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Quantitative estimation of the ecosystem services supporting the growth of Japanese chum salmon

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Abstract

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

Keywords

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

1. Introduction

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

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

Pacific salmon, including the Japanese chum, have played an important role in the lives of people living close to the coasts of the northern North Pacific. These fish reportedly confer three of four categories of the ecosystem services defined by the Millennium Ecosystem Assessment (MEA) (2005) and The Economics of Ecosystems and Biodiversity (TEEB) (2010): provisioning, culture and supporting services for human populations (Bottom et al., 2009). The clearest ecosystem service is provisioning. Pacific salmon are also important as a principal focus of the spiritual and cultural lives of native communities in North America (Bottom et al., 2009), as well as in Hokkaido, Japan (Okada, 2012). Salmon are also a principal food item in the diets of many terrestrial wildlife species (Willson and Halupka, 1995; Merz and Moyle, 2006). They are a source of marine-derived nutrients for coastal lakes and streams (Bilby et al. 1996; Cederholm et al., 1999; Finney et al., 2000), thereby providing additional support services (Bottom et al., 2009).

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

As noted above, Japanese chum populations are maintained by artificial release practices. Hence, the commercial fisheries for this species differ from capture fisheries for other species/populations. In capture fisheries, harvesting reduces the predation pressure on prey organisms and may therefore affect ecosystem structure via trophic cascades (Scheffer et al., 2005). Artificially released chum salmon consume low trophic level resources in each migration area; they return to the rivers from which they were released and are harvested there. Thus, artificially released Japanese chum salmon are likely supported by low trophic level components of the ecosystems in the Sea of Okhotsk, the North Pacific and the Bering Sea. Quantitative estimations of the supporting services for the growth and survival of Japanese chum salmon are required for evaluations of the marine ecosystem impacts of the artificial release and harvesting of this species.

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

2. Methods

2.1. Migration of Japanese chum salmon

It was assumed that 1.8×10^9 Japanese chum salmon fry (corresponding to the average number of artificially released salmon in the period 2001–2015; http://salmon.fra.affrc.go.jp/zousyoku/ok_relret.html) were released in Japan on March 1 (Fig. 2). In our analysis, we adopted the 4-box lower trophic level ecosystem model NEMURO (Kishi et al., 2007) to represent the migration habitats of Japanese chum salmon. The boxes were as follows: the Sea of Okhotsk (Stage 1), the western North Pacific (Stage 2), the Bering Sea (Stages 3, 5, 7 and 9) and the Gulf of Alaska (Stages 4, 6 and 8), according to Urawa (2000). In our study, the Sea of Okhotsk, which was not included in Kamezawa et al. (2007) or Kishi et al. (2010), was considered a part of the migration route. Japanese chum salmon are supposed to instantly migrate from one box to another as they moved from one migration stage to the next (Fig. 1). We simulated the growth of Japanese chum salmon until the end of Stage 9, immediately before the return to Japan, because the salmon stop feeding during their homing migration (e.g. Tanaka et al., 2000). The number of fish was assumed to decrease according to the survival function proposed by Kishi et al. (2012) (Fig. 2). By coupling a bioenergetics model with the NEMURO model (see 2.2 below) we were able to estimate the prey biomass consumed by individual salmon. We also calculated the prey biomass consumed by a cohort of salmon as the product of the estimated prey biomass consumed per individual and the number of fish (Fig. 2). It is important to note that the prey biomass consumed by a cohort in this study includes the prey biomass consumed by fish that died before the end of stage 9.

2.2. Bioenergetics model

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

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

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

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

$$\mathrm{C} = C_{MAX} \cdot \rho \cdot f_c(T) \qquad (2)$$

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

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

where C_{MAX} is the maximum consumption rate (g prey g fish^{-1} d^{-1}), ρ (dimensionless) is the consumption rate without temperature effects (prey dependence function for consumption), $f_c(T)$ (dimensionless) is a temperature dependence function for consumption that was formulated by Thornton and Lesserm (1978), T is water temperature (ºC), ac is the intercept of the mass dependence function for 1.0 g wet weight at the optimum water temperature (set to a constant: 0.303), and bc is the coefficient of the mass dependence (set to a constant: –0.275) (Beauchamp et al. 1989), PD is the density of prey (g wet weight m^{-3} or g prey m^{-3}), V_i is the vulnerability at stage i (dimensionless), which was set to a constant (1.0), and K_i is the half-saturation constant (g prey m^{-3}), which was set to 0.15 (Kamezawa et al., 2007; Kishi et al., 2010). Both ρ and $f_c(T)$ range from 0 to 1; high values are indicative of better prey and temperature conditions.

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

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

The prey density input to our bioenergetics model was estimated by NEMURO (Kishi et al., 2007). The NEMURO model has three categories of zooplankton: small zooplankton (ZS), large zooplankton (ZL) and predatory zooplankton (ZP) (Kishi et al., 2007). Previous studies have assumed that modeled chum salmon prey upon ZP (Kamezawa et al., 2007; Kishi et al., 2010; Yoon et al., 2015; Ueno et al., 2016) because the fish have high prey diversity across a range of zooplankton, e.g. *Themisto* spp., pteropods and gelatinous zooplankton (Tadokoro et al., 1996; Kaeriyama et al., 2004; Qin and Kaeriyama, 2016), and we incorporated this assumption. ZP, a top predator in the NEMURO model, includes all carnivorous zooplankton (i.e. gelatinous zooplankton, euphausiids and other large carnivorous species); these were not further resolved in the model.

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

$$\frac{14\,\mu g\,N}{1\,\mu\,mole\,N}\cdot\frac{10^{-6}\,g}{1\,\mu g}\cdot\frac{1\,g\,dw}{0.07\,g\,N\,dw}\cdot\frac{1\,g\,W}{0.2\,g\,dw}\cdot\frac{10^{3}\,L}{1\,m^{3}} \tag{5}$$

where *dw* is dry weight, and *W* is wet weight.

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

The seasonal variation in the temperature input in the NEMURO model was the same as that in the bioenergetics model (Fig. 3a). The seasonal variation in light intensity input in the NEMURO model (Fig. 3b) indicated the daily downward solar radiation flux (NCEP/NCAR Reanalysis 1; Kalnay et al., 1996) from 2001 to 2015 at 50°N, 150°E (Sea of Okhotsk); 50°N, 165°E (western North Pacific); 55°N, 175°W (Bering Sea); and 50°N, 145°W (Gulf of Alaska), assuming the albedo of water is 11% (Talley et al., 2011).

2.4. Estimating primary production that supports Japanese chum salmon

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

$$PP_1 = \frac{\alpha_{ZP} \cdot \mathrm{raZP2Salmon}}{P/Q\,(ZP)} \tag{6}$$

$$PP_2 = \frac{\alpha_{ZL} \cdot \beta_{ZP} \cdot \mathrm{raZP2Salmon}}{P/Q\,(ZP) \cdot P/Q\,(ZL)} \tag{7}$$

$$PP_3 = \frac{\beta_{ZL} \cdot \beta_{ZP} \cdot \mathrm{raZP2Salmon}}{P/Q\,(ZP) \cdot P/Q\,(ZL)} \tag{8}$$

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

$$PP_5 = \frac{\gamma_{ZP} \cdot \mathrm{raZP2Salmon}}{P/Q\,(ZP) \cdot P/Q\,(ZS)} \tag{10}$$

where PP_1, PP_2, PP_3, PP_4 and PP_5 are the primary production (g wet weight) consumed by Japanese chum salmon through transfer pathways 1, 2, 3, 4 and 5, respectively. *GraZP2Salmon* represents the ZP consumed by Japanese chum salmon (g wet weight).

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

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

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

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

3. Results

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

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

Figure 6a depicts a time series of ZP wet weight consumed by individual Japanese chum salmon per hour. Consumption gradually increased up to *ca*. 4 g wet weight h^{-1} as the body weight of salmon increased through the end of Stage 9, except when (i) $f_c(T)$ was low near to the time of area-transfer (Fig. 5c), or (ii) ρ was low in the midpoints of stages 6–9 (Fig. 5d). The time series of ZP wet weight consumed by a cohort of Japanese chum salmon per hour is presented in Fig. 6b (Fig. 6a was multiplied by Fig. 2 to give the plot in Fig 6b). The value also increased gradually up to *ca.* 2 × 10^5 kg wet weight h^{-1}, except when $f_c(T)$ and ρ were low.

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

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

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

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

4. Discussion

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

The values estimated in our model were almost the same as those estimated without considering the reduction in ZP by salmon consumption in the NEMURO model. For example, the difference was less than 0.01×10^9 kg (~0.2% of estimated values) for the wet weight of zooplankton consumed by a cohort of Japanese chum salmon. This is consistent with Starovoytov (2007), who reported that the influence of chum salmon on the forage resources in the Bering Sea ecosystem was insignificant, because the chum salmon biomass and consumption of plankton were much smaller than those of Walleye pollock (*Theragra chalcogramma*) based on ship survey data.

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

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

Miyakoshi et al. (2013) reported the age composition of Japanese chum salmon in Hokkaido (northern Japan) from 1983 to 2006. They observed that age-4 (Stage 7 in our model) was the dominant age among Hokkaido chum salmon. The age composition changed interannually, with the percentage of fish returning to Japan at Stages 5 and 7 varying from 50% to 75%. Considering this interannual variation, that is, assuming that only 25%–50% of salmon reached Stages 8 and 9 in our model, the total ZP consumption and primary production were estimated to be 4.2–4.7 × 10^9 kg and 2.0–2.2 × 10^9 kg C, respectively, and Japanese chum salmon were estimated to be supported by 0.17%–0.19% of the integrated primary production across all regions.

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

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

(0.1 × 10^{12}, 0.2 × 10^{12}, 1.0–1.1 × 10^{12} and 0.7–0.8 × 10^{12} Japanese yen in the Sea of Okhotsk, the western North Pacific, the Bering Sea and the Gulf of Alaska, respectively). These values were estimated considering the interannual variation in age composition (i.e. the percentage of fish returning to Japan at Stages 5 and 7 varied from 50% to 75%). The sum total (18–20 × 10^9 US dollars based on the exchange rate in 2018) far exceeds the value of the Japanese chum salmon harvest (0.06 × 10^{12} Japanese yen or 0.5 × 10^9 US dollars averaged over the period 2001–2017). Thus, the harvest of *ca*. 0.06 × 10^{12} Japanese yen was supported by a shadow cost (prey) of up to 2.0–2.2 × 10^{12} Japanese yen.

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

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Appendix A: Estimating the primary production supporting Japanese chum salmon

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

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

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

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

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

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

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

$$P/_{Q}(ZP)$$

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

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

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

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

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Table Captions

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

Figure Captions

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 (°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).

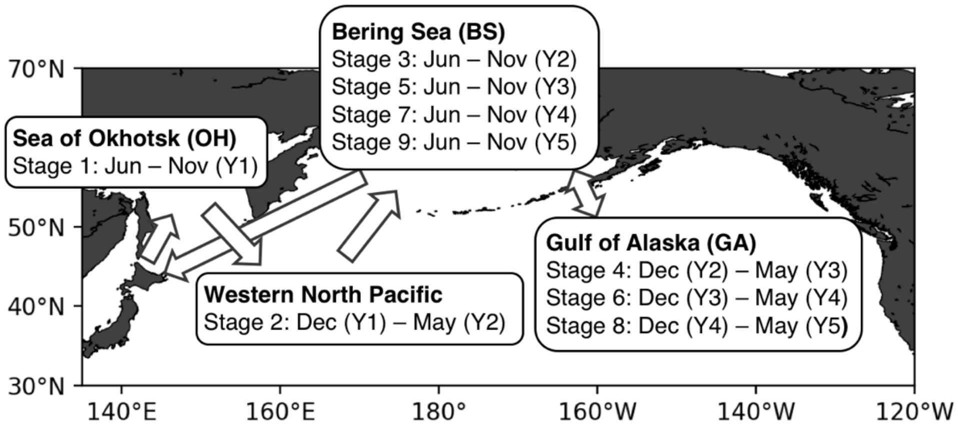
Fig. 4. Diagram of the NEMURO model showing transfer paths of organic matter from PL (large phytoplankton) and PS (small phytoplankton) to ZP (predatory zooplankton). Arrow (1) indicates a direct path from PL to ZP, arrow (2) is a pathway from PL to ZP via ZL, arrow (3) is a pathway from PS to ZP via 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 (10^8 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 (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



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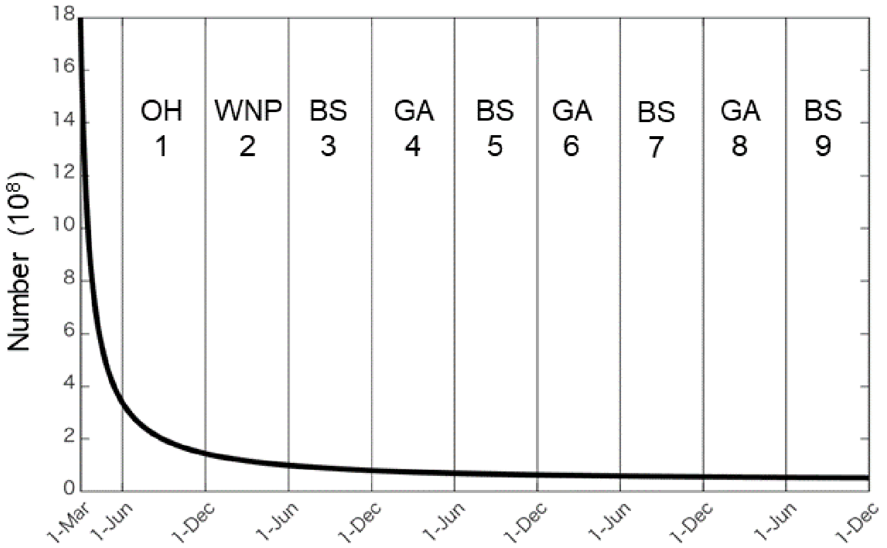
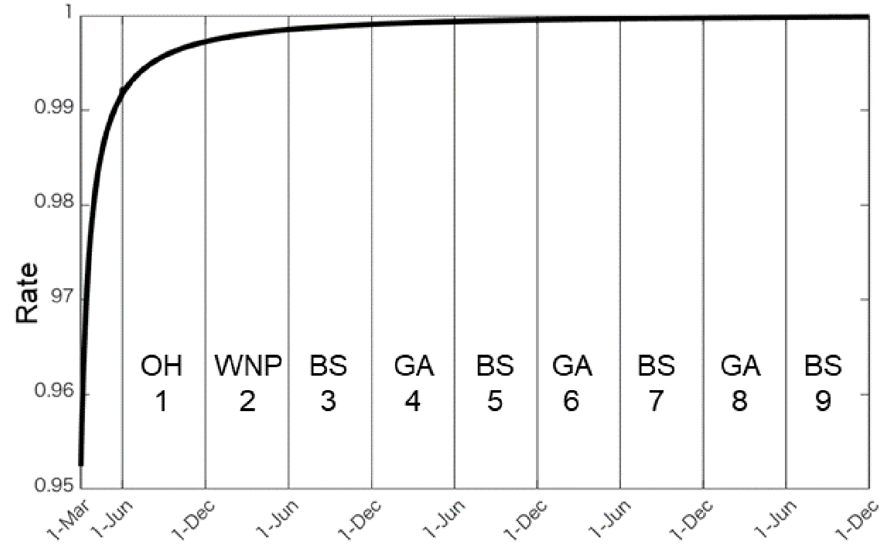
(a) Number of Japanese chum salmon



(b) Survival rate of Japanese chum salmon



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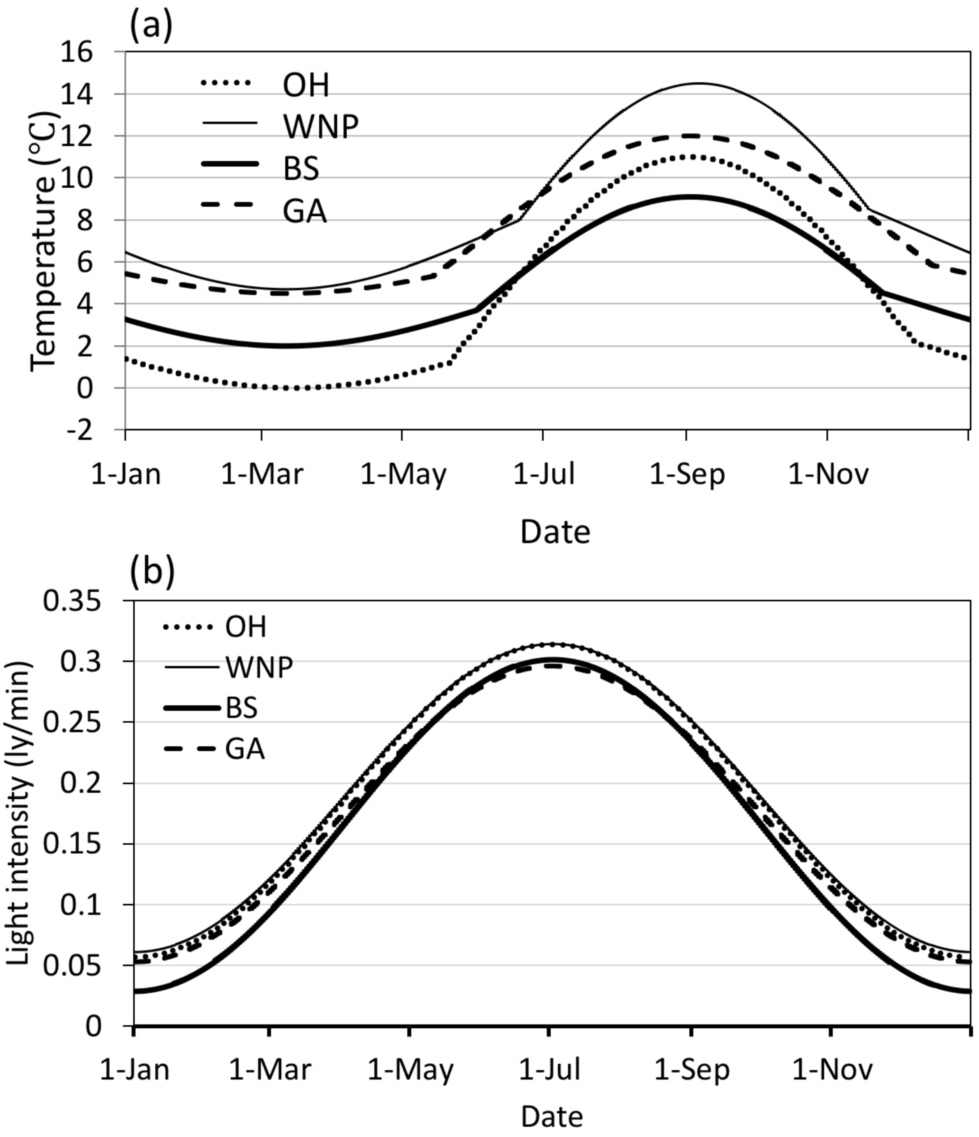

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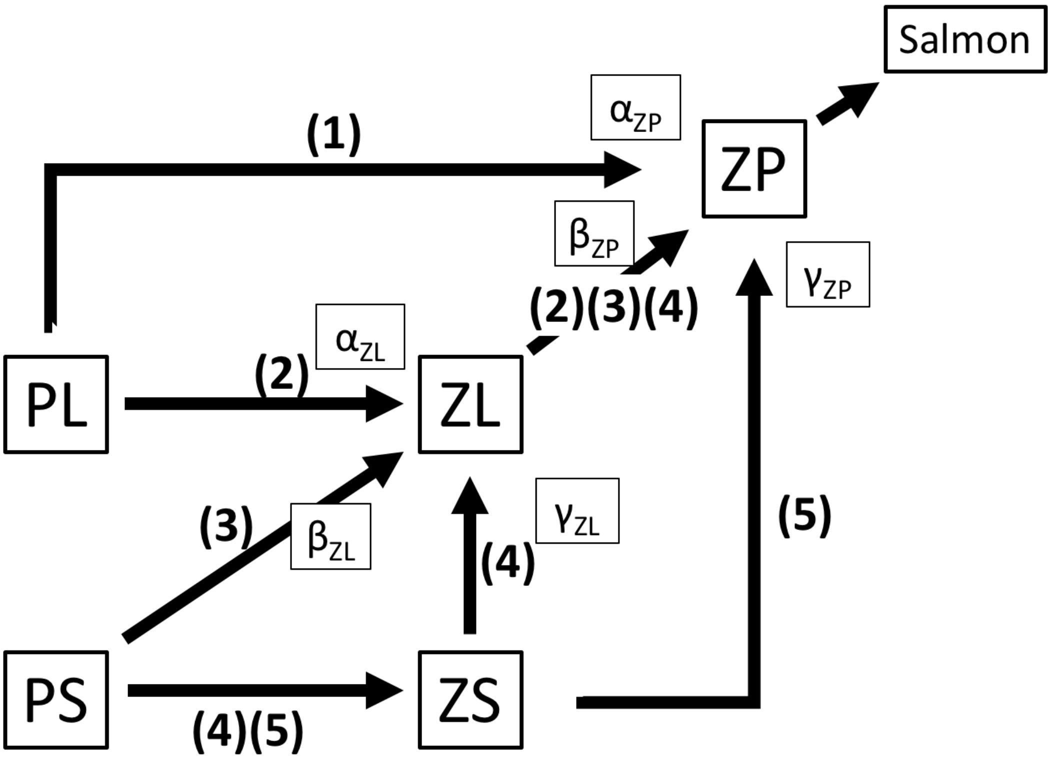

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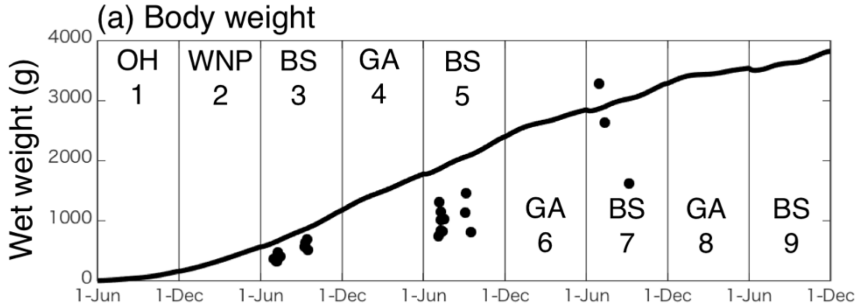

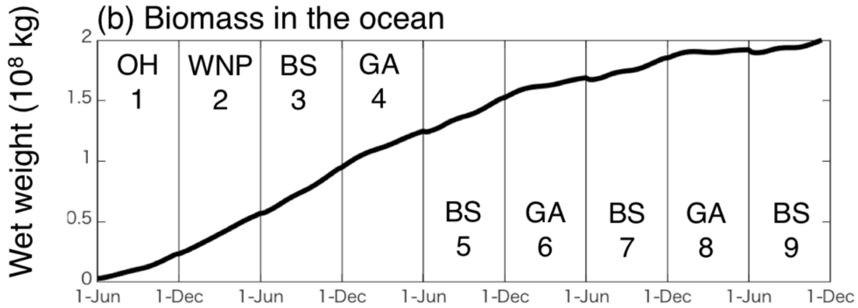

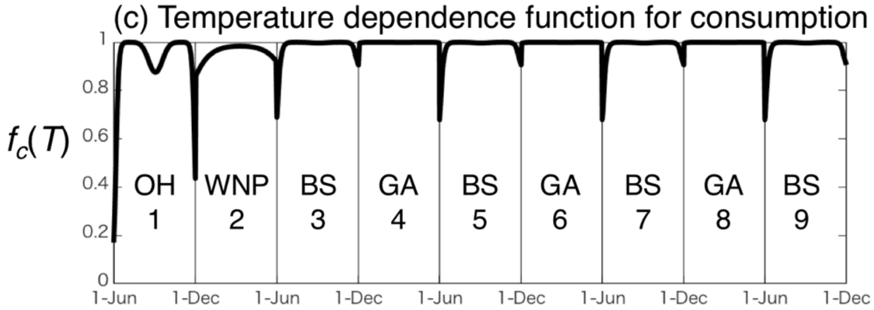

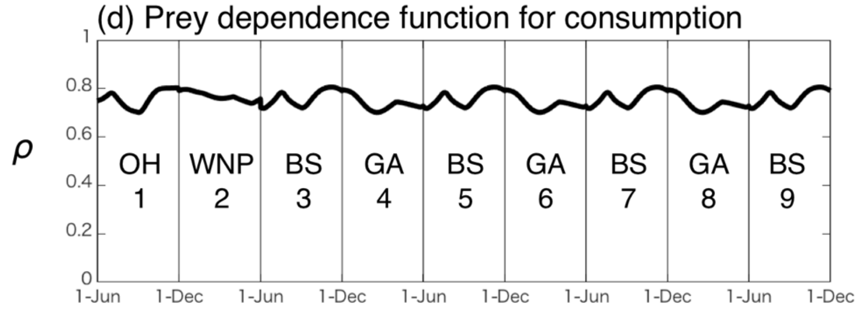

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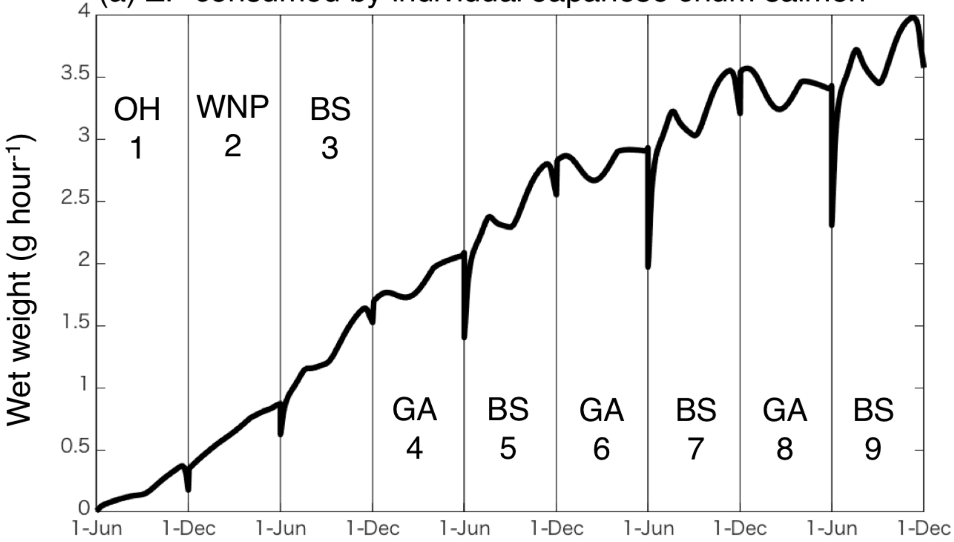
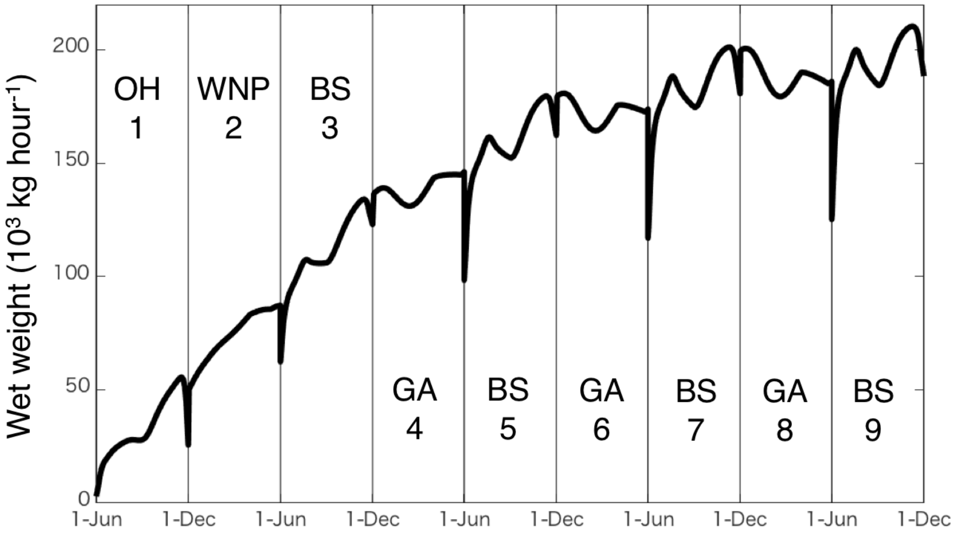


(a) ZP consumed by individual Japanese chum salmon



(b) ZP consumed by cohort Japanese chum salmon

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 (10^3 kg h^{-1}).