



# A Modeling Study on Population Dynamics of Jellyfish *Aurelia aurita* in the Bohai and Yellow Seas

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Jellyfish blooms have become a marine environmental issue with detrimental effects on marine ecosystems around the world. The jellyfish *Aurelia aurita* is one of dominant species of blooms worldwide and also in the Bohai and Yellow Seas (BYSs) of China. To investigate population dynamics and controlling factors on population biomass, a complex population-dynamic model is developed for jellyfish of *A. aurita* in the BYSS that includes three components, namely, a three-dimensional coupled physical-biogeochemical model, a Lagrangian particle-tracking model, and an energy balance model for the jellyfish life cycle. By comparison, the model well reproduces the individual growth and seasonal evolution of *A. aurita* population. During individual growth period, the temperature is a key factor controlling growth and dry weight, characterized by a nearly linear growth rate. Longer period tends to favor larger medusa size and further to promote the biomass. The yearly peak biomass shows interannual variations that are controlled by the jellyfish magnitude, food concentration, and effective accumulative temperature of growth, with their contributions quantified through statistical analyses. Only considering the effect of temperature, the yearly peak biomass can be obtained through the durations of suitable temperature ranges for strobilization and individual growth that determines the magnitude and the averaged individual weight, respectively, with longer strobilation duration leading to higher magnitude. The simplified statistical relationships would favor to understand the temperature control on population dynamics of *A. aurita*.

**Keywords:** *Aurelia aurita*, population dynamics, biomass, duration of suitable temperature range, Bohai and Yellow Seas

## 1 INTRODUCTION

In recent decades, jellyfish blooms in coastal waters have increased significantly and become a marine environmental issue of global concern, which are considered to be associated with both intensive human activities and climate change (Purcell et al., 2007; Richardson et al., 2009; Sun et al., 2015). Jellyfish blooms can cause detrimental consequences for the marine fishery, industry, and tourism, such as predation to fish eggs and larva, competition with fish for food, clogging cooling water intakes of coastal power plants, and stinging tourist by venomous species (Purcell et al., 2007;

Richardson et al., 2009; Zhang et al., 2017; Sun et al., 2019). In coastal seas of China, jellyfish blooms have been one of the most severe marine ecological problems (e.g., eutrophication, harmful algal blooms, and hypoxia), with dominant species of *Aurelia aurita*, *Cyanea nozakii*, and *Nemopilema nomurai* (Dong et al., 2010; Zhang et al., 2017). As one of the common species, *A. aurita* has a worldwide distribution in neritic waters between 70°N and 40°S (Lucas, 2001) and causes jellyfish blooms in the Bohai and Yellow Seas (BYSS) of China (Dong et al., 2010; Dong et al., 2015).

The life history of *A. aurita* includes complex strategies in which there are three main stages: the pelagic planula stage, the benthic polyp stage, and the pelagic ephyrae and medusa stage (Lucas, 2001). During the life cycle, the availability of hard substrate is of key importance for the settlement success of planula and the living of the polyp stage; temperature and food are considered the key influence factors on reproduction and growth of *A. aurita* (Lucas, 2001; Møller and Riisgård, 2007; Shi et al., 2016), while salinity has no significant impact on *A. aurita* in coastal seas of China (Fu et al., 2011). The suitable temperature for strobilation offshore China is 10°C–20°C (Wang, 2013; Wang and Sun, 2015), with the intensive strobilation at 12°C–13°C (Wang, 2013; Shi et al., 2016). Temperature can also affect the growth and metabolism of ephyrae and medusa by affecting enzymatic activities, with too low temperature (<8°C) or high temperature (>30°C) causing inhibition of growth and even death (Widmer, 2005). Experiments show that 10°C–25°C is the suitable temperature range for *A. aurita* growth in the northern Yellow Sea (Fu et al., 2011). The growth and metabolism of *A. aurita* is also modulated by food, with abundant food favoring its predation (Lucas, 1996; Goldstein and Steiner, 2020). *Aurelia aurita* has a wide range of food, involving all available zooplankton (Ma and Fan, 1998).

Previous studies indicated general seasonal evolutions of *A. aurita* population in coastal areas such as fjords and lagoon in the northern hemisphere: ephyrae beginning to appear in March and April and abundance and biomass increasing since May with zooplankton (food of *A. aurita*) increasing and decreasing in September (Møller, 1980; Olesen et al., 1994; Bonnet et al., 2012). In coastal areas of China, the seasonal evolution of *A. aurita* shows a similar pattern although slight difference in timing. Based on field survey in 2011 in the Jiaozhou Bay of the Yellow Sea, ephyrae were observed in May and June and rapidly grew and developed into jellyfish from late May to early July, but its bell diameter shrank and abundance reduced in August and September (Wang and Sun, 2015). In the Bohai Sea, jellyfish medusa was observed during July to October in the Laizhou Bay and in June and July in the Liaodong Bay (Wang B. et al., 2012; Zuo et al., 2016). Nevertheless, factors influencing seasonal and even interannual variations of *A. aurita* population in the BYSS are poorly constrained.

Population dynamics of jellyfish have been studied widely, while they mainly focus on life history strategies (Lucas, 2001; Xie et al., 2021) and feeding, growth, respiration, and bioenergetics during the life cycle (Olesen et al., 1994; Møller and Riisgård, 2007; Goldstein and Steiner, 2020; Gueroun et al., 2020; Wang et al., 2021). Statistical models have been used to explore the relationship between jellyfish

populations and environmental factors (e.g., temperature, salinity, and zooplankton) and further to predict the distribution of jellyfish (Kremer, 1976; Decker et al., 2007; Xu, 2009; Wang S. et al., 2012; Fernández-Alías et al., 2020). However, these statistical models cannot consider the influence of hydrodynamics. Jellyfish movement is mainly dominated by currents due to its weak swimming ability. To take into account currents, Lagrangian particle-tracking methods are utilized to simulate trajectories and distributions of jellyfish (Moon et al., 2010; Wei et al., 2015). However, the tracking method does not involve the individual growth of jellyfish nor quantify the jellyfish biomass. Therefore, a complex model including the individual growth and the movement of jellyfish is required to investigate population dynamics.

In this study, a population-dynamic model is developed to research population dynamics of *A. aurita* in the BYSS and explore factors controlling population variations. Based on model results, statistical relationships are established to associate the yearly peak biomass with temperature that further understand the impact of temperature on the population dynamics BYSS.

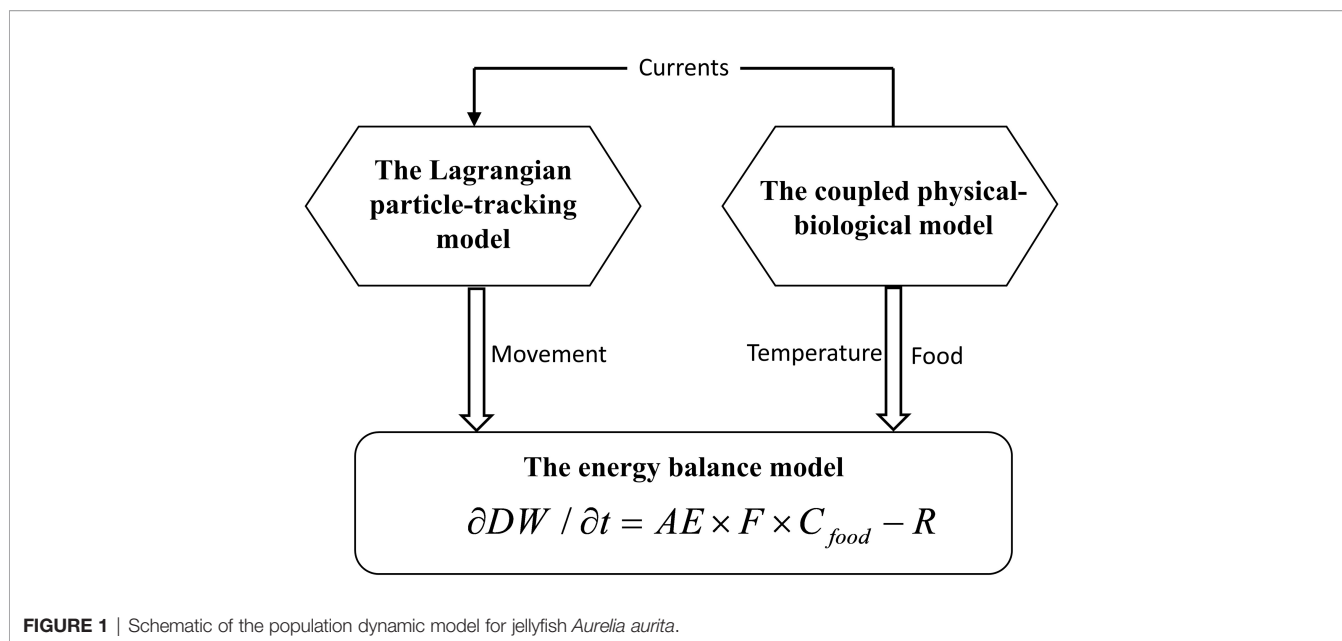
## 2 METHODS AND MATERIALS

### 2.1 Establishment of the Population-Dynamic Model for *Aurelia aurita*

The population-dynamic model incorporates three components: a three-dimensional coupled physical–biological model that provides temperature, food, and currents to influence growth and movement of *A. aurita*; a Lagrangian particle-tracking model that simulates movement and determines positions of *A. aurita*; and an energy balance model that regulates the growth of medusa (**Figure 1**).

#### 2.1.1 The Coupled Physical–Biological Model

The coupled model includes a physical and a biological component. The physical model is configured with the Regional Ocean Modeling System (ROMS; Haidvogel et al., 2008). The model domain covers the whole BS, the Yellow Sea, and part of the East China Sea, with a horizontal resolution of 2.2 km in the northern BS and 4.8 km near the open boundary in the East China Sea. The model has 30 vertical layers with enhanced resolution near the surface and bottom. The biogeochemical model is Carbon, Silicate, and Nitrogen Ecosystem (CoSiNE; Chai et al., 2002; Xiu and Chai, 2014). The state variables include two forms of dissolved inorganic nitrogen, namely, nitrate and ammonium; phosphate; silicate; two phytoplankton functional groups, namely, picophytoplankton and diatoms; two classes of zooplankton, namely, microzooplankton and mesozooplankton; and two classes of detritus, namely, slow-sinking small detritus and fast-sinking large detritus. The microzooplankton and mesozooplankton in the model serve as food for *A. aurita*. More detailed model descriptions can be found in Zhang et al. (2022). The coupled model has been implemented for ecosystem



**FIGURE 1** | Schematic of the population dynamic model for jellyfish *Aurelia aurita*.

research in the BYSs (Li et al., 2021a; Li et al., 2021b; Nan et al., 2022; Zhang et al., 2022).

### 2.1.2 The Lagrangian Particle-Tracking Model for *Aurelia aurita* Drift

The Lagrangian particle-tracking model is Lagrangian TRANSPORTmodel (LTRANS; Schlag and North, 2012), a three-dimensional offline particle tracking model that can be fully coupled to the instantaneous flow field output from the ROMS hydrodynamic model and that can simulate the motion of passive particles, sediment, or floating objects. The LTRANS model predicts the particle displacement through physical processes of advection and turbulent diffusion. In this model, the external time interval was 1 h for inputs from the physical–biological model, and the internal time interval was 20 min for movement computation. Only the horizontal movement are considered for *A. aurita* drift in this study.

### 2.1.3 The Energy Balance Model

Specific growth of *A. aurita* individuals is dependent on energy balance. The energy balance generally involves ingestion, respiration, and excretion that associate with temperature and food (Olesen et al., 1994; Møller and Riisgård, 2007). In previous studies, specific formula relating to energy balance and growth rate has been presented in different forms (Supplementary Table S1). Referring to Møller and Riisgård (2007), the formula for *A. aurita* bioenergetics in the BYSs is given as

$$\frac{\partial DW}{\partial t} = AE \times F \times C_{food} - R \tag{1}$$

where *DW* denotes dry weight, *AE* is assimilation efficiency, *F* is clearance rate, *C<sub>food</sub>* is food concentration, and *R* represents respiration. The dry weight (mg) can be estimated from umbrella diameter (mm) for *A. aurita* ephyrae and medusa. The relationship for ephyrae (Båmstedt et al., 1999) is expressed as

$$DW = 1.913 \times 10^{-3} \times UD^{2.998} \tag{2}$$

and the relationship for medusa (Møller and Riisgård, 2007) is

$$DW = 0.004 \times UD^{2.7} \tag{3}$$

where *UD* is the umbrella diameter.

Expressions of terms in Eq. (1) and related processes have been deeply discussed (Uye and Shimauchi, 2005; Møller and Riisgård, 2007; Wang and Li, 2012). The formula is further expressed as

$$\begin{aligned} \frac{\partial DW}{\partial t} = & AE \times (K_1 e^{K_2 T} \times DW^{K_3}) \times (C_s + r_0 C_l) \\ & \times (r_1 \times r_2) - K_4 e^{K_5(T-T_0)} \times r_3 \times DW \end{aligned} \tag{4}$$

where *T* denotes temperature, and *C<sub>s</sub>* and *C<sub>l</sub>* represent microzooplankton and mesozooplankton concentrations, respectively. Parameters in Eq. (4) are given in Table 1 for ephyrae and medusa, respectively.

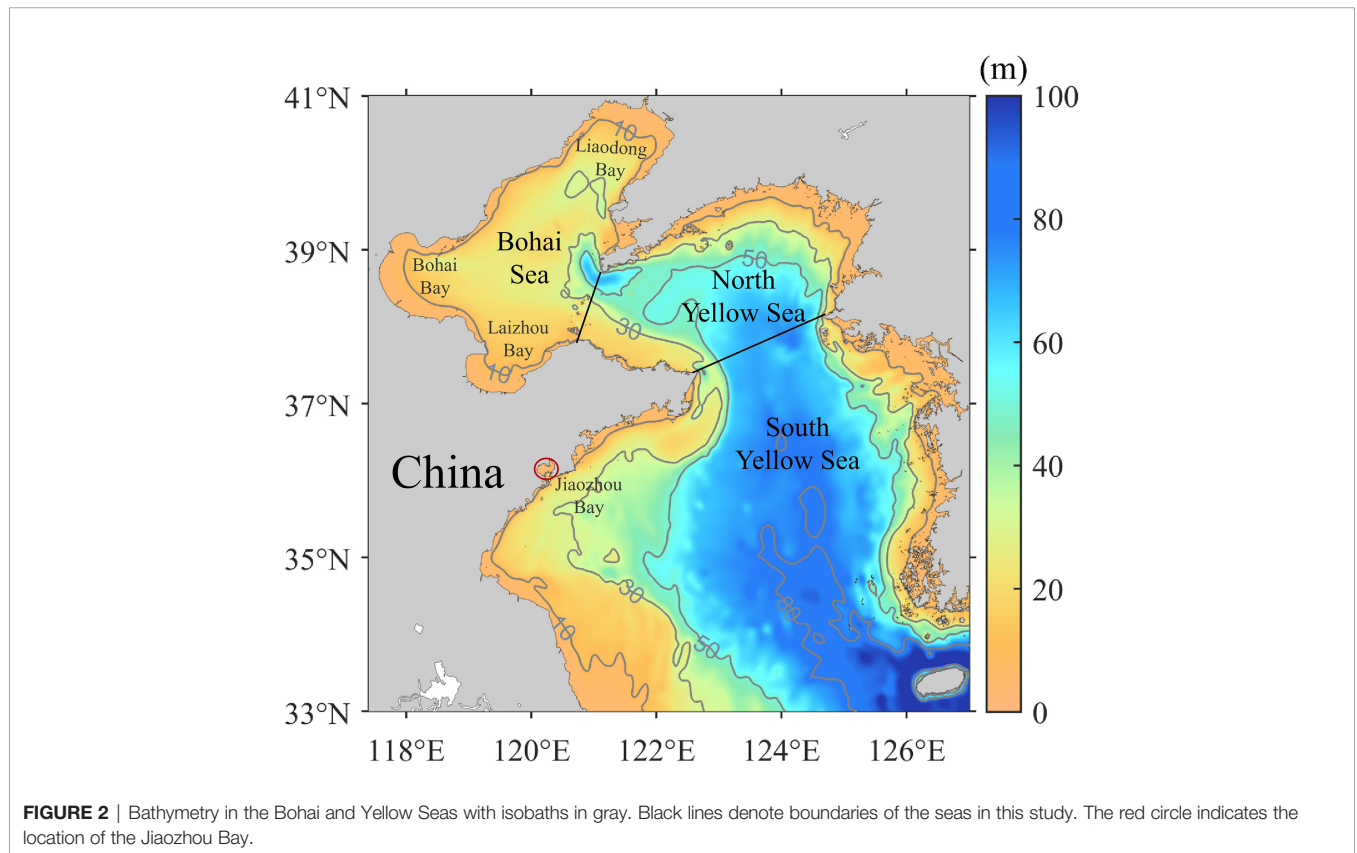
### 2.1.4 Model Configuration

Coastal substrate is of key importance for the benthic polyp stage and then the ephyrae release through strobilation (Toyokawa et al., 2011; Lucas et al., 2012). To indicate possible substrate in the BYSs, the initial condition of *A. aurita* in the model is ephyrae released in coastal areas with water depth <10 m (Figure 2). The release of ephyrae is dependent on temperature. Referring to Wang (2013; 2015) and Shi et al. (2016), ephyrae are released when temperature is during 10°C–16°C, with intensive release at temperature of 12°C–13°C (Table 2). Based on surveys in 2011 in Jiaozhou Bay by Wang S. et al. (2012), one ephyrae particle represents 1,000 *A. aurita* individuals (1 particle = 1,000 *A. aurita*).

Considering that *A. aurita* is observed in the upper layer of the water column, particles representing ephyrae are placed in the upper layer (with depth of 3.5 m) and moved at this depth. Under influence of currents, the horizontal movement speed of *A. aurita*

**TABLE 1** | Parameters in the formula of *Aurelia aurita* bioenergetics.

Parameters	Parameter description	Values for ephyrae	Values for medusa
$AE$	Assimilation efficiency	0.85	0.65
$K_1$	–	0.066	1.24
$K_2$	–	0.006	0.048
$K_3$	Influence index of dry weight on feeding rate	0.22	0.5
$r_0$	Ratio of feeding on large zooplankton	0.75	0.8
$r_1$	Ratio of dry weight to carbon content	3.6/0.13	3.6/0.13
$r_2$	Coefficient related to ratio of N to C	$12 \times 6.625/1,000$	$12 \times 6.625/1,000$
$K_4$	–	19.03	13
$K_5$	–	0.166	0.17
$T_0$	Suitable growth temperature for ephyrae or medusa-	20	25
$r_3$	Ratio of dry weight consumption to respiratory oxygen consumption	$1/(3.66 \times 50)$	$1/(2.24 \times 50)$



**FIGURE 2** | Bathymetry in the Bohai and Yellow Seas with isobaths in gray. Black lines denote boundaries of the seas in this study. The red circle indicates the location of the Jiaozhou Bay.

**TABLE 2** | The temperature range suitable for the strobilation of polyps and the number of ephyrae released in the model, inspired by Wang (2013; 2015) and Shi et al. (2016).

Temperature range (°C)	Number of ephyrae (ind ephyrae <sup>-1</sup> day <sup>-1</sup> )
10–11.5	1
11.5–12	2
12–13	3
13–13.5	2
13.5–16	1

accounts for about 60% of the current velocity based on field surveys in the southwestern areas of the Korean Peninsula in the Yellow Sea (Yoon et al., 2018). Therefore, this result is used to

simulate movement of *A. aurita* in the BYSS. The population-dynamic model is running from 2011 to 2017 with the time interval of 20 min for computation. Model outputs are saved daily for analyses. In addition, to further understand effects of temperature/currents and zooplankton on interannual variations of *A. aurita* population, sensitivity experiments are conducted with temperature/currents and zooplankton of 2011 repeated in these years, respectively.

## 2.2 Data From Laboratory Experiments and Field Surveys

Data for model validation are from laboratory experiments and field surveys. *Aurelia aurita* ephyrae were incubated at 18°C with food concentration of 0.1 mg C L<sup>-1</sup> and without food in the

laboratory to get the respiration and growth processes. The feeding rate of *A. aurita* medusae with bell diameter of 2 cm at different food concentrations was obtained by incubation experiments. Ephyrae and medusae in the experiments were sampled from the Jiaozhou Bay. Details on laboratory experiments can be found in Wang (2015). Bell diameters from May to September in 2011 were obtained by surveys conducted in the Jiaozhou Bay. Ephyrae and young medusae were selected and identified under a dissecting microscope immediately after towing and measured with a vernier caliper. For detailed descriptions, refer to Wang and Sun (2015).

## 2.3 Statistical Analyses Methods

The multiple linear regression method is utilized to quantify the relationship of interannual variations of *A. aurita* biomass with controlling factors. It is a statistical technique that uses several explanatory variables to predict the outcome of a response variable. When analyzing the links of *A. aurita* abundance and individual weight with temperature, one-variable linear regression is used for abundance against temperature duration suitable for strobilation, and a quadratic equation is established between the individual weight and temperature duration suitable for *A. aurita* growth.

## 2.4 Model Validation With Laboratory Experiments and Field Observations

Simulated respiration, growth, and feeding rate are calibrated with laboratory experiments (Figures 3A–C). DW of *A. aurita* ephyrae indicates an exponential decreasing trend against incubation time under respiration, with a determination coefficient of 0.86 between the simulation and laboratory experiment results. With temperature at 18°C and food concentration at 0.1 mg C L<sup>-1</sup>, DW of ephyrae rises monotonically with a determination

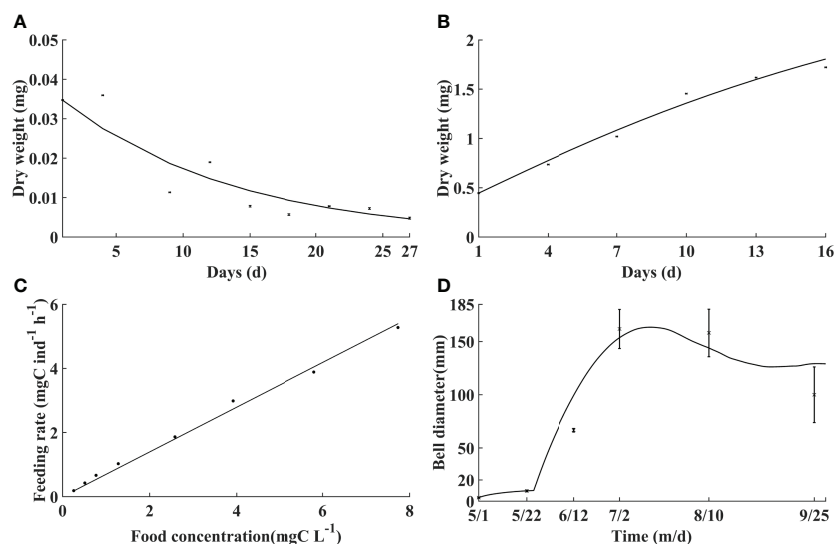
coefficient of 0.98. The feeding rate of *A. aurita* medusa increases monotonically against food concentration with a determination coefficient of 0.99.

Simulated bell diameter during *A. aurita* growth period is compared with field observations in the Jiaozhou Bay in the Yellow Sea (Figure 3D). The simulated variation of the bell diameter is similar to that of the observations. The bell diameter is overall <10 mm in early and mid-May, suggesting that the ephyrae is released shortly. It increases markedly through the end of May to July, with the maximum bell diameter of about 175 mm in mid-July. After the peak time, the bell diameter begins to decrease. The comparison suggests that the model well reproduces the individual growth of *A. aurita*.

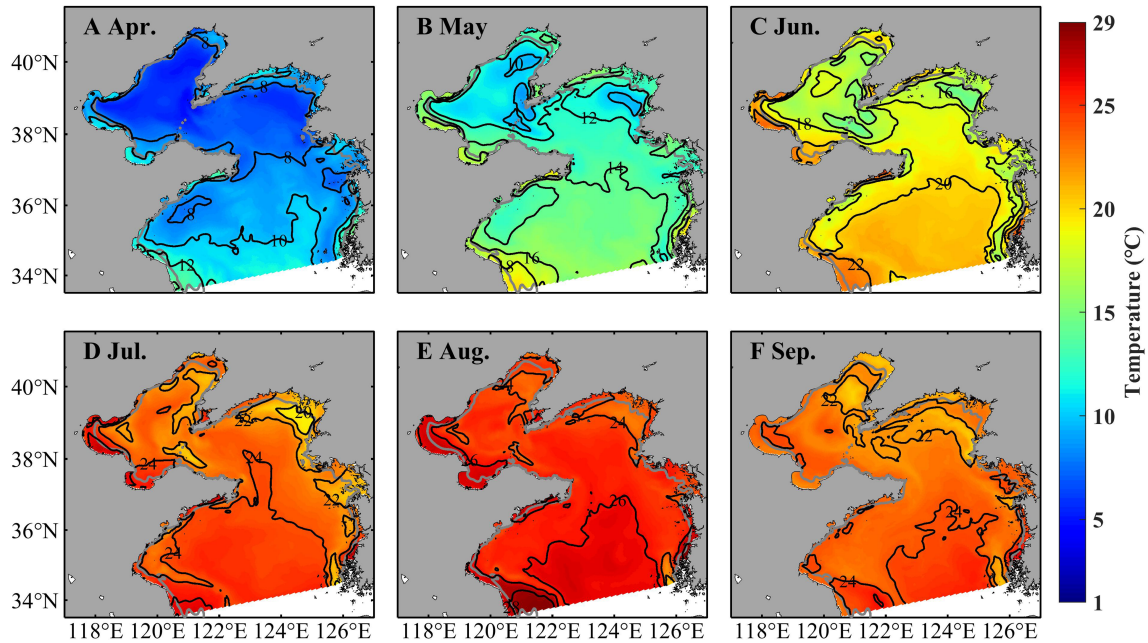
## 3 RESULTS

### 3.1 Seasonal Variations of Temperature, Zooplankton, and Currents

Temperature, zooplankton, and currents influence strobilation, growth, movement, and further population dynamics of *A. aurita*. Figures 4–6 shows monthly distributions of temperature, zooplankton, and currents during April–September in 2011 to present their seasonal variations. Temperature in the upper layer (3.5 m) shows significantly seasonal fluctuations (Figure 4). In April, it is cold in most of the Bohai Sea and northern Yellow Seas with temperature of about 7°C, but relatively warm in the southern part of the Yellow Sea and coastal areas with temperature even >10°C. Considering the temperature of 10°C–16°C for strobilation, ephyrae start to be released in April. In May, temperature increases markedly with most areas >12°C but <16°C and is suitable for strobilation. Temperature continues to



**FIGURE 3** | Comparisons of the model with laboratory experiments and field observations (black dots with/without error bars). Dry weight variation of ephyrae against time without (A) and with (B) food, feeding rate against food concentration (C), and bell diameter variation against time in the Jiaozhou Bay in 2011 (D).

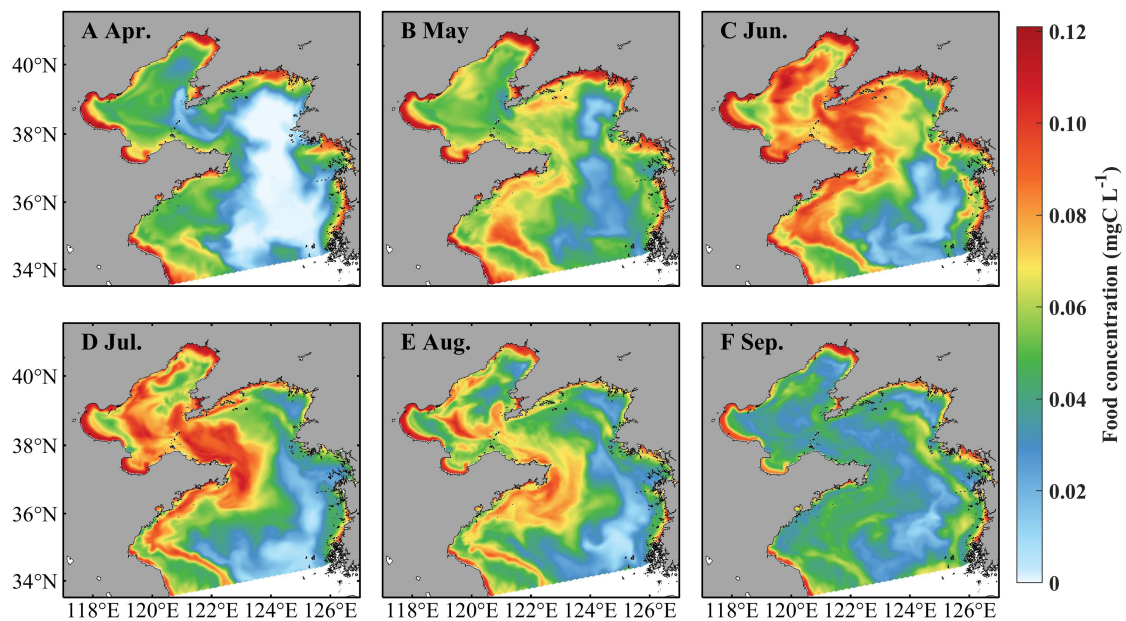


**FIGURE 4** | Simulated monthly temperature at 3.5 m in April (A), May (B), June (C), July (D), August (E), and September (F) in 2011.

rise with values between 16°C and 24°C in June and July and over 24°C in August, but decreases slightly in September.

Zooplankton indicates prominent spatiotemporal variations, with high concentrations in coastal areas and during June–

August (Figure 5). In April, the zooplankton concentration is about 0.06 mg C L<sup>-1</sup> in the Bohai Sea and shallower areas of the Yellow Sea and over 0.12 mg C L<sup>-1</sup> in the vicinity of the coast. It increases in May, June, and July and maintains a high level with



**FIGURE 5** | Simulated monthly food concentration (sum of microzooplankton and mesozooplankton) at 3.5 m in April (A), May (B), June (C), July (D), August (E), and September (F) in 2011.

concentrations over  $0.12 \text{ mg C L}^{-1}$ . The zooplankton concentration decreases in August with values over  $0.06 \text{ mg C L}^{-1}$  in most areas but decreases drastically in September. During April–September, strong currents occur near temperature fronts (indicated by positions with surface-bottom temperature difference of  $0.2^\circ\text{C}$ , Zhang et al., 2020), especially through July–September (Figure 6). In the Bohai Sea, a basin-scale anticyclonic gyre is present in the central area. Overall, the currents flow southward in the west part of the Yellow Sea and northward in the east part.

### 3.2 Seasonal Variations of *Aurelia aurita* Population

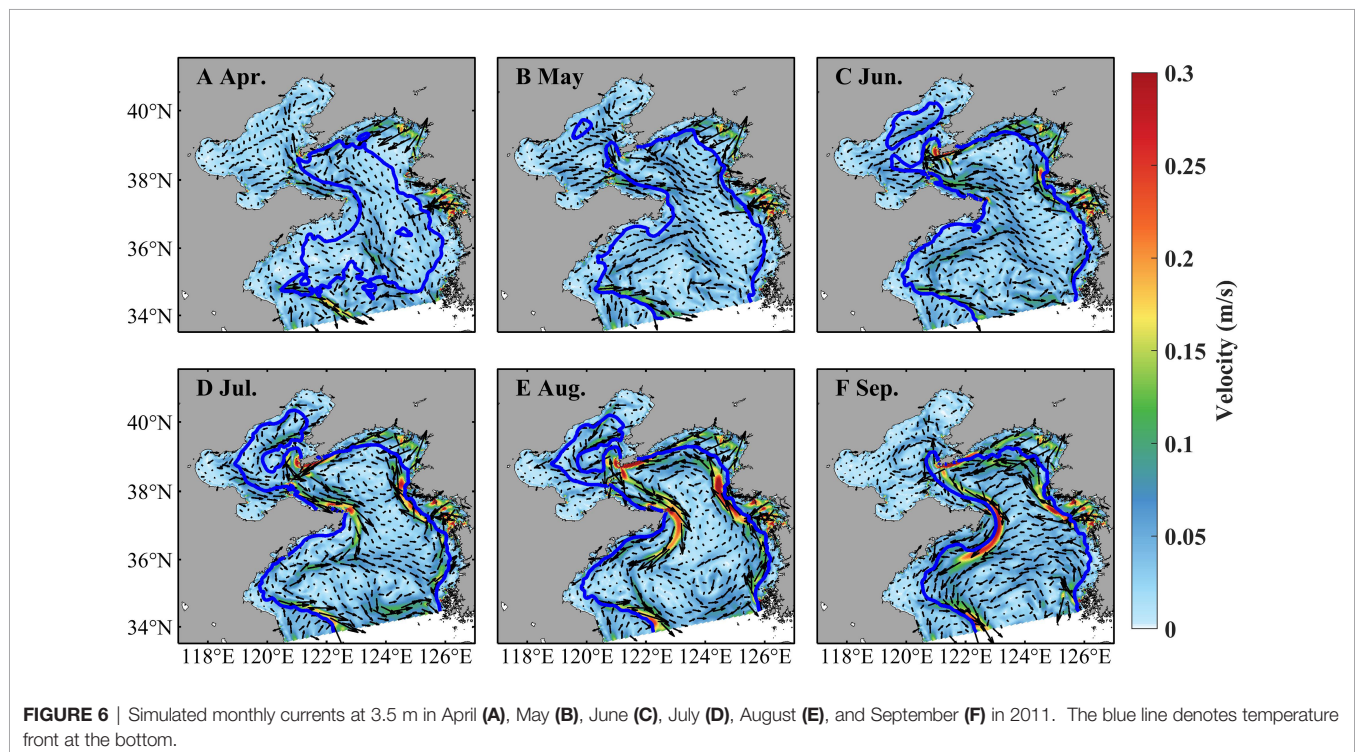
Seasonal variations of *A. aurita* population abundance are presented in Figure 7. In April, ephyrae begin to appear in some coastal areas with low abundance. In May, the abundance becomes prominently high but still near the coast. The jellyfish is apparently dispersed during June to September that suggests the impact of currents on jellyfish distribution. The abundance presents notable spatial differences, with relatively high values more than  $1,000 \text{ ind km}^{-2}$  in coastal areas and the middle Bohai Sea. The bell diameter is small in April and May, increases drastically in June and July, and reaches its maximum around 18 cm in July, but then decreases in August and September (Supplementary Figure S1). The biomass, affected by the abundance and the individual size, indicates a similar variation with the bell diameter (Supplementary Figure S2). The spatial distribution of the bell diameter indicates the characteristic with relatively larger size in the more northern region and smaller size in the more southern region.

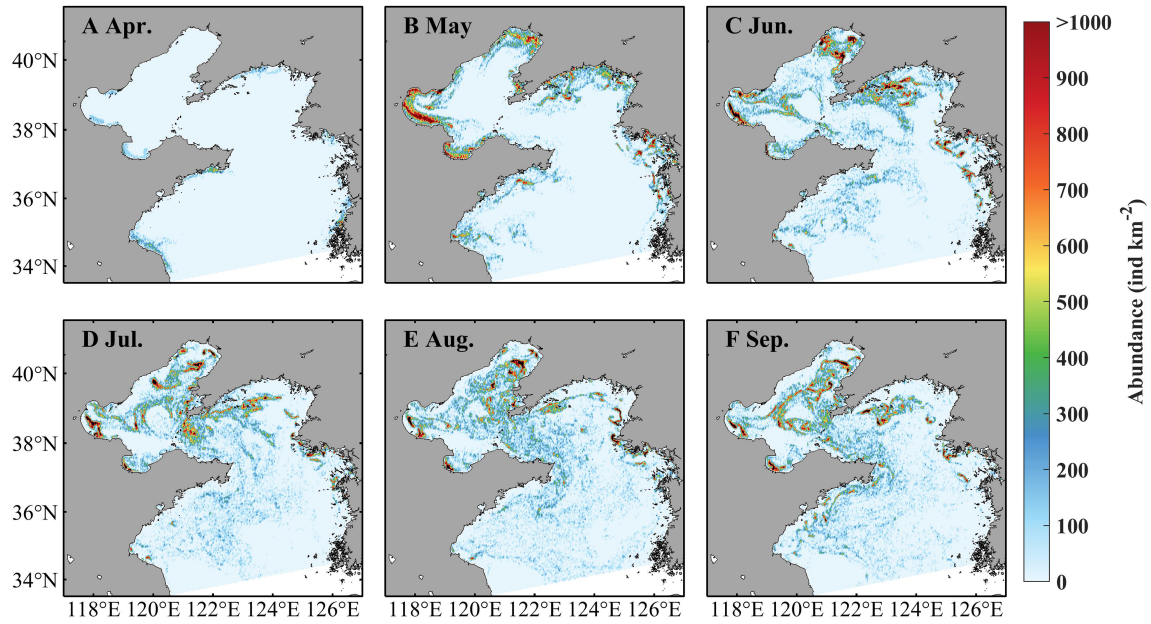
Figure 8A shows the time series of *A. aurita* total biomass, magnitude (total amount), food concentration, and temperature during jellyfish growth period in the BYSS. In early April, the magnitude began to increase due to ephyrae release through strobilization, with the average temperature over  $10^\circ\text{C}$ . The magnitude increases rapidly with the rising temperature in May. In early June, it becomes stable as the temperature reached approximately  $16^\circ\text{C}$ , and the strobilization is almost done in this year. Due to the low magnitude and the short period of growth, the total biomass was relatively small in April and May. The biomass increases rapidly in June as a result of the rapid growth medusa. In July, the biomass continued to increase and peaked in mid-July. After then, it gradually decreases that associates with the too high temperature and decreasing food concentrations.

### 3.3 Interannual Variations of *Aurelia aurita* Population

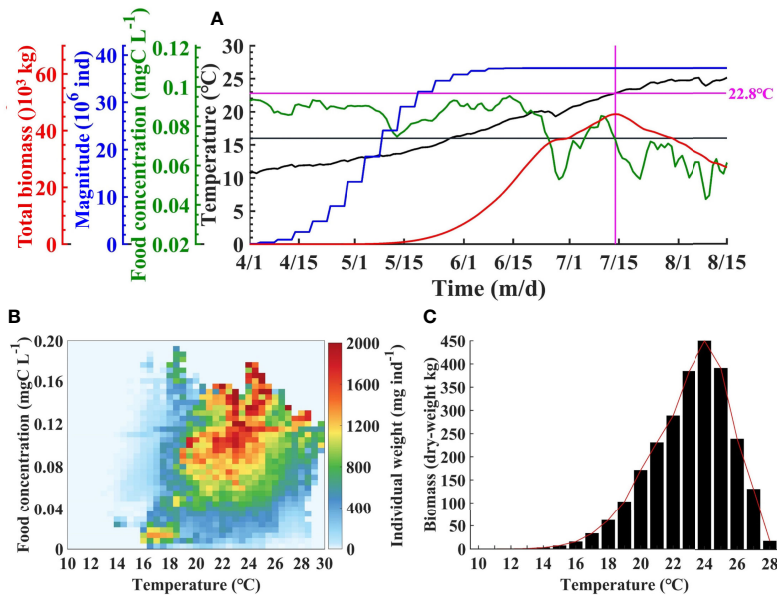
Seasonal and spatial distributions of *A. aurita* abundance in 2012–2017 show similar patterns with that in 2011, which reflects the principle seasonal cycle of the marine system of the BYSS (Supplementary Figures S3–S8). However, quantitative differences exist during these years. Figure 9A indicates variations of yearly peak biomass, the magnitude, and the averaged food concentration during the growth period through 2011–2017. There are notable differences in the peak biomass and the abundance, with the least biomass and abundance in 2013 and the highest biomass in 2017 and the greatest abundance in 2014.

The variations in total biomass and magnitude are not completely consistent. Relatively higher magnitude corresponds to higher biomass during 2012–2015, while this is not case in other





**FIGURE 7** | Simulated monthly averaged abundance of *Aurelia aurita* in April (A), May (B), June (C), July (D), August (E), and September (F) in 2011.

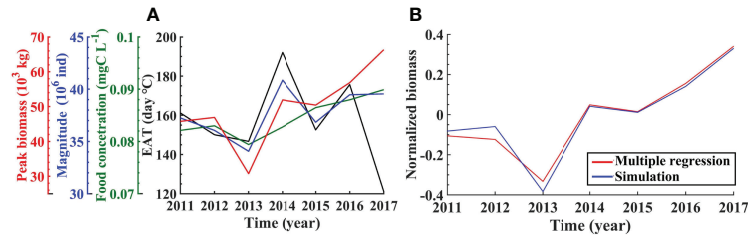


**FIGURE 8** | Time series of total biomass, magnitude, mean food concentration, and temperature in the Bohai and Yellow Seas in 2011 (A). The vertical line indicates the position of the peak biomass. Individual weight of *Aurelia aurita* against food concentration and temperature (B). Integrated biomass against temperature (C).

years. It is also noted that the variation in the magnitude is <20%, while it is more than 100% for the biomass. This means that both the magnitude and the jellyfish size are important for the biomass variations. The magnitude is controlled by ephyrae release through

strobilization that is related to temperature, and the jellyfish size is the result of individual growth that is affected by the food supply and temperature. Factors influencing interannual variations will be discussed in the following section.





**FIGURE 9** | Interannual variations of peak biomass and corresponding magnitude, averaged food concentration during the growing period, and the effective accumulated temperature (EAT) (A), simulated and multiple-regressed interannual variations of normalized biomass (B) based on model results from 2011 to 2017.

## 4 DISCUSSION

### 4.1 The Population-Dynamic Model of *Aurelia aurita* in the BYSs

This study develops a population-dynamic model to investigate seasonal and interannual variations of the *A. aurita* population in the BYSs. The model is able to reproduce metabolic processes and individual growth of jellyfish by quantitative comparison with laboratory experiments and field observations and is thus used to research population dynamics. Compared with previous modeling studies, such as the life-cycle model without movement of jellyfish (Henschke et al., 2018; Xie et al., 2021) and simulation of jellyfish movement without considering the individual growth (Moon et al., 2010; Wei et al., 2015; Wu et al., 2017), the model in this study considers both the bioenergetics and the effect of currents on movement of jellyfish *A. aurita*. It is also noted that the environment factors (such as temperature and zooplankton) at the jellyfish's position determine its growth. Thus, the model attempts to simulate jellyfish dynamics in the actual ecosystem.

Nevertheless, due to the complexity of the life strategies and habitat of *A. aurita* and difficulties of adequate field observations, there exist shortcomings in this model. Polyps tend to settle on hard substrate in coastal shallow areas (Toyokawa et al., 2011; Lucas et al., 2012). However, the actual distribution and abundance of polyps in the BYSs is unknown. Therefore, the substrate is assumed to be evenly distributed in waters shallower than 10 m for ephyrae release through strobilation in the model. Vertical mitigation of *A. aurita* could exist, which is associated with temperature and/or zooplankton distribution, but it differs geographically (Barz and Hirche, 2005; Kogovsek et al., 2012). No vertical mitigation is considered in the current model. Hence, further understanding of these aspects in the BYSs would help improve the model performance.

### 4.2 Seasonal Variations and Controlling Factors on Individual Growth

The ephyrae of *A. aurita* began to appear in April, and the abundance rises rapidly in May. The biomass increased rapidly in June and peaked in July but decreased markedly in August, which is consistent with the previous general understanding of the abundance and biomass of *A. aurita* population in the Northern Hemisphere (Möller, 1980; Olesen et al., 1994; Bonnet et al., 2012).

In coastal areas of BYSs, ephyrae are observed as early in April, and medusa is observed in June, July, and August (Wang B. et al., 2012; Wang and Sun, 2015; Xue et al., 2021). These observations are consistent with the results of simulations. Spatially, these relatively high abundance and biomass in three bays of the Bohai Sea are in agreement with field observations (Zuo et al., 2016; Wang et al., 2020). In addition, the simulated spatial distribution in these years also indicates aggregation near Hongyanhe Power Plant at the east coast of the Liaodong Bay where jellyfish including *A. aurita* clogged the cooling water intakes repeatedly in summer (Sun et al., 2019; Zhang et al., 2019).

In order to explore the key influencing factors on the individual growth of *A. aurita*, the relationship between the average individual dry weight (IW) and food concentration and temperature is statistically analyzed (Figure 8B). It is indicated that the relatively higher IW corresponds to a certain range of food concentration and temperature (Figure 5A). Overall, when the temperature was >16°C, the IW began to increase significantly. The IW is kept in relatively high levels with temperatures between 16°C and 26°C and food concentration >0.06 mg C L<sup>-1</sup>. By integration of IW along food concentration, Figure 8C shows the variation of the biomass with temperature. The biomass is quite low with slow increasing rate when temperature is lower than 16°C, increases almost linearly during 16°C–24°C with peak at 24°C, and begins to decrease drastically as temperature continues to rise. When the temperature reaches 28°C, the biomass just remains <5% of the peak.

It is suggested that 16°C–24°C is a suitable temperature range for individual growth of *A. aurita* in the BYSs, characterized by a nearly linear growth rate against temperature. Longer duration of this range would promote individual growth and therefore higher biomass of *A. aurita* population. Specifically in the BYSs, the duration is 51, 50, and 45 days for the Bohai Sea, the North Yellow Sea, and the South Yellow Sea (Table 3). The

**TABLE 3** | The duration days of SST suitable for the growth of *Aurelia aurita* and the bell diameter of *Aurelia aurita* in the Bohai and Yellow Seas.

	Bell diameter (cm)	Duration days of suitable growth (days)
Bohai Sea	11.5	51
North Yellow Sea	10.7	50
South Yellow Sea	10.2	45

corresponding bell diameter is 11.5, 10.7, and 10.2 cm, respectively, suggesting the effect of duration for growth on the individual size. The characteristic of relatively larger size in the more northern region and smaller size in the more southern region is in agreement with observations (Wang et al., 2020).

### 4.3 Controlling Factors on Interannual Variations of Biomass

To further analyze influencing factors on interannual variations in the biomass, a statistical relationship is established between the biomass and the abundance, effective accumulated temperature (EAT), and the food concentration. The EAT here is defined as the sum of mean temperature subtracting 16°C at jellyfish positions during the growth period from the start time of 16°C to time of the biomass peak. The food concentration is also averaged during this period. First, normalize these four variables through dividing the anomalies by the mean values through years of 2011–2017. Then, get the relationship by the multiple regression method. The regression equation is given as

$$pW = -0.35 \times pT + 2.45 \times pF + 2.15 \times pN \quad (5)$$

where  $pW$  denotes the normalized biomass;  $pT$ ,  $pF$ , and  $pN$  are normalized EAT, food concentration, and the abundance, with the determination coefficient  $R^2$  over 0.9 (Figure 9).

The contributions of  $pT$ ,  $pF$ , and  $pN$  to interannual variations of  $pW$  are quantified in Table 4, indicating their different roles in different years. The biomass shows the lowest in 2013, with the normalized value of -33.4% in which  $pT$ ,  $pF$ , and  $pN$  account for 2.3%, -14.8%, and -20.9%, respectively. Therefore, the relatively less magnitude, dependent on strobilization of ephyrae, is mainly

responsible for the lowest biomass in 2013, followed by the food concentration. The highest biomass in 2017 corresponds to a normalized value of 34%, with  $pT$ ,  $pF$ , and  $pN$  accounting for 15.6%, 10.4%, and 8.0% respectively, suggesting the consistent contribution of the EAT, food concentration, and the abundance. Sensitivity experiments further confirm the combined effects of these factors on interannual variations (Supplementary Figure S9).

If only considering the effect of temperature, another statistical method is introduced. As the biomass is the product of the magnitude and the averaged IW, the magnitude and the averaged IW at the timing of the biomass peak can be singly regressed against temperature-related variables, respectively. The abundance is mainly determined by strobilization of ephyrae. Hence, the abundance is linearly regressed against the duration of the temperature for strobilization (10°C–16°C) (Figure 10A). The equation is given as

$$N = 0.94 \times 10^6 x_b + 1.10 \times 10^6 \quad (6)$$

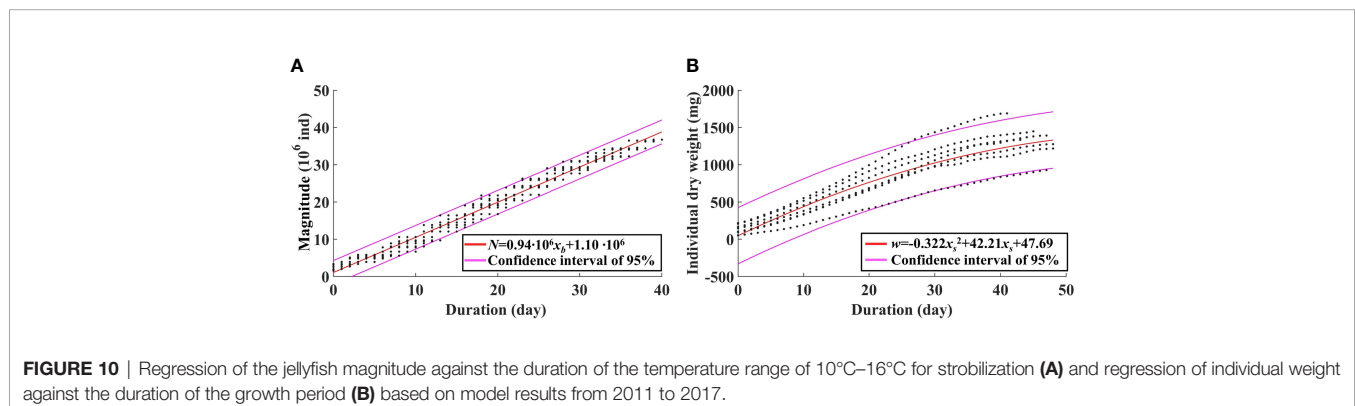
where  $N$  is the magnitude, and  $x_b$  is the duration of 10°C–16°C, with the determination coefficient  $R^2$  of 0.98. Therefore, the biomass can be represented by temperature and food concentrations that are variables in the marine environment. Analysis in Section 3.2 reveals a suitable temperature range for growth of *A. aurita*. The averaged IW is regressed against the duration of EAT (Figure 10B). The equation is given as

$$w = 0.322x_s^2 + 42.21x_s + 47.69 \quad (7)$$

where  $w$  is the averaged IW, and  $x_s$  is the duration of EAT, with the determination coefficient  $R^2$  of 0.79.

**TABLE 4** | Contributions of EAT, food, and the abundance to interannual variations of the yearly peak biomass during 2011–2017.

%	2011	2012	2013	2014	2015	2016	2017
$pT$	2.6	-4.3	-6.5	22.3	-2.7	11.9	-22.9
$(-0.35 \times pT)$	-0.9	1.5	2.3	-7.8	0.9	-4.2	8.0
$pF$	-2.8	-1.8	-6.0	-2.1	2.3	4.1	6.4
$(2.45 \times pF)$	-7.0	-4.4	-14.8	-5.1	5.7	10.0	15.6
$pN$	-1.3	-4.4	-9.7	8.3	-2.4	4.6	4.8
$(2.15 \times pN)$	-2.7	-9.5	-20.9	17.9	-5.1	9.9	10.4
$pW$	-10.8	-12.4	-33.4	5.1	1.5	15.7	34.0



The effect of temperature variations on *A. aurita* dynamics has been assessed in some coastal regions under the background of climate warming, with the conclusion of climate warming benefiting *A. aurita* (Holst, 2012; Ruiz Segura et al., 2012). The simplified relationships can reflect the linkage between temperature and jellyfish magnitude and biomass in some ways, despite the complexity of the marine ecosystem. They would contribute to further understanding the impact of temperature on the population dynamics in the warming BYSs (Lu et al., 2021).

## 5 SUMMARY AND CONCLUSIONS

In this study, a complex population-dynamic model is developed for jellyfish *A. aurita* in the BYSs that incorporates three components, a three-dimensional coupled physical-biological model, a Lagrangian particle-tracking model, and an energy balance model of *A. aurita*. By comparison with observations, the model well reproduces the individual growth and seasonal evolution of *A. aurita* population. During individual growth period with the suitable range of 16°C–24°C, the temperature is a key factor controlling growth and dry weight, characterized by a nearly linear growth rate. Longer duration of the temperature range tends to favor larger medusa size and further to promote the peak biomass.

The yearly peak biomass shows interannual variations that are controlled by the magnitude, food concentration, and EAT. Only considering the effect of temperature, the magnitude determined by strobilization of polyps can be expressed through the duration of strobilization, with longer duration leading to higher magnitude. The averaged IW corresponding to the peak biomass can be parameterized by the duration of individual growth period. Thus, the peak biomass can be obtained by the product of the magnitude and the averaged IW that finally relate to temperature. The simplified statistical relationship would help understand the temperature control on population dynamics and provide instructive insights into the impacts of ocean warming on *A. aurita* population. In addition, the actual distribution and abundance of polyps and the vertical

mitigation property of *A. aurita* in the BYSs would favor improvement of the current population-dynamic model.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

HW, HZ, and JX designed the research. GZ, YW, and JX contributed to the model establishment. GZ, YL, GS, and HW performed the data analyses. HZ prepared the manuscript with input from all other authors. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.842394/full#supplementary-material>

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