Prey Abundance Regulating the Response of an Important Marine Eel Species Conger Myriaster Growth to Water Temperature

Xiuxia Mu (✉ 11180522032@stu.ouc.edu.cn )
Ocean University of China  https://orcid.org/0000-0001-5997-3243

Chongliang Zhang
Ocean University of China - Yushan Campus

Binduo Xu
Ocean University of China - Yushan Campus

Yupeng Ji
Ocean University of China - Yushan Campus

Ying Xue
Ocean University of China - Yushan Campus

Yiping Ren
Ocean University of China - Yushan Campus

Research Article

Keywords: Conger myriaster, sea temperature, prey availability, interaction effects, mixed-effects model

DOI: https://doi.org/10.21203/rs.3.rs-400737/v1

License: ☑️ This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License
Abstract

Whitespotted conger (Conger myriaster) is a commercially important species in East Asia but the fisheries stock has drastically declined in recent years. Environmental changes are assumed to have profound impacts on the growth pattern of this species, yet the mechanisms that regulate growth remain poorly understood. Here we used otolith measurements to establish growth chronologies of 9-year period (2010–2018) for whitespotted conger in the Yellow Sea and evaluated the effects of environmental variables on the growth pattern. Linear mixed-effects models were used to explain growth variation with abiotic and biotic environmental variables, including seasonal water temperature, prey availability, and population density, and to assess age-dependent responses in growth and the interactions between abiotic and biotic factors. The results indicated that the growth of whitespotted conger positively correlated with spring sea bottom temperature (March-May) and prey per capita, and the influence of prey availability became larger with increasing ages. The model detected significant negative interactions between sea temperature and prey availability, indicating a higher degree of temperature-dependent growth when prey availability was low. Our findings imply that the growth of whitespotted conger is less likely to be influenced by food availability when the spring water temperature is high in the Yellow Sea, and a combination of cold spring and low food availability may result in substantial constrained growth. This study provided the first evidence for the joint effects of abiotic and biotic factors on the growth variation of whitespotted conger, and the information may contribute to sustainable management policies.

1 Introduction

Whitespotted conger Conger myriaster (Brevoort 1856) is an eel species distributed in the coastal to deep waters around China, Korean Peninsula and Japan (Tokimura 2011). This population, which supports an important fishery shared in East Asia, has been exploited mainly in the Yellow Sea and the East China Sea. As an economically important fish species, the population has been under intensive fishing pressure and drastically declined in recent decades (Gorie and Tanda 2004; FAO 2016). Although there are increasing concerns about the population declines and many researchers and managers have been taking actions, restoring the population is challenging due to limited understanding of their complex life histories, which is typical for eel species. In addition, as coastal areas are characterized by dynamic and complicated environments driven by climate changes (Harley et al. 2006) and human activities (Selkoe et al. 2008), many biological processes of whitespotted conger may be largely impacted, making management of this species even more challenging.

Growth is one of the most important factors determining population dynamics, and modeling of body growth constitutes an essential part of fisheries stock assessments (Lorenzen 2016). Currently, most fisheries assessments models assume that the growth parameters are consistent for given species (Lorenzen, 2016), although many studies have shown that growth patterns actually change over time (e.g., Morrongiello et al. 2014), in response to environmental factors, e.g. temperature (e.g. Heather et al. 2018; Lee and Punt 2018) and food availability (Weatherley 1990). Ignoring the variation in growth may
result in errors in stock assessment and misleading in fisheries management, given the prevalent influence of global climate changes (Rahikainen and Stephenson 2004).

Given the complex life history of this species, whitespotted conger is likely to be more vulnerable to the changes in environmental conditions. Growth of whitespotted conger has been investigated in several geographical areas (Katayama et al. 2002; Kim et al. 2011; Mu et al. 2019); however, few field or laboratory studies have examined the environmental effects. At present, it is largely unknown how environmental change and human activities may affect the growth pattern of whitespotted conger. Research of growth variation requires long-term length-at-age data in contrast environmental conditions, whereas collecting those data is often difficult and costly for marine fish populations, which hamper deeper understanding of the drivers of growth variation (Lee and Punt 2018). Fortunately, analysis of otolith provides an alternative approach for studying the growth of fish and other organisms. Growth history can be established through measuring translucent and opaque zones in otoliths, which reflect annual somatic growth with age and correspond to environmental factors (Campana and Thorrold 2001).

Many studies have revealed that temperature and habitat conditions have significant effects on the growth patterns of fish, and less evidences have been provided for the effects other than abiotic factors, such as prey availability. In addition, there are experimental studies showing interaction between prey availability and temperature that can affect marine organism growth (Zhang and Runham 1992; Ballesta et al. 2017), whereas the effect has not been well illustrated in natural waters in large spatial scales. A comprehensive understanding of the regulation of fish population dynamics requires investigating the combined effects of abiotic and biotic factors.

In this study, we used inter-annual measure of otolith increments as a proxy of somatic growth of whitespotted conger and adopted mixed-effects models to analyze individual growth trajectory regarding the influence of temperature and population density on individual growth. We also evaluate prey availability effects by relating growth rates to the prey biomass data, as well as to assess age-dependent responses in growth and the interactions between prey availability and water temperature. This study aims to demonstrate the growth pattern of whitespotted conger in China Sea and evaluate the effects of the abiotic and biotic factors that regulate the growth of this species. The improved understanding of the growth patterns may provide critical information for responding to climate changes and contribute to management policies for sustainable fisheries.

2 Materials And Methods

2.1 Sample collection

*C. myriaster* individuals were collected over the region 33–36°N, 119.5–123°E (Fig. 1), from 2011 to 2017 with bottom trawl surveys, with supplementary samples provided by local fishermen using longlines in 2017–2018 (Table 1). A total of 532 individuals were randomly selected from the catch, and the total length and body weight were measured and their sagittal otoliths were removed and cleaned for further
analyses. Males were rarely captured in our surveys and all females and unsexed individuals were used in this study.

| Sampling date | Sample size | Total length range (mm) |
|---------------|-------------|-------------------------|
| 2011          | 56          | 175–452                 |
| 2013          | 64          | 130–390                 |
| 2015          | 23          | 256–628                 |
| 2016          | 20          | 178–575                 |
| 2017          | 307         | 165–795                 |
| 2018          | 62          | 217–832                 |

2.2 Otolith measurements

The otoliths were embedded in epoxy resin (Epofix; Struers, Copenhagen, Denmark), then sectioned along the dorsal-ventral axis across the core with a diamond circular saw (Isomet low speed, Buehler). The sections (2 mm) were mounted on glass slides and polished with 800–1200 grit grinding paper (Minimet 1000 grinder-polisher, Buehler) until a clear view of the primordium was evident, and then pictured by optimal microscope (Olympus bx51). Sections with unclear annulus were discarded for subsequent age determination and measurement. We estimated age by counting annuli on the otolith images, where individual ages were represented as numbers of complete annuli. Ages were read twice from the otolith images and re-read after half a month, and the results that differed in two reading were then re-examination by another well-experienced reader. The birth-date of was assumed to be 1, December according to literature (Lee and Byun 1996). Using the ‘list year’ technique by subtracting the age from the collection year, we aligned each annual increment into the appropriate calendar year of the formation (Yamaguchi 1991). Then, annuli were measured from the nucleus to the edge along the axis of maximum growth, which was perpendicular to growth-increment boundaries.

Increment width series were constructed using ImageJ image analysis software (Rasband 1997–2012). The first increments (birth year) were removed because the increment width mainly depended on the birth date rather than the corresponding annual environmental variables. Marginal increments were also removed from analysis because they did not comprise a complete year of growth. In total, 264 otolith samples were used to establish the growth chronologies of whitespotted conger (Supplementary Fig. S1). Some samples were excluded because of the low annulus clarity (N = 167) or small age (N = 101). Additional analyses were conducted to ensure the increment of otolith was proportional to somatic growth (Supplementary Fig. S2), which is the precondition for using otolith increments to construct the biological chronology.
2.3 Influencing factors of growth

Firstly, the variability in growth patterns were examined for *C. myriaster*. The tested factors included the age of fish when a given increment in otolith was formed (age), the calendar year of the increment formed (Year), and the identity of fishes (Fish ID). The first factor account for expected age-related trends, the second account for the effects of annual variation, and the last Fish ID allowed individual to have diverged growth from average and handled the correlations among increment measurements of the same individuals (Morrongiello and Thresher 2015).

We then considered both biotic and abiotic factors that influence the growth rate of *C. myriaster*. Environmental factors included three categories of variables, seasonal bottom temperature, prey availability, and population density (Supplementary Fig. S3). Average bottom temperatures of survey region were obtained from the FVCOM from 2010 to 2018 (unpublished data). Bottom temperature was aggregated to seasonal averages (spring, March to May; summer, June to August; autumn, September to October; winter, December to February), and each of was were tested separately to identify the key season that affect fish growth. To estimate population density of *C. myriaster*, catch per unit efforts (CPUE) was used, for which commercial catches were obtained from the local fisheries administration and fishing efforts were measured by the number of fishing boats operating eels. The main prey species including *Engraulis japonicus*, *Ammodytes personatus*, and *Trachypenaeus curvirostris* were identified according to stomach studies in the survey region (Liu et al. 2015; Mu et al. 2019). We used total catch of three forage species divided by the catch of whitespotted conger to represent the food availability per capita (PPC).

2.4 Mixed-effect modeling

Hierarchical mixed effect models have been developed to determine growth variation following Morrongiello and Thresher (2015). We used the data of 2–7 ages to generate a general population chronology, i.e., an estimate of the mean inter-annual growth rates, which was developed by extracting the conditional effects from models (Morrongiello and Thresher 2015). Our model used otolith increments as response variables, and used the factors mentioned above as explanatory variables. Growth increments were log-transformed to meet model assumptions.

The models were developed by analyzing fixed effect (Age) with a series of random effect structures (combinations of random slope and/or intercepts of Fish ID, Age, Year). Models were compared using Akaike's information criterion (AIC; Bozdogan, 1987), and the model that results in the smallest AIC was chosen as the optimal model. To facilitate model convergence and interpretation of interaction terms, all predictor variables were mean centered (Morrongiello et al. 2014).

The effects of seasonal sea bottom temperature, PPC and population density were added to the model separately. Significantly correlated variables (Pearson's product-moment correlation P < 0.05) were not be included in the model simultaneously. To assess the potential synergistic effects of different factors, interaction terms were fitted among the combination of environmental variables. Specifically, we
examined the age-specific and density-dependent response of conger growth to water temperature, which were derived from the interaction effects of the mixed effects models.

The variance of the model was assessed on marginal $R^2$ describing the variance of fixed effects (Morrongiello and Thresher 2015). We obtained the predictions and confidence intervals using the arm and Effects packages (Fox 2003; Gelman and Hill 2006). All the data analyses were implemented in R 3.3.2.

3. Results

3.1 Variability in growth

Different combinations of fixed and random effects made up the intrinsic models for chronologies. The best intrinsic models included the fish ID random intercept and the year random intercept (Table 2). The selected model with both random and fixed effects explained 29.3% of the variance in otolith growth according to the marginal $R^2$.

“Age” as a fixed effect explained a large portion of the variance of growth, and a relatively high proportion of otolith growth was explained by Year and Fish ID, and a considerable level of unexplained variance persisted as residuals (Table 4). The growth rates of otolith decreased gradually with increasing age (Fig. 2a). Best linear unbiased predictors for the Year random effect showed considerable inter-annual variation in whitespotted conger growth over the last 9 years (Fig. 2b). Marked below-average growth rates were observed in 2010–2011, whereas above-average growth was detected in 2016–2018 (Fig. 2b).

Table 2 Selection of optimal random effects structures (highlighted in italics) in annual models. Random slope term designated with $x | y$.

| Model   | Random effects structure | K | AIC  | Marginal $R^2$ | Conditional $R^2$ |
|---------|--------------------------|---|------|----------------|------------------|
| Rm1     | 1|FishID                  | 4 | -93.21 | 0.132          | 0.763            |
| Rm2     | 1|Year                    | 4 | -265.04 | 0.258          | 0.737            |
| Rm3     | Age|FishID                 | 6 | -94.88 | 0.151          | 0.790            |
| Rm4     | Age|FishID+1|Year | 5 | -352.77 | 0.274          | 0.875            |
| Rm5     | 1|FishID+1|Year | 7 | -354.77 | 0.293          | 0.897            |

3.2 Biotic and abiotic effects

We further examined the effects of conger density, prey per capita, and seasonal bottom temperature. AIC scores showed that spring (March-May) bottom temperature was the most critical factors for growth modelling among the seasonal averages (Table 3). Model AIC was lowest when including fish age, spring
bottom temperature (Spring BT), PPC, and interaction between age and PPC and between Spring BT and PPC (Table 3). Including these fixed effects increased model marginal $R^2$ by 0.264. However, density was not included into the optimal model.

The spring bottom temperature showed a significant positive influence on otolith growth, with an average increase rate of 21.63% per 1 °C (Table 4, Fig. 3a). The prey per capita also had a significant positive influence on otolith growth (Table 4, Fig. 3b). High prey per capita resulted in an increase of 39.38% in mean growth of otolith (Table 4, Fig. 3b).

Table 3 Results of mixed effect model optimization stage of increasing complexity for *Conger myriaster*.

| Model structure                          | df  | AIC    | Marginal R² |
|------------------------------------------|-----|--------|-------------|
| M1 Age +SpringBT+1|FishID+1|Year   | 6    | -367.24 | 0.524 |
| M2 Age + Summer BT+1|FishID+1|Year   | 6    | -362.86 | 0.474 |
| M3 Age + Autumn BT+1|FishID+1|Year   | 6    | -351.61 | 0.253 |
| M4 Age + Winter BT+1|FishID+1|Year   | 6    | -366.60 | 0.529 |
| M5 Age + Density +1|FishID+1|Year   | 6    | -356.64 | 0.319 |
| M6 Age + PPC+1|FishID+1|Year   | 6    | -365.19 | 0.461 |
| M7 Age +SBT+PPC+1|FishID+1|Year   | 7    | -370.46 | 0.515 |
| M8 Age+SBT+Density+1|FishID+1|Year   | 7    | -374.30 | 0.553 |
| M9 Age +PPC+ SBT +Density+1|FishID+1|Year   | 8    | -373.87 | 0.541 |
| M10 Age +SBT+ PPC +Age: SBT+1|FishID+1|Year   | 8    | -373.65 | 0.557 |
| M11 Age +SBT+ PPC +Age: PPC+1|FishID+1|Year   | 8    | -376.01 | 0.551 |
| M12 Age +SBT+ PPC +SBT: PPC +1|FishID+1|Year   | 8    | -380.24 | 0.556 |
| M13 Age+SBT+PPC+SBT:PPC+Age:SBT +1|FishID+1|Year   | 9    | -381.91 | 0.561 |
| M14 Age+SBT+PPC+SBT:PPC+Age:PPC +1|FishID+1|Year   | 9    | -386.41 | 0.557 |
| M15 Age+SBT+PPC+SBT:PPC+Age:SBT+Age:PPC+1|FishID+1|Year   | 10   | -384.96 | 0.559 |

Notes, SBT means spring bottom temperature, PPC means prey per capita

Table 4. Variance components and estimates of random and fixed effects of the optimal model describing otolith growth for *Conger myriaster*. 
### 3.3 Interaction effects

The interaction between Age and PPC showed a significant positive relationship with species growth (Table 4, Fig. 4a). Based on the optimal model, high PPC resulted in a 14.47% increase in otolith growth of individual with 2 years and 69.81% in 7 years fish otolith growth (Supplementary Table. S1). Furthermore, we found a significant negative relationship of species growth with Spring BT and PPC interaction (Table 4, Fig. 4 b), indicating a higher degree of temperature-dependent growth when prey availability was low. The coefficients of interaction implied that increase of 1°C in spring BT led to 41.22%, 27.59%, 16.11%, and 5.89% growth increase when PPC was at the level of 1, 1.5, 2 and 2.5, respectively (Fig. 4).

### 4. Discuss

Our study used otolith increments to reconstruct the growth trajectory of whitespotted conger and illustrated a considerable inter-annual variation in their growth rates in recent years. After accounting for the intrinsic variations of growth rates resulting from age and the individual levels, we identified significant effects of environmental factors that drive annual growth, which enabled important implication for stock assessments and sustainable management for fisheries.

The study identified a remarkable pattern of increasing growth rate of whitespotted conger over the last nine years. Specifically, marked below-average growth rates were observed in 2010–2011, and above-average growth was detected in 2016–2018. The variation may be attributable to the large-scale climate events. During 2010, the tropical Pacific had a persistent La Niña event, with a second-year sea surface cooling that occurred in the autumn of 2011 (Feng et al. 2015). The cool ocean conditions may slow
down metabolism and temporarily decrease primary production, resulting in lower food availability, which, in turn, eventually might result in decreasing fish growth. Instead, extreme ocean warming events occurred during boreal summers in 2016 to 2018 in the South Yellow Sea and the East China Sea (Gao et al. 2020). Warm ocean conditions caused increases in metabolic rates, extending the whitespotted conger growing season. Therefore, the remarkable inter-annual variation of whitespotted conger growth could be a consequence of climate events which induced changes in aquatic temperature and food availability, though other factors such as eutrophication and fishing pressure may also have played a role.

Our study showed that growth of whitespotted conger was sensitive to changes in spring temperature rather than other seasons. The spring bottom temperature showed a significant positive influence on otolith growth, with an average increase rate of 21.63% per 1°C. The distinguishing effects of spring temperature may correspond to the fast growth period of conger eel (Gorie and Tanda, 2004; Bae et al. 2018). This response of whitespotted conger to temperature might be related to various ecological processes, for example, temperature may directly affect metabolic and physiological processes then determine growth rates (Boltana et al. 2017). Besides, the effects can also be caused indirectly by altering fish assemblage structure and productivity of ecosystems through food web mechanisms (Pörtner and Peck 2010; Breeggemann et al. 2015), which determine the prey availability and consequently growth. For many marine fish species, a slight increase in their thermal window is likely to benefit growth (Thresher et al. 2011; Tao et al. 2018). Whitespotted conger lives in the waters with temperature range of 8–27°C (Tang and Wu 1988; Hori et al. 2019), and temperature ≥ 26°C had a negative effect on the whitespotted conger activity (Hori et al. 2019). In the last nine years, the spring and summer mean-bottom temperature in study area was ranged of 10.81–12.60 °C and 21.11–22.75 °C, respectively. Therefore, the increase of temperature in the coastal water of the Yellow Sea still fell into the broad suitable temperature range of whitespotted conger and benefit its growth rates in recent years. By the end of this century, sea surface temperature in the Bohai, the Yellow Sea and the East China Sea will rise by 2°C and 4°C under the high and medium concentration emission scenarios, respectively (Tan et al. 2018). Combined climate predictions, temperature-dependent growth could lead to a significant implication for the management of whitespotted conger.

The positive correlation between growth and prey availability is in accord with the common sense that high food availability would increase fish growth. In addition, the whitespotted conger growth was influenced by the prey per capita depending on fish age, and the older were more sensitive to the increase of prey availability. The ontogenetic shift in diet were observed in this species (Mu et al. 2019), and different food resources were consumed by small and large conger eels (Mu et al. 2019), which may lead to differential growth suppression among age classes (Walters and Post, 1993). Additionally, we found prey availability influenced the temperature effect on otolith growth of whitespotted conger. When prey resource was relatively poor, the growth rates were significantly improved with the increased of temperature, and when the prey was abundant, the growth rate was at a higher level and was less affected by the water temperature. The results implied a combined effect on growth limitation by low water temperature and prey per capita. This response could be related to the predation success of
whitespotted conger. Feeding rate is a function of the encounter rate between predator and prey, the predator’s attack frequency, and the capture success (Elliott and Leggett 1997). Swimming speeds and activity rates are two most important factors determine the encounter rates (Gerritsen and Strickler 1977), and generally increase with temperature range from 10 to 26°C for whitespotted conger (Hori et al. 2019). The attack rate of predators has also been shown to increase with temperature (Elliott and Leggett 1996). Therefore, the influences of high temperature on conger’s behaviors are likely to benefit predation success when prey resource is poor, and conversely, the capture ability of fish predators would be reduced at low temperatures (Persson 1986; Bergman 1987). Consequently, the increasing water temperature in the future enables whitespotted conger to remain high predation pressure on their preys when the forage population fall to a low level, which may result in substantial changes in community structure.

Many previous researches support an inverse relationship between growth of eel and its density (Machut et al. 2007; Boulenger et al. 2016), e.g., a negative linear relationship was found of density-dependent growth for European eel in a small river of western France (Boulenger et al. 2016). Density-dependent regulation of growth is often related to intraspecific competition (Lorenzen and Enberg 2002), and occurrence of different forms of density-dependent growth depending on the nature of the life history and individual behaviors (Post et al.1999). Although the density effect was not selected into the optimal model, the prey-per-capita, which calculated by total catch of three forage species divided by the catch of whitespotted conger, takes into account the effect of intraspecific competition. In addition, the interspecific competition may also influence the results, as there are more diverse species completing for the same preys in the marine environment, which was not considered in our study.

Conclusions

This study examined the otolith growth of whitespotted conger with explicit consideration of biotic and abiotic variables in mixed effects models to reveal the critical driving factors. We identified that spring temperature and prey availability had significant influence on conger growth. This study provided the first evidence for the joint effects of abiotic and biotic factors on the growth variation of whitespotted conger. The improved knowledge is essential for effective management of these ecologically important species, and is key to understanding the broad implications of global climate change.

Declarations

Acknowledgment

We are grateful to the members of Ecosystem Assessment and Evaluation Laboratory from College of Fisheries in Ocean University of China for the sample collections.

Funding

This work was supported by Supported by the National Key R&D Program of China (2018YFD0900904, 2018YFD0900906).
Conflicts of interest

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

Ethics approval

All fish captures and handling were conducted in accordance with the guidelines of concerned government ministries in China.

Data/Code Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Authors' Contribution

Xiuxia Mu: Conceptualization; Methodology; Software; Formal Analysis; Investigation; Data Curation; Writing- Original draft

Chongliang Zhang: Writing – Review & Editing, Funding Acquisition

Binduo Xu: Writing – Review & Editing

Yupeng Ji: Writing – Review & Editing

Ying Xue: Writing – Review & Editing

Yiping Ren: Writing- Reviewing and Editing, Supervision, Project Administration; Funding Acquisition

References

1. Bae JH, Bae HJ, Park HM, Park HS, Kim HG, Oh CW (2018) Age determination and growth estimates of the white-spotted conger eel, Conger myriaster (Brevoort, 1856) in marine waters of South Korea. J Appl Ichthyol 34(3):542–549. https://doi.org/10.1111/jai.13587

2. Ballesta I, Janssen R, vanderMeer J, Witbaard R (2017) Interactive effects of temperature and food availability on the growth of Arctica islandica (Bivalvia) juveniles. Mar Environ Res 133. https://doi.org/10.1016/j.marenvres.2017.12.004

3. Bergman E (1987) Temperature-dependent differences in foraging ability of two percids, Perca fluviatilis and Gymnocephalus cernuus. Environ Biol Fishes 19(1):45–53. https://doi.org/10.1007/BF00002736

4. Boulenger C, Alain C, Charrier F, Roussel JM, Feunteun E, Acou A (2016) Difference in factors explaining growth rate variability in European eel subpopulations: the possible role of habitat carrying capacity. Ecol Freshw Fish 25:281–294. https://doi.org/10.1111/eff.12209
5. Bozdogan H (1987) Model selection and akaike's information criterion (AIC): the general theory and its analytical extensions. Psychometrika 52(3):345–370

6. Breeggemann J, Kaemingk M, DeBates T, Paukert C, Krause J, Letvin A, Stevens T, Willis D, Chipps S (2015) Potential direct and indirect effects of climate change on a shallow natural lake fish assemblage. Ecol Freshw Fish 25(3):487–499. https://doi.org/10.1111/eff.12248

7. Campana S, Thorrold S (2001) Otoliths, increments, and elements: Keys to a comprehensive understanding of fish populations? Can. J Fish Aquat Sci 58:30–38. https://doi.org/10.1139/cjfas-58-1-30

8. Elliott JK, Leggett WC (1996) The effect of temperature on predation rates of a fish (Gasterosteus aculeatus) and a jellyfish (Aurelia aurita) on larval capelin (Mallotus villosus). Can J Fish Aquat Sci 53:1393–1402. https://doi.org/10.1139/cjfas-53-6-1393

9. Elliott JK, Leggett WC (1997) Influence of temperature on size-dependent predation by a fish (Gasterosteus aculeatus) and a jellyfish (Aurelia aurita) on larval capelin (Mallotus villosus). Can J Fish Aquat Sci 54(12):2759–2766. 10.1139/cjfas-54-12-2759

10. Feng LC, Zhang RH, Wang ZG, Chen XR (2015) Processes leading to second-year cooling of the 2010–12 La Niña event, diagnosed using GODAS. Adv Atmos Sci 32(3):424–438. https://doi.org/10.1007/s00376-014-4012-8

11. Francis R (2006) Back-calculation of fish length: A critical review. J Fish Biol 36:883–902. https://doi.org/10.1111/j.1095-8649.1990.tb05636.x

12. Gao G, Marin M, Feng M, Yin B, Yang D, Feng X, Yang D, Song D (2020) Drivers of marine heatwaves in the east china sea and the south yellow sea in three consecutive summers during 2016–2018. J Geophys Res-Oceans 125. 10.1029/2020JC016518

13. Gelman J. Hill (2006) Applied Regression and Multilevel. (Hierarchical) Models General Information 45(1):94–97

14. Gerritsen J, Strickler JR (1977) Encounter Probabilities and Community Structure in Zooplankton: a Mathematical Model. J Fish Res Board Canada 34:73–82. https://doi.org/10.1139/f77-008

15. Gorie S, Tanda M (2004) Growth and stomach contents of juvenile white-spotted conger Conger myriaster. Suisanzoshoku 52:139–144. https://doi.org/10.11233/aquaculturesci1953.52.139

16. Harley C, Hughes A, Hultgren K, Miner B, Sorte CJB, Thornber C, Rodriguez LF, Tomanek L, Williams S (2006) Erratum: The impacts of climate change in coastal marine systems. Ecol Lett 9:228–224. https://doi.org/10.1111/j.1461-0248.2006.00917.x

17. Heather FJ, Childs DZ, Darnaude AM, Blanchard JL, Patrick P (2018) Using an integral projection model to assess the effect of temperature on the growth of gilthead seabream sparus aurata. Plos One 13(5):e0196092. 10.1371/journal.pone.0196092

18. Hori T, Noda T, Wada T, Iwasaki T, Arai N, Mitamura H (2019) Effects of water temperature on white-spotted conger Conger myriaster activity levels determined by accelerometer transmitters. Fish Sci 85(2):295–302. https://doi.org/10.1007/s12562-019-01289-0
19. Katayama S, Ishida T, Goto K, lizuka K, Karita K (2002) A new aging technique by UV light observation of burnt otoliths for the conger eel *Conger myriaster* (Brevoort). Ichthyol Res 49(1):81–84. https://doi.org/10.1007/s102280200009

20. Kim YH, Lee EH, Kim JN, Choi JH, Oh TY, Lee DW (2011) Age and Growth of Whitespotted Conger *Conger myriaster* in the Southern Coastal Waters of Korea. Korean J Fish Aquat Sci 44(6):689–694. https://doi.org/10.5657/KFAS.2011.0689

21. Lee Q, Punt A (2018) Extracting a time-varying climate-driven growth index from otoliths for use in stock assessment models. Fish Res 200:93–103. https://doi.org/10.1016/j.fishres.2017.12.014

22. Lee TW, Byun JS (1996) Microstructural growth in otoliths of conger eel (*Conger myriaster*) leptocephali during the metamorphic stage. Mar Biol 125(2): 259–268. Doi: https://doi.org/10.1007/BF00346306

23. Liu XF, Liu H, Xue Y, Ji YP, Li SY, Han DY (2015) Feeding ecology of *C. myriaster* in Haizhou Bay. Journal of Fishery Sciences of China 22(3):517–527

24. Lorenzen K, Enberg K (2002) Density-Dependent Growth as a Key Mechanism in the Regulation of Fish Populations: Evidence from Among-Population Comparisons. Proc Biol Sci 269:49–54. https://doi.org/10.1098/rspb.2001.1853

25. Lorenzen K (2016) Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fish Res 180:4–22. https://doi.org/10.1016/j.fishres.2016.01.006

26. Machut L, Limburg K, Schmidt R, Dittman D (2007) Anthropogenic impacts on American eel demographics in hudson river tributaries, New York. Trans Amer Fish Soc 136:1699–1713. https://doi.org/10.1577/T06-140.1

27. Morrongiello JR, Thresher RE (2015) A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. Ecol Monogr 85:93–115

28. Morrongiello J, Walsh C, Gray C, Stocks J, Crook D (2014) Environmental change drives long-term recruitment and growth variation in an estuarine fish. Glob Chang Biol 20 (6). https://doi.org/10.1111/gcb.12545

29. Mu X, Zhang C, Xue Y, Zhang C, Xu B, Ren Y (2019) Fishery biology of whitespotted conger Conger myriaster (Brevoort, 1856) in the Yellow Sea and East China Sea. Acta Oceanol Sin 38(6):18–24. https://doi.org/10.1007/s13131-018-1271-8

30. Persson L (1986) Temperature-induced shift in foraging ability in two fish species; roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. J Anim Ecol 55:829–840

31. Pörtner HO, Peck M (2010) Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. J Fish Biol 77:1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

32. Rahikainen M, Stephenson RL (2004) Consequences of growth variation in northern Baltic herring for assessment and management. ICES J Mar Sci 61(3):338–350. https://doi.org/10.1016/j.icesjms.2004.02.005
33. Rasband WS (1997–2012) ImageJ. US National Institutes of Health, Bethesda, MD.
   http://imagej.nih.gov/ij/
34. Selkoe KA, Kappel CV, Halpern BS, Micheli F, Hunter SL (2008) Response to Comment on “A Global
    Map of Human Impact on Marine Ecosystems”. Sci 321:948–952.
    https://doi.org/10.1126/science.1158007
35. Tan HJ, Cai RS, Yan XH (2018) Projecting changes of marine environment in coastal China Seas over
    21st century based on CMIP5 Models. Journal of Applied Oceanography 37(02):151–160
36. Tang YM, Wu CW (1988) On biologic habits and resources distribution of common Japanese conger
    Astro C. myriaster (Brevoort). Journal of Zhejiang College of Fisheries 7(1):19–26
37. Tao J, Kennard M, Jia Y, Chen Y (2018) Climate-driven synchrony in growth-increment chronologies
    of fish from the world’s largest high-elevation river. Sci Total Environ 645.
    https://doi.org/10.1016/j.scitotenv.2018.07.108
38. Thresher R, Lyle J, Semmens J, Neuheimer A (2011) Tolerance limit for fish growth exceeded by
    warming waters. Nat Clim Chang 1. https://doi.org/10.1038/nclimate1084
39. Tokimura M (2011) Fisheries and their resources in the East China Sea. Nippon Suisan Gakkaishi
    77:919–923. https://doi.org/10.2331/suisan.77.919
40. Walters CJ, Post JR (1993) Density-dependent growth and competitive asymmetries in size-
    structured fish populations: a theoretical model and recommendations for field experiments. Trans
    Amer Fish Soc 122(1):34–45
41. Weatherley AH (1990) Approaches to understanding fish growth. Trans Amer Fish Soc 119:662–672
42. Yamaguchi DK (1991) A simple method for cross-dating increment cores from living trees. Can J
    Forest Res 21:414–416
43. Zhang Z, Runham NW (1992) Effects of food ration and temperature level on the growth of
    Oreochromis niloticus (L.) and their otoliths. J Fish Biol 40(3):341–349.
    https://doi.org/10.1111/j.1095-8649.1992.tb02581.x

**Figures**
Figure 1

Locations of Conger myriaster specimen collections for otolith biochronology analysis Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.
Figure 2

Intrinsic effects for Conger myriaster with 95% CIs in the Yellow Sea

Figure 3

The effect of spring bottom temperature, density, and prey availability on otolith growth rates of Conger myriaster.
Figure 4

Predicted effect of the significant extrinsic interaction of (a) Age with Prey per capita and (b) the Spring bottom temperature with Prey per capita on Conger myriaster otolith growth. PPC means prey per capita (total catch of three forage species divided by the catch of whitespotted conger)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterial.docx