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Modelling seasonal growth of captive yellowfin tuna (Thunnus albacares) using repeated measurement data

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#### Abstract

Although several studies have shown the spatial variation in growth of yellowfin tuna (Thunnus albacares) in the Pacific Ocean, the current stock assessment model used in the WCPFC assumes the single growth curve in the whole assessment region, which may lead to uncertainty in the assessment results. To investigate the growth pattern of yellowfin tuna in a temperate region, we analyzed longitudinal growth data of 121 captive fish collected in southwestern water of Japan. We found that the fish shows higher growth rate in summer than winter, suggesting that the seasonal variability of water temperature or other associated factors play a key role in shaping the variations in growth. Our findings indicate that the fish in temperate waters can show different growth patterns than that in tropical waters.


## Introduction

The current stock assessment for yellowfin tuna (Thunnus albacares) in the Western and Central Pacific Ocean (WCPO) assumes a single stock and uses a single growth curve in the entire assessment region (Vincent et al., 2020). However, several studies have suggested the differences in the growth pattern among regions (Farley et al., 2018; Hoyle et al., 2009). Ignoring the spatial variations in growth could be a potential factor leading to uncertainty in the assessment outcomes. Growth is one of the most important factors in stock assessment models and significantly influences assessment outcomes. Therefore, understanding the spatial variation in the growth of yellowfin tuna is important to improve the stock assessment.

Regional differences in oceanographic condition can be a major factor causing spatial variations in growth. Temperature is among the most important factors regulating individual growth (Atkinson, 1994; Kooijman, 2010). Temperate regions are characterized by distinct seasonal variability in water temperature. Seasonal variability in water temperature in temperate regions can significantly influence the growth patterns of fish, which can result in differences compared to the tropical regions.

We previously reported the seasonal differences in growth in captive yellowfin tuna
(Okamoto et al., 2022). The monthly growth rate of young fish was higher in summer than winter. However, we did not account for the nonindependence of repeated measures in the analysis. Growth can considerably vary among individual fish (Goodrich \& Clark, 2023). To include the individual variability in growth, a growth model incorporating individual effects is needed.

Here, we used longitudinal records of body length in individually measured captive yellowfin tuna to investigate the seasonal effect on individual growth. By using additionally collected data to the previous report, we fitted a model estimating the growth of individual fish, assuming that the growth rate can change between summer and winter. We then compared the estimated growth rate parameter between the two seasons and discussed the seasonal effect on growth.

## Method

Young yellowfin tunas were collected in the coastal waters of the Amami Archipelago ( $27^{\circ} 24^{\prime} \mathrm{N}-28^{\circ}$ $45^{\prime} \mathrm{N}, 128^{\circ} 24^{\prime} \mathrm{E}-129^{\circ} 56^{\prime} \mathrm{E}$ ) by pole and line fishery in October 2020 and May 2021 (Fig.1). Captured fish were kept in a tank of the fishing vessel and later transported to the offshore sea cages ( 18 m and 20m diameters each) of Japan Fisheries Research and Education Agency, Fisheries Technology Institute, Amami Field Station ( $28^{\circ} 09^{\prime} \mathrm{N}, 129^{\circ} 15^{\prime} \mathrm{E}$ ). Upon arrival at the sea cage, each fish was measured for fork length to the nearest 1 mm (Fig.2) and tagged with plastic tipped dart tag (PDA Tag, Hallprint, Australia; 15cm length) and/or passive integrated transponder (PIT) tag (HPT9, Biomark, USA) for individual identification, and then released into the sea cage. Fish were fed mainly sand eels (Ammodytidae), sardines (Clupeiformes) and occasionally krills (Euphausiidae) to satiation for one to four times per day except for the staff's holidays. Daily seawater temperature was recorded during the study (Fig.3)

To observe the longitudinal change in the body size of an individual fish, we repeatedly recaptured captive fish with rod and reel, measured their fork length and released them back into the cage. Prior to each measurement, the fish were starved for approximately two weeks to increase the effectiveness of recapture. The measurements were taken every three to five months to observe the seasonal variation in growth. Note that all fish were not collected at every measurement, resulting in some missing data for certain individuals. Length at death were also recorded.

In total, 121 fish were used in the analysis, with 92 fish caught in 2020 and 29 fish caught in 2021. Data for fish that died within 50 days after introduction to the sea cage were not included due to some of those data showing negative growth records. Length-at-death data were used only if the record is obtained more than a month from the previous measurement.

To estimate the growth trajectory of individual fish, we developed a growth model that incorporates both seasonal and individual effects based on Richards growth model. Tuna species commonly show linear growth in the juvenile phase, followed by a rapid change to slower growth rates around the transition to adulthood (Laslett et al., 2002). Richards equation was chosen as it
allows more flexibility in parameter estimation compared to other commonly used growth models (Aires-da-Silva et al., 2015; Schnute, 1981).

Richard growth equation describes the length of fish at time $t$ as:

$$
\begin{equation*}
L_{t}=L_{\infty}\left(1+\frac{1}{p} e^{-K\left(t-t_{0}\right)}\right)^{-p} \tag{1}
\end{equation*}
$$

where $L_{\infty}$ is asymptotic length, $K$ is the growth rate, t0 is the inflection point on the curve, and $p$ is a shape parameter at the inflection point.

Transforming equation (1) yields:

$$
\begin{equation*}
\frac{1}{p} e^{-K(t-t 0)}=\left(\frac{L_{t}}{L_{\infty}}\right)^{\frac{1}{p}}-1 \tag{2}
\end{equation*}
$$

Now, consider a fish recaptured after a certain period of time ( $\Delta$ ). From equation (1), the length of this fish can be described as:

$$
\begin{gather*}
L_{t+\Delta}=L_{\infty}\left(1+\frac{1}{p} e^{-K\left(t+\Delta-t_{0}\right)}\right)^{-p} \\
L_{t+\Delta}=L_{\infty}\left(1+\frac{1}{p} e^{-K\left(t-t_{0}\right)} * e^{-K \Delta}\right)^{-p} \tag{3}
\end{gather*}
$$

Integrating equation (2) and (3) yields:

$$
\begin{equation*}
L_{t+\Delta}=L_{\infty}\left[1+\left\{\left(\frac{L_{t}}{L_{\infty}}\right)^{\frac{1}{p}}-1\right\} e^{-K \Delta}\right]^{-p} \tag{4}
\end{equation*}
$$

We assumed growth rate (K) has seasonal and individual variability. Incorporated this in equation (4) yields:

$$
\begin{equation*}
L_{t+\Delta, i}=L_{\infty}\left[1+\left\{\left(\frac{L_{t}}{L_{\infty}}\right)^{\frac{1}{p}}-1\right\} e^{-K_{s, i} \Delta}\right]^{-p} \tag{5}
\end{equation*}
$$

Here, $K_{\text {s,i }}$ i is a individual growth rate in season $s$, which is defined as:

$$
K_{s, i}=\mu+\text { season }+I
$$

In which $\mu$ is the population mean, season is the seasonal variability with specific values for summer and winter, and $I$ is the individual variability. In this study, we defined summer as between May to October and winter as between November to April. We assumed individual variability follows normal distribution with the mean equals to 0 and the standard deviation equals to $\sigma_{k}$.

$$
I=N\left(0, \sigma_{k}\right)
$$

Statistical analyses were conducted using R 4.2.0 (R Core Team, 2022). Using the nlme function from the nlme package (Pinheiro et al., 2010), we fitted a nonlinear mixed effects model with maximum likelihood estimation. The model can account for the nonindependence of repeated measures of individuals by including individual variability as a random effect. To determine the effects
of seasonality on growth, we developed two models: one without the seasonal effect (model_null) and the model with the seasonal effect (model_season). We then compared these models using Akaike's information criterion (AIC; Akaike, 1974) to determine if including seasonality improves the model.

## Results

Longitudinal changes in fork length of individual fish are shown in Fig.4. Fish caught in October 2020 exhibited a slower growth phase during winter, followed by a faster growth phase in summer, whereas fish caught in May 2021 experienced the faster growth phase in summer initially, then followed by a slower growth phase in winter. Both groups of fish displayed slightly slower growth during the winter of 2022, followed by the second summer with faster growth.

Comparing the monthly growth rate among different seasons revealed that fish grow faster in summer than in winter (Fig.5). On average, fish showed a monthly growth rate of 3.0 cm (standard deviation (SD): 0.6 ) during summer, whereas the rate declined to 1.8 cm (SD: 0.8 ) during winter.

Individual growth also depends on body size. Generally, the growth rate declines as a fish approaches its asymptotic length. To account for this, we developed a growth model predicting the length of individual fish as a function of the length at the previous measurement ( $L_{t}$ ) and the number of days elapsed between the measurements ( $\Delta$ ), while including season as a fixed effect and individual as a random effect (equation (5)). As we did not have sufficient data for large fish to reliably estimate $\mathrm{L}_{\infty}$, we fixed the value at 150 cm , which was estimated by the growth model used in the stock assessment. Table 1 presents the comparison between the models that do not include the seasonal effect (model_null) and the model that includes the seasonal effect (model_season). According to their AIC values, the model incorporating the seasonal effect provided a better fit to the data. The estimated parameter $k$ was higher in summer ( 0.87 ) than in winter ( 0.57 ), suggesting that fish showed a higher growth rate during summer compared to winter. While almost no individual effect was observed in the null model ( $\sigma_{\mathrm{k}}: 0.00$ ), it was more noticeable for the model incorporating the seasonal effect ( $\sigma_{\mathrm{k}}$ : 0.05).

## Discussion

We found that including the seasonal effect on the growth rate improved the growth model, highlighting the significance of considering seasonal variability in growth rate when estimating the growth of yellowfin tuna. Fish growth is strongly influenced by ambient temperature, generally being slower in cold waters and faster in warm waters (Atkinson, 1994). In line with this general pattern, our results demonstrated that captive yellowfin tuna grow faster in summer and slower in winter. Yellowfin tuna inhabit both tropical waters where the water temperature remains relatively constant across seasons, and temperate waters where water temperature shows distinct seasonal fluctuations.

Therefore, growth patterns may also vary among regions. Previous studies have reported geographical differences in growth in the WCPO (Farley et al., 2018; Hoyle et al., 2009), but most of them focused on tropical regions. As we have shown that different growth patterns between temperate and tropical waters are possible, further research on growth in temperate regions is needed.

Food availability could also be a major determinant of an individual growth (Kooijman, 2010). In this study, to isolate the effect of food availability from temperature on growth, we did not consider the seasonal changes in food availability and fed the fish to satiation. Therefore, our results do not reflect the influence of food availability. However, in natural environments, food availability can vary with the season and become a factor causing seasonal variability in growth. To explain the seasonal variability in growth in the wild, it is essential to consider both temperature and food availability. Although quantifying the specific food availability experienced by individual fish is extremely challenging, recent studies have demonstrated that the consumption rate of wild fish can be estimated from archival tagging data in some tuna species (Aoki et al., 2017; Muhling et al., 2022; Whitlock et al., 2013). This approach could also be applied to yellowfin tuna, which allows us to discuss the effect of food availability on seasonal growth.

In this study, we used a fixed value for the asymptotic length, assuming that the value remains invariant regardless of the seasons the fish experienced. However, temperature can also affect the size at maturity and the asymptotic size of fish (Atkinson \& Sibly, 1997). There might be seasonal effects on these parameters as well, but we could not investigate this because there was no data available for large fish at this time. In future research, we will continue to collect growth data of captive fish with repeated measures and examine the seasonal effect on the growth of adult fish.

## Conclusion

To investigate the seasonal variation in growth of yellowfin tuna, we analyzed repeated measurement data of fork length from fish reared in a temperate environment. The growth model incorporating seasonal effects revealed that fish had a higher growth rate in summer compared to winter. Our findings suggest that fish in temperate regions can show different growth patterns when compared to fish in tropical regions. This study offers valuable insights into understanding spatial differences in the growth of yellowfin tuna in the WCPO.

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## Tables

Table 1. Comparison of the models with the estimated parameters. "model_null" represents the model without seasonal effect and "model_season" represents the model including seasonal effect.

| Model | loglik | AIC | Season | Parameter estimates |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | p | k | $\sigma_{\mathrm{k}}$ |
| model_null | 452 | -896 | - | 1.51 | 0.78 | 0.00 |
| model_season | 531 | -1053 | Summer | 1.80 | 0.87 | 0.05 |
|  |  |  | Winter | 1.80 | 0.57 | 0.05 |

Figures


Fig. 1 The dots indicate the positions where yellowfin tunas were collected and the red point represents the position where the offshore sea cage is located


Fig. 2 Size-at-catch frequency of captive fish. Fish were caught in October 2020 and May 2021.


Fig. 3 Seawater temperature recorded during this study. Blue and red stripes refer to winter and summer defined in the analysis, respectively.


Fig. 4 Temporal variation in fork length of captive fish. Each line shows the growth trajectory of individual fish.


Fig. 5 Monthly growths rate for different seasons. "Winter_2021" and "Summer_2021" correspond to the periods between November 2020 and April 2021, and May 2021 and October 2021, respectively. "Winter_2022" and "Summer_2022" correspond to the periods between November 2021 and April 2022, and between May 2022 and October 2022, respectively.

