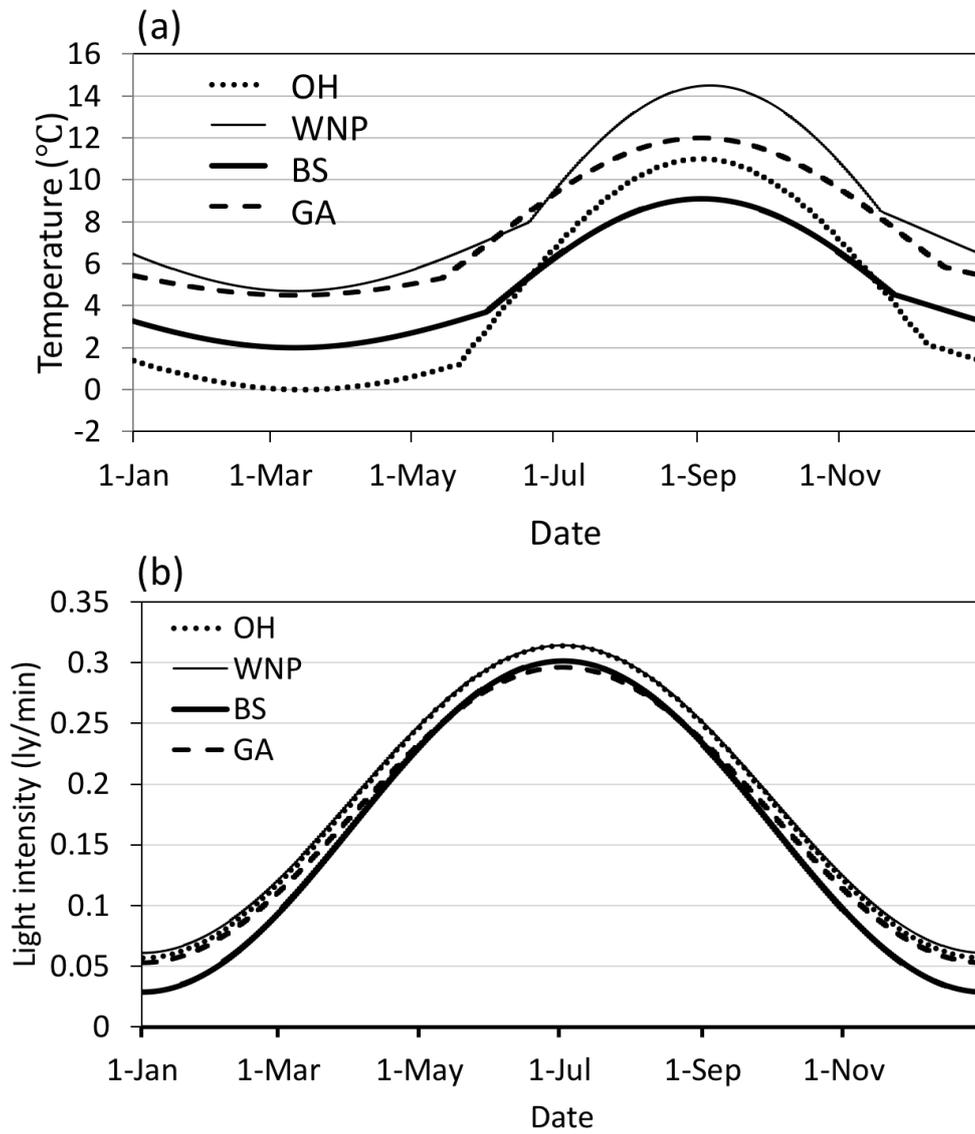


Fig. 3. Seasonal variation in (a) sea surface temperature ($^{\circ}\text{C}$) and (b) light intensity (ly min^{-1}) in the Sea of Okhotsk (OH), western North Pacific (WNP), Bering Sea (BS) and the Gulf of Alaska (GA) that were input to the bioenergetics model and NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography).

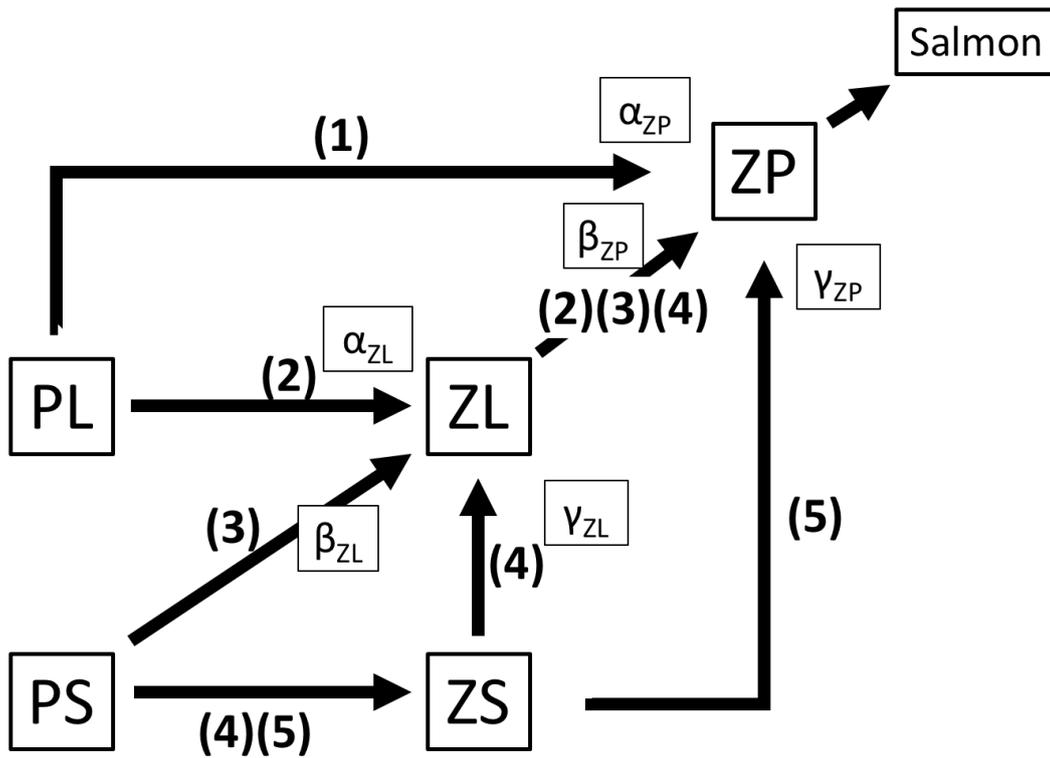


Fig. 4. Diagram of the NEMURO model showing transfer paths of organic matter from PL (large phytoplankton) and PS (small phytoplankton) to ZP (predatory zooplankton). Arrow (1) indicates a direct path from PL to ZP, arrow (2) is a pathway from PL to ZP via ZL, arrow (3) is a pathway from PS to ZP via ZL, arrow (4) is a pathway from PS to ZP via ZS and ZL, and arrow (5) is a pathway from PL to ZP via ZS. α_{ZP} , β_{ZP} , γ_{ZP} and α_{ZL} , β_{ZL} , γ_{ZL} are the ratios of prey consumed by ZP and ZL, respectively.

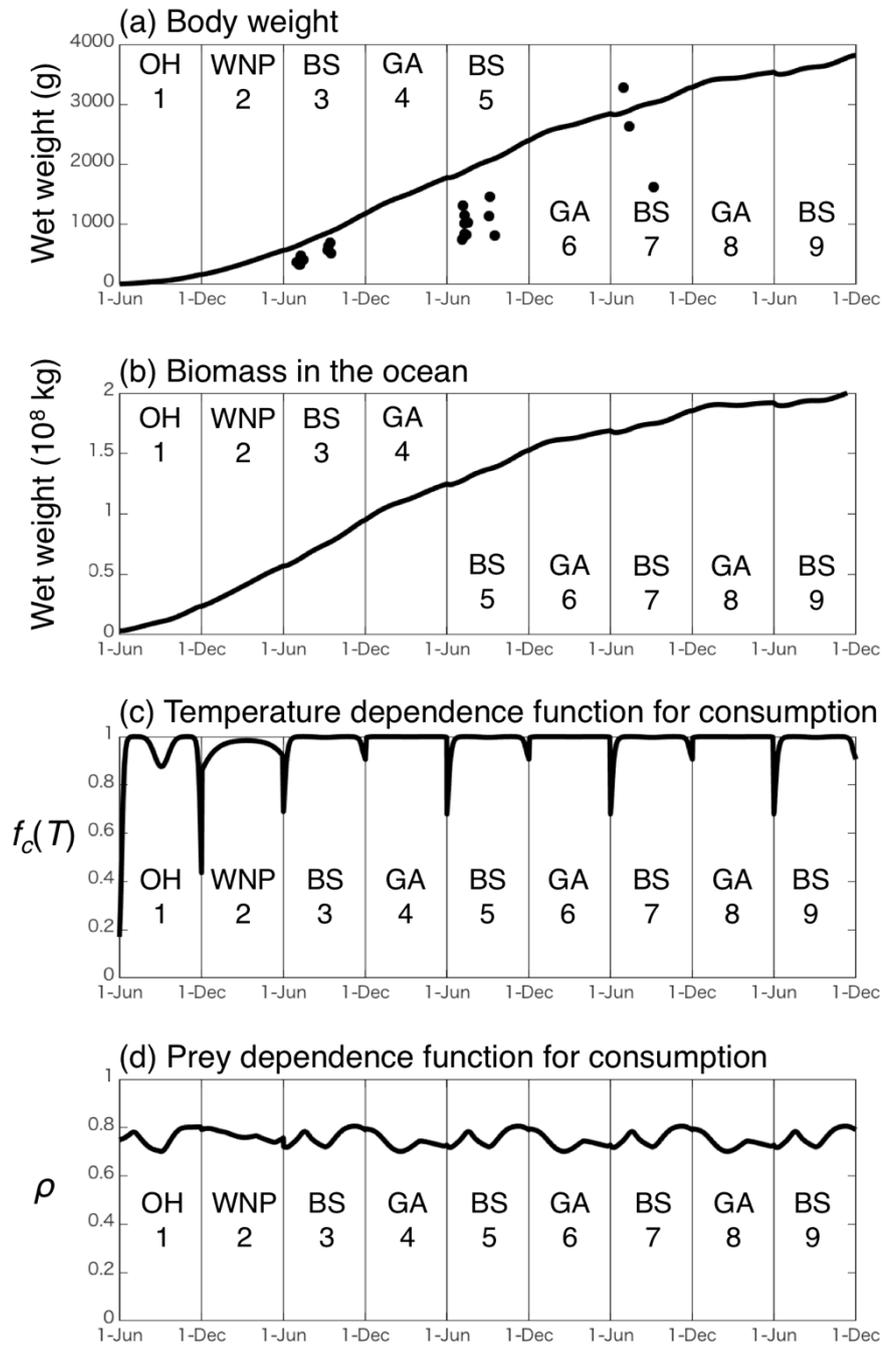


Fig. 5. Time series of (a) simulated body weights of Japanese chum salmon (g wet weight), (b) biomass in the ocean (10⁸ kg wet weight), (c) $f_c(T)$ (temperature dependence function for consumption), and (d) ρ (prey dependence function for consumption).

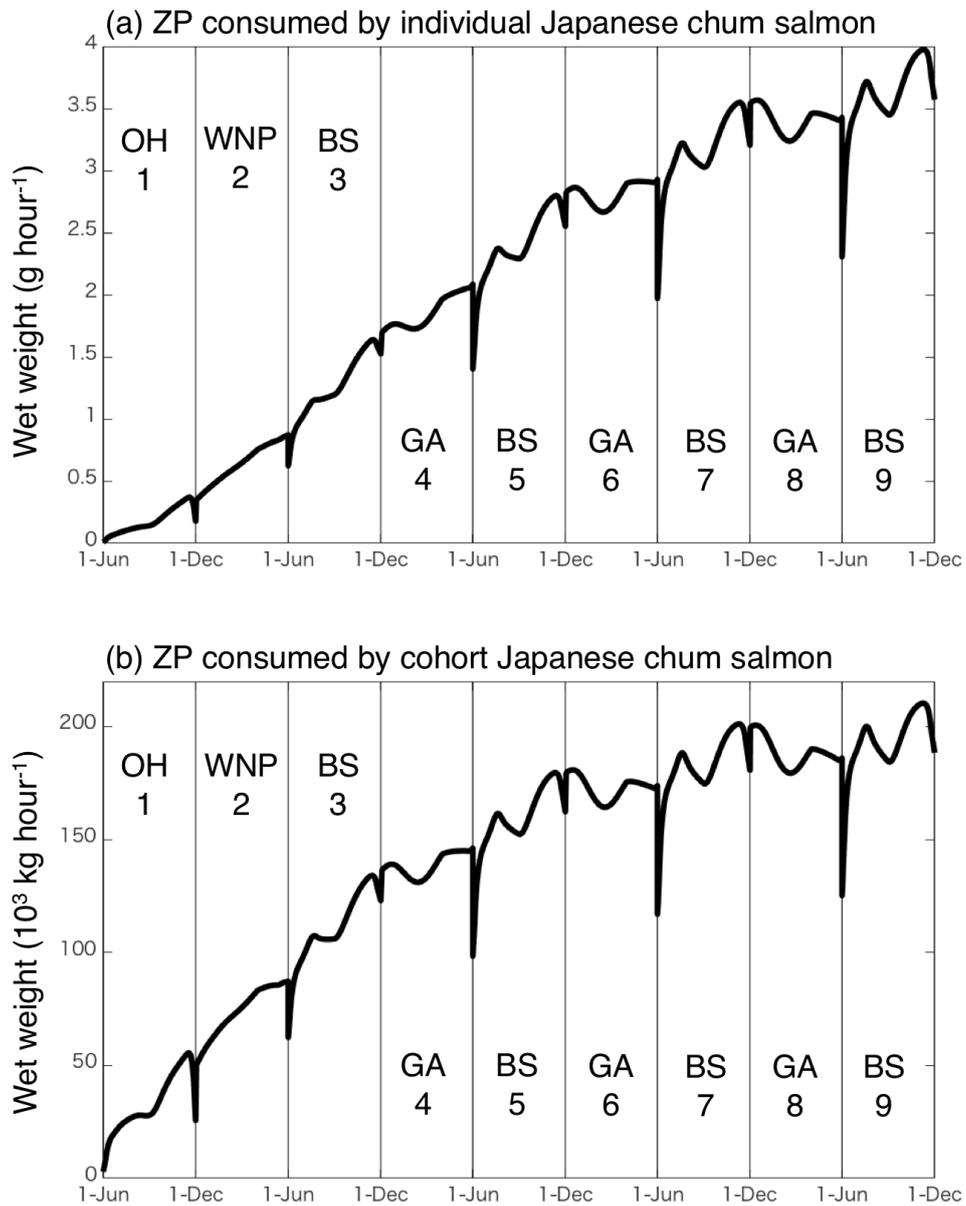


Fig. 6. Time series of ZP wet weights consumed by (a) individual Japanese chum salmon per hour (g h⁻¹) and (b) a cohort of Japanese chum salmon per hour (10³ kg h⁻¹).