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Relationships between daily growth of different groups of swordtip squid (*Uroteuthis edulis*) and environmental variables in the East China Sea

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Abstract

Swordtip squid (*Uroteuthis edulis*) is one of the important economical fishing target species in the East China Sea. *Uroteuthis edulis* is characterized by rapid growth, extensive migration, and long spawning period and sensitive to surrounding environment. In order to assess its stock status, it is necessary to explore its spawning season, growth patterns of different populations and their relationship with the environment in advance. In this paper, based on the samples of *U. edulis* collected in the East China Sea from September 2017 to March 2018, we explored the relationships between daily growth of statolith microstructure and environmental variables by gradient forest method and generalized additive model. The spawning season of *U. edulis* was found to be nearly one year, and two dominant season groups were found: the spring group with the peak period of April and the summer group with the peak period of August. Water temperature in the depth of 25 m (Temp_25), sea surface temperature (SST) and zonal velocity were the key environmental variables for the daily growth of April-spawning group. The most suitable environmental conditions for the growth of April-spawning group were water temperature (24–27°C) and velocity (0.1–0.3 m/s). SST, Temp_25 and mixed layer depth were the key environment variables for the daily growth of August-spawning group. The most suitable environmental conditions for the growth of August-spawning group were water temperature (21–28°C) and water depth (0–50 m). Key environmental variables of different groups suggested that early growth was significantly affected by seasonal changes of water temperature, current velocity and prey abundance. This study explored the relationships between early growth and environmental variables and provided the scientific guidance for the management and conservation of *U. edulis*.

Key words: East China Sea, *Uroteuthis edulis*, statolith microstructure, environmental variables

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1 Introduction

Swordtip squid, *Uroteuthis edulis*, is an important species of Loliginidae widely distributed in the subtropical and tropical area of the northwestern Pacific Ocean and the coastal waters of the eastern Africa as well as northern Australia (Sin et al., 2009; Jereb and Roper, 2010). Since the 1990s, *U. edulis* has gradually replaced the high-catch species *Sepiella japonica* and become one of the new economic fishery species with an annual landing of about 1.5×10^4 t in the East China Sea (Chen et al., 2019; Jereb and Roper, 2010). According to the all-year spawning characteristics of *U. edulis*, its population is divided into spring-, summer-, autumn- and winter-hatching groups (Chen et al., 2019). The growth and development of each group are obviously affected by environmental factors (Wang et al., 2013). Generally, the population hatching in the cold water period was larger in size and grew faster (Wang, 2009; Yamaguchi et al., 2015). The growth of individuals at different stages was obviously affected by the prey abundance and sea temperature, especially the growth from the embryonic stage to the larval stage, which was positively correlated with the early survival of the population (Bounket et al., 2019).

The age estimation and growth analyses can provide important information on population structure and growth difference (Arkhipkin, 2005; Ceriola and Jackson, 2010; Fang et al., 2016).

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The statolith of squid has the characteristics of stable structure, corrosion resistance, and clear growth increment and is the good material recording the entire life history, including growth pattern and ecological information (Liu et al., 2011; Arkhipkin and Shcherbich, 2012; Chen et al., 2015; Fang et al., 2018; Jin et al., 2019). Ceriola and Jackson (2010) proved the daily periodicity of the statolith growth pattern of *Loliolus noctiluca* with the laboratory feeding method and reported that the growth rate of statoliths showed the gender difference. Moreover, statolith microstructure and its chemical composition archived a variety of environmental and ontogenetic events experienced by the individual during the entire life history (Jackson, 2004; Zumholz et al., 2007). Several intrinsic and extrinsic factors affect statolith growth and formation such as temperature, ontogenetic shifts and available foods (Pecl, 2004; Ceriola and Jackson, 2010).

The population growth and survival of aquatic animals were highly influenced by some environmental variables, including water temperature, chlorophyll *a*, and salinity, which also played an important role in the regulation of population dynamics and marine ecosystem (Sun et al., 2020). For example, previous studies indicated that *Loligo vulgaris* deposited thicker increments in their statolith during the embryonic stage due to the increase in water temperature, thus resulting in larger statolith morphology (Miyahara et al., 2006; Moreno et al, 2012). Too high or low salinity leads to a significant decrease in the survival rate of embryo and a large fluctuation in salinity may be fatal to eggs (Şen, 2005). In the East China Sea, the interaction between the Kuroshio Current with high temperature and high salinity, and coastal current with low salinity, and high nutrients jointly affected the spatial and temporal distributions and characteristics of marine environmental variables under global climate change (Wang, 2009; Yamaguchi et al., 2018a). The current velocity affected the vertical movement and migration distance of individuals, which determined their habitat environment and food selection for early growth (Yamaguchi et al., 2019). In addition, rich nutrients carried by freshwater of the Changjiang River increased the primary productivity of the sea area and provided abundant foods for growth (Sun et al., 2020). However, recent studies have shown that the East China Sea is one of the fastest-warming large-scale marine ecosystems in the global oceans and this warming phenomenon may be one of the most important abiotic factors affecting squid growth (Takahara et al., 2017; Pang et al., 2018).

The study aims to explore the spawning season and growth characteristics of different hatching groups in the East China Sea based on statolith information, screen the key environmental factors affecting early growth of *U. edulis* by the gradient forest method and analyze the differences of key factors among different hatching groups. The study revealed the environmental causes for the differences in early growth of different hatching groups of *U. edulis*.

2 Materials and methods

2.1 *Sampling information and study area*

A total of 121 *U. edulis* samples were randomly captured by a commercial trawler vessel (*Zhelingyu 23860*) in the East China Sea (27°–32°N, 122°–127°E, Table 1) from September 2017 to March 2018. Samples were frozen at –20°C and transported to the laboratory for the subsequent analysis. Mantle length and sex ratio of samples were determined (Table 1).

Table 1. Sampling information of *Uroteuthis edulis* from the East China Sea

Sampling time	Location	Number	Mantle length range/mm	Age range/d	Sex ratio F:M
September 2017	30°30′N, 127°00′E	15	69–198	176–224	1.4:1
November 2017	31°00′N, 126°30′E	19	110–234	175–273	0.9:1
December 2017	31°30′N, 126°30′E	23	86–223	153–254	1.2:1
January 2018	31°30′N, 127°00′E	24	93–180	175–228	1:1
February 2018	28°30′N, 123°00′E	17	87–158	176–233	2:1
March 2018	27°30′N, 124°30′E	23	92–154	169–215	0.7:1

Note: F:M represents female amount vs. male amount.

Uroteuthis edulis is one of the most abundant cephalopod species in the East China Sea, an important feeding and spawning ground (Wang et al., 2015a). With the strengthening of the Kuroshio Current and Taiwan Warm Current, individuals migrate to the northeast for feeding in April. When the squid becomes mature, *U. edulis* moves from the feeding ground toward the spawning ground in September (Liao et al., 2018). The swimming speed of squid is different, and its migration speed varies from 0.18 km/h to 0.55 km/h (Natsukari and Tashiro, 1991). Therefore, it is reasonably assumed that *U. edulis* inhabits the areas of 26°–29°N and 122°–125°E in the early 90 d with 0.18 km/h and then the zones of 28°–31°N and 123°–126°E in the next 60 d with 0.25 km/h (Fig. 1).

2.2 *Age estimation and statolith microstructure*

Statolith had been used as a good material for the cephalopod study on individual age and growth as well as ecological information due to the stable structure, corrosion resistance and irreversible daily increments (Arkhipkin et al., 2018). For each specimen, both statoliths were extracted from statocysts, then cleaned and stored with 75 % ethyl alcohol. Each statolith was embedded with acrylic resin and mounted on a microscope slide (Liu et al., 2011). Statolith was grounded on a longitudinal plane with 3M commercial waterproof sandpaper (600 grit, 1 200 grit, 2 000 grit and 2 500 grit) and polished with alumina powder (0.3 μm) until the nucleus and daily increments were visible

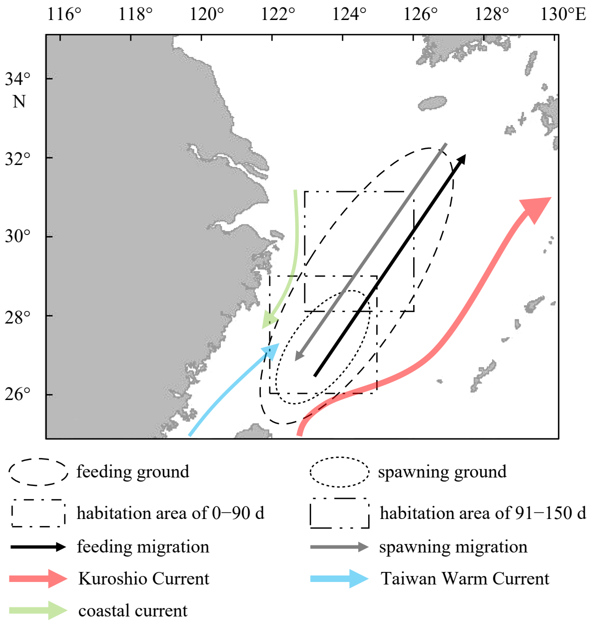

Fig. 1. Spawning and feeding ground of *Uroteuthis edulis*.

(Liu et al., 2015). Photos of statolith slices were taken under 20× magnification with a charge-coupled device. Daily age was read with Photoshop and then the hatching dates were calculated with the date of capture and daily age. Daily increment width was measured by Image-J. All increments of statolith were counted and measured along the same axis (Figs 2a–d). The counting and measurement results were read twice by two readers to ensure the accuracy.

2.3 *Environmental variables*

Water temperature, especially sea surface temperature (SST) is considered to be an important environmental factor affecting squid population growth and reproduction (Fang et al., 2019; Yamaguchi et al., 2020). Mixed layer depth (MLD) is related to the nutrient abundance of squid in the habitat area and chlorophyll *a* concentration also affects the distribution and richness of its prey (Yu et al., 2016). The convergence and divergence of nutrition mass transport in the surface layer of the ocean respectively result in positive and negative sea levels (Polito et al., 2000). Therefore, sea surface height (SSH) represents a potential aggregating mechanism of planktons as well as their predators (squid) (Chen et al., 2011; Wang et al., 2015b). The strength and direction of current affects the migration distance and food availability of squid, making individuals hatching in the south of the East China Sea migrate to the northeast offshore area for feeding along with current. So current is one of the key environmental variables that determine the survival rate of individuals (Yamaguchi et al., 2019). Coastal current is obviously affected by freshwater of the Changjiang River in winter and sea surface salinity (SSS) can be selected as an indicator to represent the features of alongshore currents (Kako et al., 2016). Therefore, these environmental variables were selected as the indicators of statolith daily increments in this study (Table 2).

Daily environmental variables of sampling location and hypothetical early habitat, including SST, Temp_25, MLD, SSH, SSS, ZV and VV, were derived from National Oceanic and Atmospheric Administration (NOAA) High-resolution Blended Analysis (http://apdrc.soest.hawaii.edu/las/v6). The daily chlorophyll *a* data were downloaded from the NOAA OceanWatch (http://oceanwatch.pifsc.noaa.gov/). The spatial resolutions of all downloaded environmental variables were processed according to the value of 0.25°×0.25° in Matlab 2018 (Fig. 3). All the daily environmental variables corresponded to the daily growth data of *U. edulis* hypothesized migration area (Fig. 1).

2.4 *Statistical analysis*

Specimens hatched in the same month were grouped into the same month group based on the calculated hatching date. In each month group, daily increment widths of specimens and corresponding environment variables were averaged to obtain the growth and environmental data of a given day. The daily increment width of statolith was measured to the smallest age (153 d)

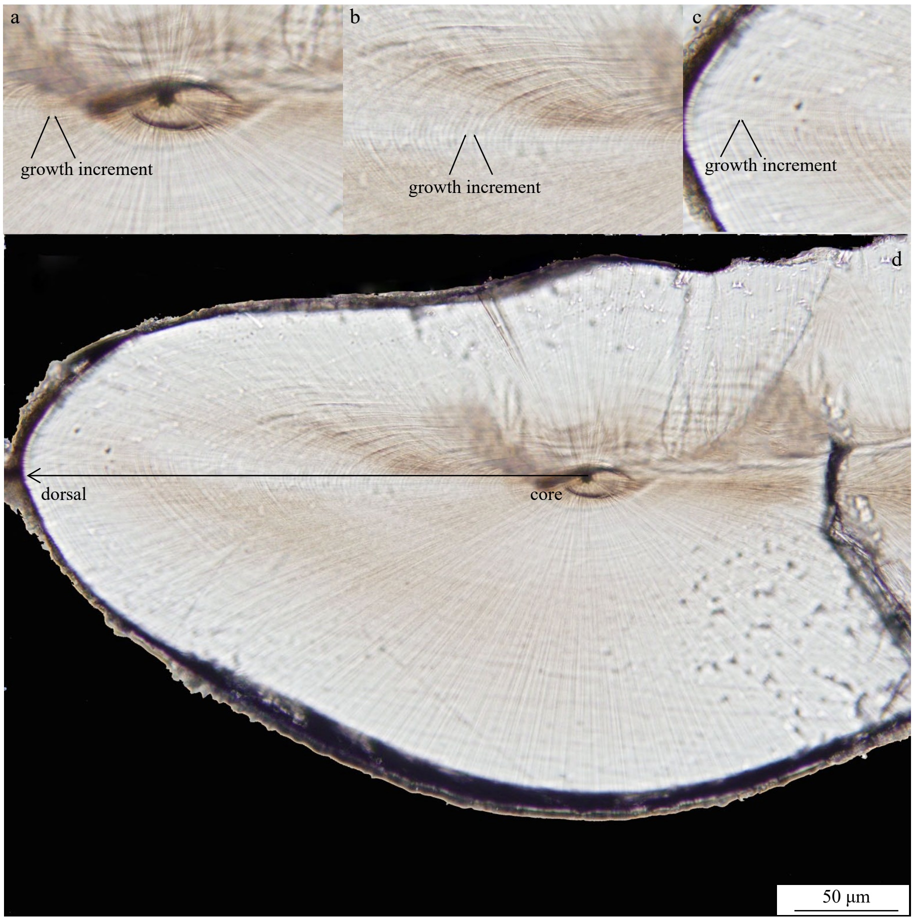

Fig. 2. Polished statolith of *Uroteuthis edulis* aged 200 d. All increments were counted and measured along the same axis from core to dorsal. a. Growth increments within nuclear zone; b. growth increments within lateral dome; c. growth increments within dorsal dome; d. polished statolith.

Table 2. Descriptions of environmental variables

Environmental variable	Description
SST	sea surface temperature
Temp_25	water temperature at the depth of 25 m
MLD	mixed layer depth
SSH	sea surface height
SSS	sea surface salinity
Chl *a*	chlorophyll *a* concentration
ZV	zonal current velocity
VV	vertical current velocity

to ensure the consistency of the overall specimen. Analysis of variance (ANOVA) was used to analyze the daily increment width of monthly groups, and *t*-test was used to explore sexual differences.

In order to quantify the relationship between daily increment of statolith and environmental variables, the gradient forest method was used to screen key environmental variables (Ellis et al., 2012). The gradient forest method can use multiple potentially correlated variables as predictors and provide the goodness-of-fit to the response variables and the importance weight of each predictor (Ellis et al., 2012). Therefore, the average daily increment width was used as the response variable, and environmental variables were used as the prediction variable. The analysis was conducted with “gradientForest” and “extendedForest” package in R (Ellis et al., 2012; Sun et al., 2020).

According to the importance weight of the predictor variable obtained by the gradient forest method, the key environmental variables with the cumulative importance weight greater than 0.7 were selected to clarify the quantitative relationship between daily increment of statolith and environmental variables with generalized additive model (GAM) (Sun et al., 2020). Based on the collinearity and consistency of environmental variables, the multiple linear regression analysis was performed with the key environmental variables selected by gradient forest method. If there was no collinearity among these key environmental variables, daily statolith increment was modeled as a smoothing function of multiple environmental variables. Otherwise, the single environmental variable model was established. Thus, GAM model could be written as

$$\mathrm{DIW}_t = S(\mathrm{PV1}_t) + S(\mathrm{PV2}_t) + S(\mathrm{PV3}_t) + \varepsilon_t, \qquad (1)$$

where DIW_t is response variable representing daily increment width at Day *t*; $\mathrm{PV1}_t$, $\mathrm{PV2}_t$ and $\mathrm{PV3}_t$ are predictor variables representing key environment variables; $S(\,)$ is nonlinear function; ε_t is the random error. Daily increment width data are normally distributed after log transformation. Akaike Information Criterion (AIC) and R^2 were used to test the model goodness and select the best model (Fang et al., 2019). The analysis was conducted by MGCV package.

3 Results

3.1 *Hatching date and daily statolith growth*

The relationship between statolith increment and mantle length is assumed linear function, which allows back-calculations of *U. edulis* somatic growth based on statolith (Wang et al, 2010). The accumulated statolith daily increments for specimens are indeed linearly correlated with mantle length (Fig. 4), suggesting that statolith daily increments for the *U. edulis* can well represent their somatic growth.

The hatching dates of the 121 specimens ranged from January to September 2017 and the peak hatching period was from April to June and August, respectively, accounting for 52% and 27% of the overall specimens (Fig. 5). Therefore, the specimens of the squid were divided into four hatching groups and two dominant hatching groups of *U. edulis* were identified: spring-spawning group with the peak spawning period of April and summer-spawning group with the peak spawning period of August.

The samples of different groups in the peak period were selected for the subsequent analysis. ANOVA results showed that the daily increment width of statolith between April and August groups showed the significant growth difference (P<0.05), but the difference between genders was not significant (P>0.05). The daily increment width of April-spawning group reached a maximum value of 1.78 μm on the 63rd day after hatching and then declined on the 100th day (Fig. 6). The daily increment width of August-spawning group reached a maximum value of 1.62 μm on the 58th day after hatching and then declined on the 99th day (Fig. 6). On the whole, the daily increment width of April-spawning group was wider than that of August-spawning group. The daily increment width of statolith in April- and August-hatching groups increased first and then decreased after reaching the peak. However, the daily increment growth ranges of the two hatching groups were different. The difference in the daily increment width of statolith between April and August-hatching groups was confirmed.

3.2 *Key environmental variables*

As for the April-spawning group, Temp_25, SST, and ZV were selected as the key environmental variables affecting the daily increment width of statolith according to the gradient forest meth-

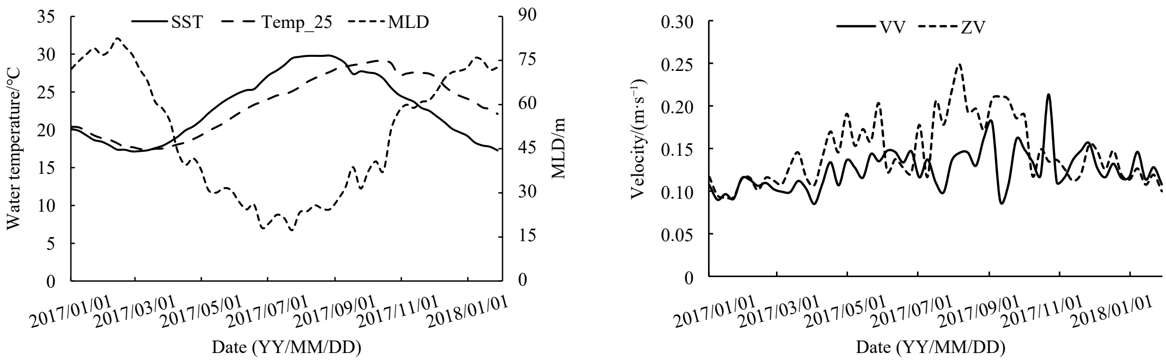

Fig. 3. Environmental variables in the sampling area, including sea surface temperature (SST), water temperature at the depth of 25 m (Temp_25), mix layer depth (MLD), vertical current velocity (VV) and zonal current velocity (ZV).

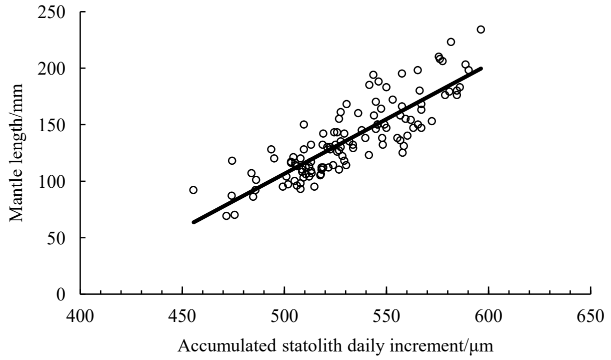

Fig. 4. Linear relationship between mantle length and accumulated statolith daily increment.

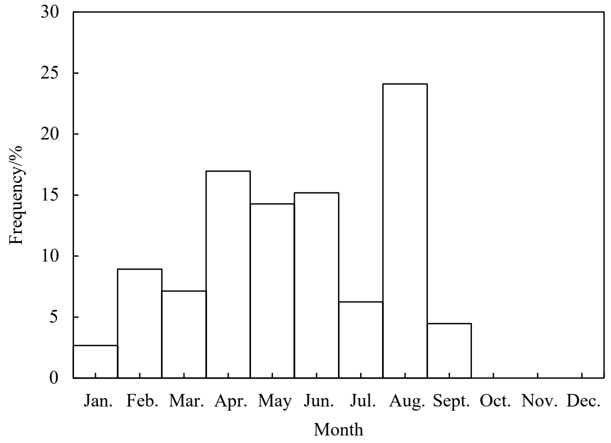

Fig. 5. Distribution of the hatching date of *Uroteuthis edulis* caught from September 2017 to March 2018 in East China Sea.

od. The cumulative importance weight was greater than 0.7 (Fig. 7a). The daily increment of statolith respectively showed strong threshold responses to Temp_25 (24°C), SST (25°C) and ZV (0.07 m/s), and the second strong threshold responses for these three variables were respectively 27°C, 28°C and 0.13 m/s (Figs 8a–c). As for the August-spawning group, SST, Temp_25 and MLD were selected as the key environment variables affecting the daily increment width of statolith. The cumulative importance weight was greater than 0.7 (Fig. 7b). The daily increment of statolith showed strong threshold responses to SST (20–22°C), Temp_25 (21–23°C) and MLD (55–60 m), respectively (Figs 8d–f).

3.3 *Key environment effects of statolith daily increment*

GAM analyses showed that the key environmental variables selected by the gradient forest method had the significant correlation with the daily increment of statolith, suggesting the consistency of the two statistical approaches in identifying key environmental variables. Multiple linear regression analysis suggested that there was a linear relationship between SST and Temp_25 for the April-spawning group and August-spawning group, so the effects of the above two environmental variables on the daily increment of statolith should be considered separately in the establishment of GAM. The GAM established with the combination of Temp_25 and ZV environmental variables was identified as the best model to explain the daily incremental growth of statolith in April-spawning group based on the lowest AIC and the overall interpretation rate of the deviation was 82.6% (Table 3). As for August-spawning group, GAM established with SST was identified as the best model to explain the daily incremental growth of statolith based on the lowest AIC and the overall interpretation rate of the deviation was 97.1% (Table 3).

As for the April-spawning group, the daily increment of statolith was positively correlated with Temp_25 and SST within the range of 20–26°C and negatively correlated with Temp_25 and SST above 26°C. The threshold responses of the daily increment of statolith to Temp_25 around 26°C were indeed found (Figs 9a, b). ZV was positively correlated with the daily increment of statolith in the range of 0.05–0.15 m/s (Fig. 9c). As for the August-spawning group, the daily increment of statolith was positively correlated with SST and Temp_25 within the range of 16–25°C. The threshold responses of daily increment of statolith to SST and Temp_25 around 25°C were found (Figs 9d, e). The daily increment of statolith was positively correlated with MLD within the water depth range of 0–50 m, negatively correlated with MLD within the water depth range of 50–60 m and gradually positively correlated with MLD above 60 m. The threshold response of the daily increment of statolith to MLD around 60 m was found (Fig. 9f).

4 Discussion

4.1 *Spawning seasonality and daily growth*

Uroteuthis edulis spawns in all seasons with two dominant hatching peaks in this study: April to June and August, which were different from the peaks in March and April, October and November in the southern part of the East China Sea (Wang, 2009). As a year-round spawning cephalopod, different hatching groups of *U. edulis* had different suitable spawning temperatures (Wang et al., 2010). The hatching and mortality as well as survival rates of individuals were significantly affected by the surround-

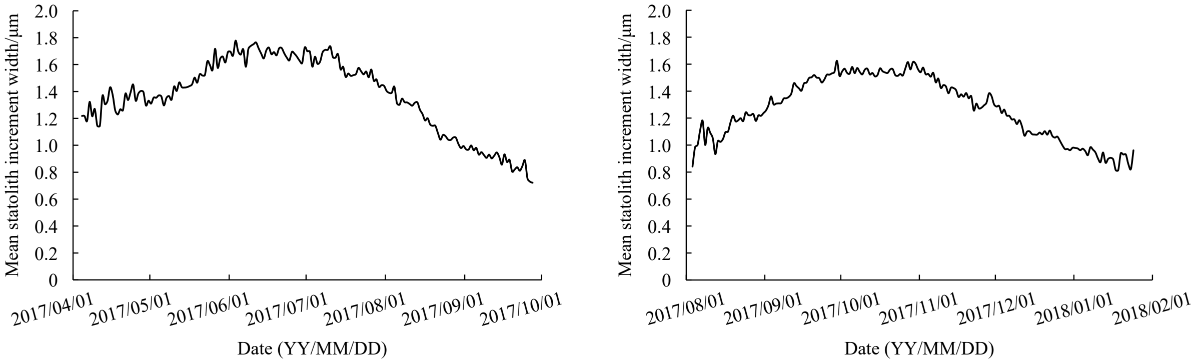

Fig. 6. Mean daily increment width of April-spawning and August-spawning groups in 2017.

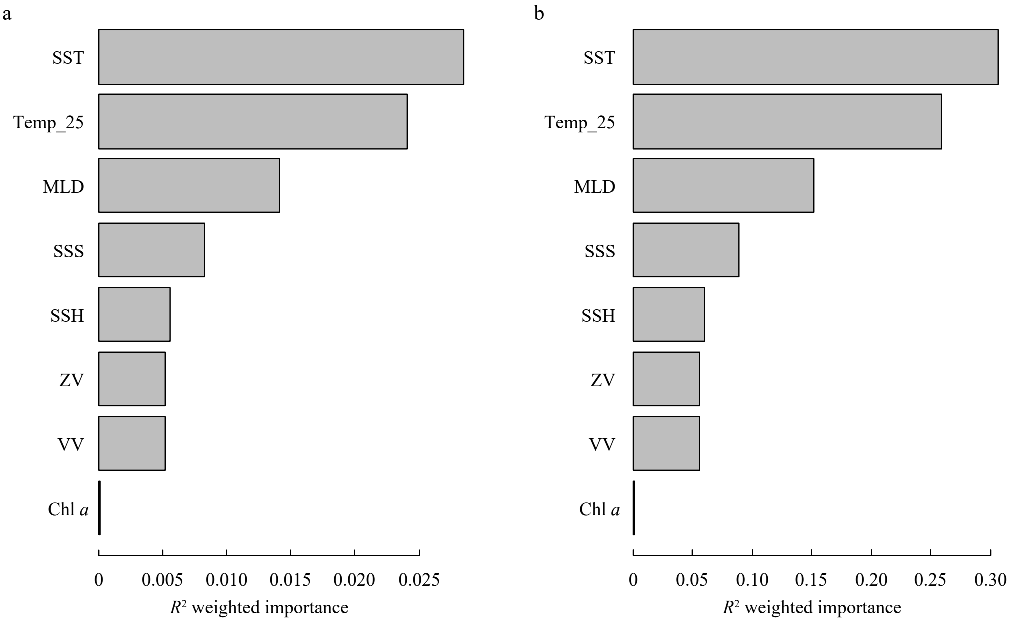

Fig. 7. Importance of environmental variables in response to mean daily increment width of April-spawning group (a) and August-spawning group (b) in 2017. SST is the abbreviation of sea surface temperature; Temp_25, water temperature at depth of 25 m; MLD, mix layer depth; SSS, sea surface salinity; SSH, sea surface height; VV, vertical current velocity; ZV, zonal current velocity; Chl *a*, chlorophyll *a* concentration.

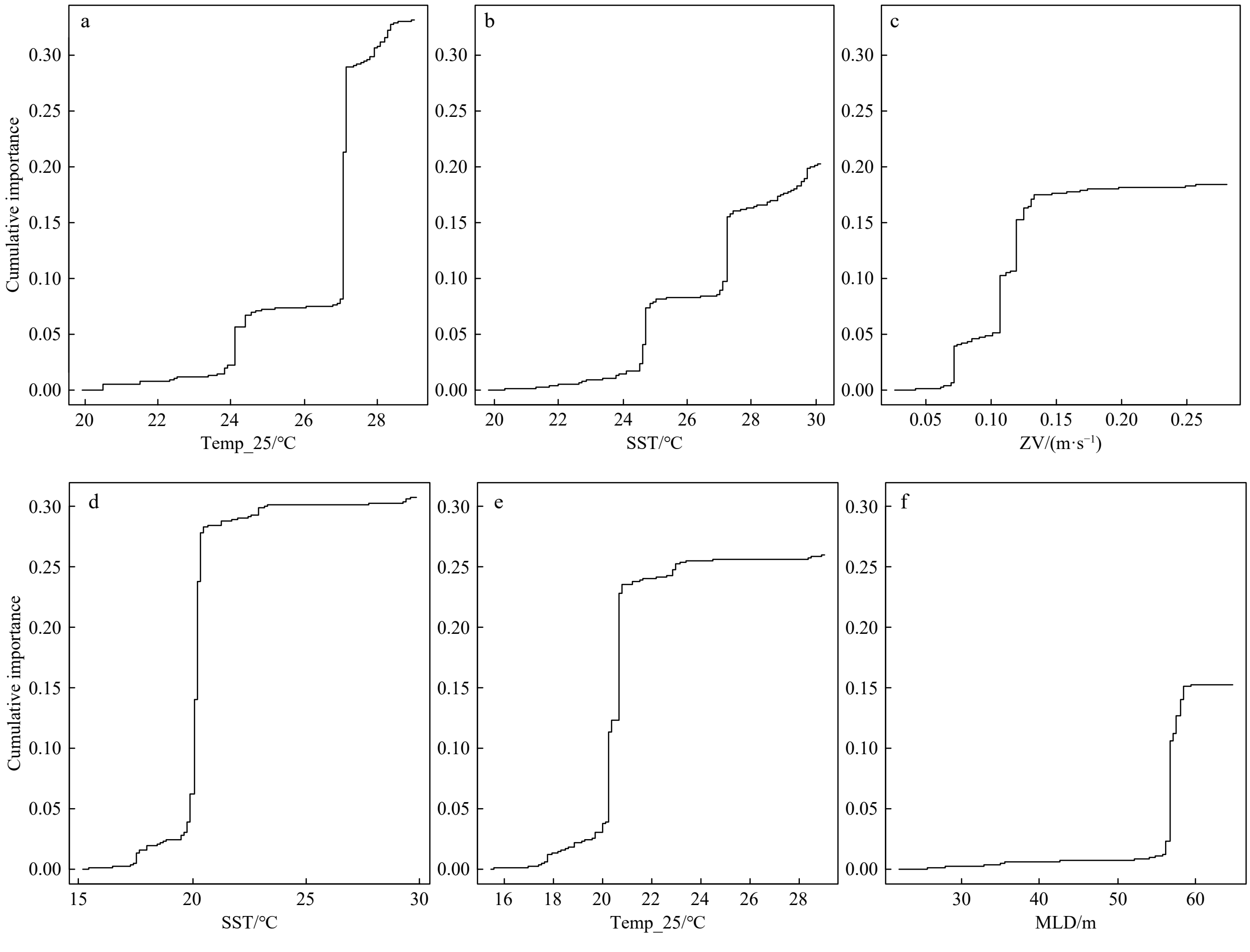

Fig. 8. Cumulative importance of environmental variables in relation to daily increment width of statolith for April-spawning group (a–c) and August-spawning group (d–f). Temp_25 is the abbreviation of water temperature at the depth of 25 m; SST, sea surface temperature; ZV, zonal current velocity; MLD, mix layer depth.

Table 3. Key environmental variables of April- and August-spawning groups identified based on the analysis results of the generalized additive model (GAM)

Group	Environmental variable	AIC	R^2	Deviance explained/%	P-value	Significance
April-spawning	Temp_25	−238.50	0.72	73.1	0.000	***
	SST	−106.51	0.40	43.0	0.000	***
	ZV	−165.57	0.57	58.6	0.000	***
	Temp_25+ZV	−299.13	0.81	82.6	0.000	***
	SST+ZV	−239.13	0.72	73.8	0.000	***
August-spawning	**SST**	−674.92	0.97	97.1	0.000	***
	Temp_25	−651.80	0.96	96.8	0.000	***
	MLD	−348.80	0.82	82.5	0.000	***

Note: AIC is the abbreviation of Akaike Information Criterion; Temp_25, water temperature at the depth of 25 m; SST, sea surface temperature; ZV, zonal current velocity; MLD, mix layer depth. Model significance: *, $P<0.05$; **, $P<0.001$; and ***, $P<0.000\,1$. Environmental variables in bold are the highest goodness-of-fit based on GAM.

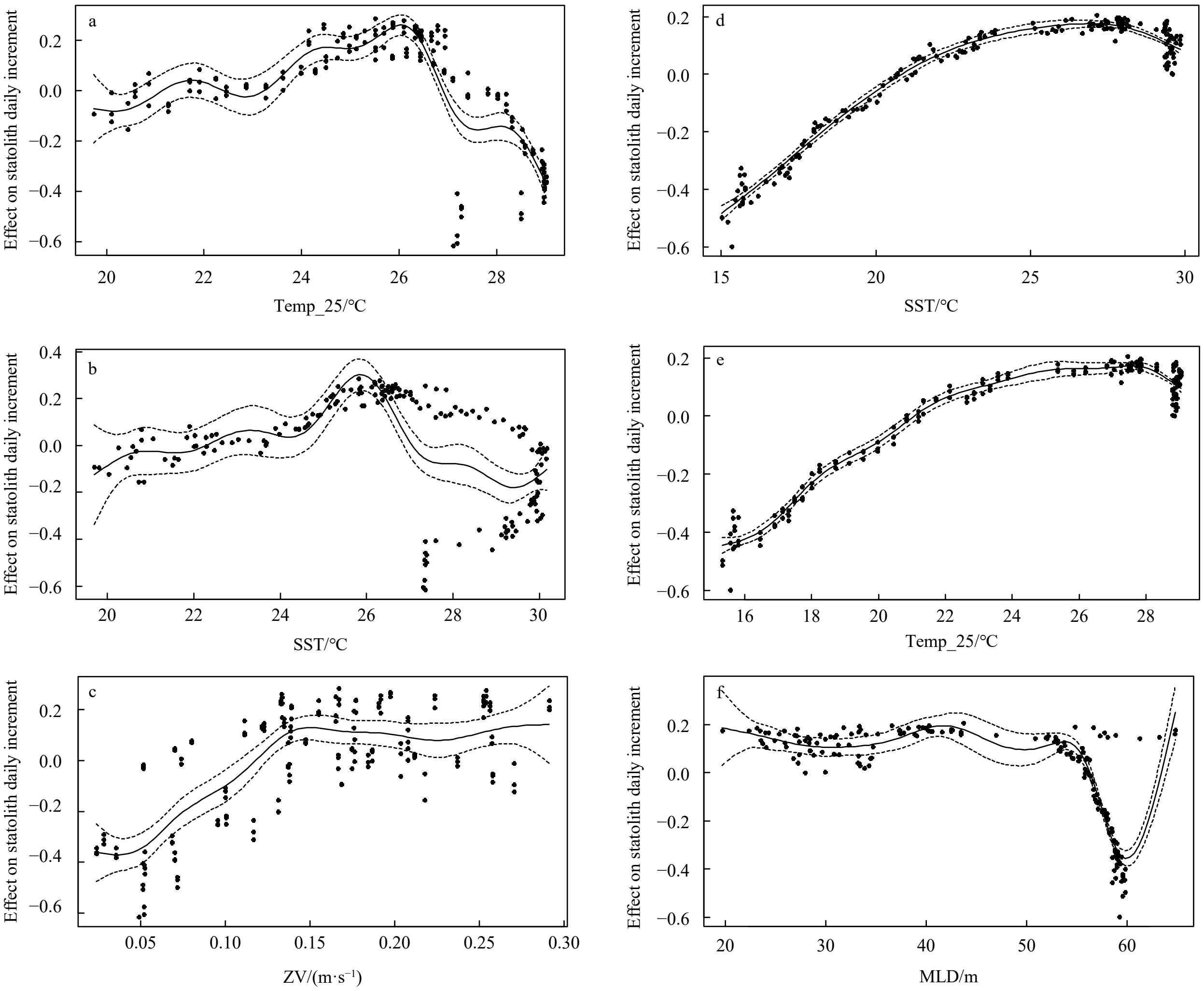

Fig. 9. Effective of environmental variables on daily increment width for April-spawning group (a–c) and August-spawning group (d–f) based on generalized additive model (GAM) analyses. Temp_25 is the abbreviation of water temperature at the depth of 25 m; SST, sea surface temperature; ZV, zonal current velocity; MLD, mix layer depth.

ing environment (Wang et al., 2013), which also led to different hatching periods of various groups in different seasons. In addition, it was difficult to obtain the samples in the fishing ban period according to Chinese fishery regulation, so the data of hatching groups in October–December were not determined in the study. More specimens will be collected and examined in future studies in order to confirm this finding and exclude the possibility that the spawning specimens captured from October to December was not enough.

The daily increment width of statolith could be used as an indicator to explore the growth and development of an individual (Bounket et al., 2019). As the individual growth and feeding activity increased, the daily increment width of statolith gradually became wider (Kikko et al., 2019). The rise of water temperature in the habitat also made it wider (Sun et al., 2020). In this study, daily increment widths of April-spawning and August-hatching groups were the largest respectively on the 63rd day and the 58th day, indicating that these two groups had the more suitable habitat and the fastest growth rate in this stage. In addition, within 150 d after hatching, the water temperature of the environment of the April-spawning group was higher than that of the August-spawning group, thus resulting in the wider daily increment width of statolith in the April-spawning group. The daily increment of statolith increased firstly and then decreased, reflecting the individual growth process. The results also suggested that the characteristics of the individual life history were adjusted by oceanographic environmental factors (Pecl and Jackson, 2008).

The year-round reproductive and spawning traits of *U. edulis* enable it to reproduce under the changing marine environment and sufficient foods. It may be the response mechanism of the population to climate change (Wang et al., 2013). Seasonal changes in water temperature may also affect the distribution and abundance of prey, which improves the availability of food and promotes the growth and reproduction of individuals (Wang et al., 2011).

4.2 *Key environmental variables*

The spawning and hatching of the population directly affected its early growth and survival as well as its subsequent recruitment process, which was closely related to its ambient environment, including water temperature and food availability (Arkhipkin and Shcherbich, 2012; Kurota et al., 2020). In East China Sea, water temperature affected the timing and duration of the spawning season of cephalopods and the abundance and distribution of foods, which in turn affected early growth of population and the dynamics and structure of the ecosystem (Takahara et al., 2017). ZV, VV and MLD reflected the features of ocean currents, and the distribution of MLD was closely related to water temperature (Morgan et al., 2013). In summer, coastal current brought rich nutrients and enhanced the primary productivity of the study area, as indicated by the change in chlorophyll *a* concentration (Wang, 2009; Yu et al., 2015). The key environmental variables identified by the gradient forest method was consistent with those obtained by GAM. The results provide the basis for understanding the complex interaction between squid growth and multiple environmental variables.

SST, Temp_25 and ZV were the three main environmental variables affecting daily incremental growth of statolith for April-spawning group. Since April, eggs or larvae had no swimming ability, so the group moved to the northeast along with the strengthening effect of the Kuroshio Current and Taiwan Warm Current to feed from spawning ground to feeding ground (Wang, 2009). The result indicated that temperature was the main environmental variable affecting the daily incremental growth of statolith of August-spawning group. MLD was also another important environmental variable of August-spawning group since the intense thermocline in summer caused the phenomenon of water stratification (Hao et al., 2012). Therefore, the growth of statolith was related to environmental variables, and the key environmental variables in different spawning months were different. Sea water temperature and current were the key environmental variables affecting squid growth.

4.3 *Environmental effects on squid growth*

Squid individuals within 150 d after hatching were in the early stages of life history, including the embryonic, juvenile and larva stages. The growth and development of individuals at each stage were closely related to the environmental variables of habitat and the abundance of foods (Pecl and Jackson, 2008; Alabia et al., 2016; Yamaguchi et al., 2018b). Generally, *U. edulis* usually hatched in the temperature range from 15°C to 20°C and the hatching rate gradually increased when the water temperature increased from 15°C to 20°C. The juvenile inhabit was in the temperature of 17–21°C (Yamaguchi et al., 2018b, 2019). Water temperature after hatching was relatively low for April-spawning group due to the low temperature (20–24°C) in the stages of embryos and juveniles. The squid gradually entered the larval stage in the range of 24–27°C and the swimming range and feeding opportunity were also improved with the enhancement effect of Kuroshio Current. Therefore, they grew faster. Too high water temperature might affect the metabolic rate of marine organisms, thus restraining the metabolism and activity ability (Rosa and Seibel, 2008). Therefore, *U. edulis* growth in early life stage became slow when SST exceeded 27°C. In addition, individuals at different stages of life history had different temperature tolerances (Wang et al., 2013). As for the August-spawning group, water temperature and food abundance were relatively high after hatching and *U. edulis* grew rapidly in the temperature range of 21–28°C. Water temperature was the most important factor affecting early growth of *U. edulis*. Therefore, the increase in water temperature within a suitable range was beneficial to the growth of individuals. The seasonal change of water temperature had a significant effect on the growth of different hatching groups, and the suitable growth temperatures in different life history stages were different.

The East China Sea is mainly affected by the Kuroshio Current and Taiwan Warm Current, which affect the distribution and migration range of marine species, including *U. edulis* (Wang, 2009; Xing et al., 2020). As for the April-spawning group, squids could move to a wider area for feeding along the direction of Kuroshio Current, thus increasing the availability of foods and greatly contributing to the growth of individuals. MLD increase indicated that the power of the ocean currents such as coastal current was weakened, so the nutrient input for August-spawning group was reduced (Sun et al., 2020). When the MLD was 55–60 m, the vertical distribution of water temperature was severely affected by the thermocline, and the organism foods were less, thus limiting its growth (Hao et al., 2012).

5 Conclusions

The spawning season of *U. edulis* was nearly one year around in the East China Sea with two dominant seasons of spring and summer. Early growth of April- and August- hatching groups had different responses to environmental variables, but their responses to water temperature were the most significant. In addition, the spawning area of spring-spawning group expanded due to the ocean current, thus promoting the availability of foods. The species and abundance of foods of summer-spawning group were rich, and significantly affected by temperature and MLD. Therefore, early growth of *U. edulis* was influenced by temperature, currents and food supply. This study revealed the main environmental causes for the differences in different hatching groups of *U. edulis* and provided the basis for the management and conservation of *U. edulis* in the East China Sea.

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