

## Article

# Species Selection for Oyster Reefs: Growth Simulations of Three Oysters Across Multiple Habitats

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## Abstract

Oysters, as sessile organisms, are highly influenced by environmental conditions affecting their growth and reproduction. Therefore, unfavorable conditions can directly compromise the effectiveness of oyster reef restoration efforts. The study applied the dynamic energy budget (DEB) theory to model the growth of the Suminoe oyster (*Crassostrea ariakensis*) and estimated the model's main parameters through linear and nonlinear regression methods. Meanwhile, the parameters of the existing DEB models for the Pacific oyster (*Crassostrea gigas*) and the Portuguese oyster (*Crassostrea angulata*) were optimized to improve the model performance. Model accuracy was confirmed by comparing the simulated and observed values of shell height and wet weight for three oyster species. The validated models were subsequently applied to three distinct habitats: Qianhu Bay, the Yangtze River Estuary, and Jiaozhou Bay, to simulate the individual dynamic growth and survival processes of the three oyster species. The simulations of shell height and wet weight for the three oyster species showed strong agreement with observations, with a mean coefficient of determination ( $R^2$ ) of 0.98. The mean NRMSE value of the three models was 0.16, indicating low model-prediction error. The simulation of various habitat scenarios suggested that *C. ariakensis* exhibited faster growth in the Yangtze River Estuary and Qianhu Bay, and *C. gigas* in the Yangtze River Estuary. Additionally, *C. angulata* experienced mortality in the Yangtze River Estuary (February) and Jiaozhou Bay (January). The findings of this study can provide scientific guidance on selecting species for oyster reefs across various marine environments to effectively enhance their ecological restoration outcomes.

**Keywords:** dynamic energy budget; Suminoe oyster; Portuguese oyster; Pacific oyster; species selection for oyster reefs



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**Key Contribution:** This study developed and validated the first DEB model for the Suminoe oyster and improved the accuracy of Pacific and Portuguese oyster models through critical parameter re-estimation. Species-specific habitat suitability analyses further provided a science-based framework for oyster reef restoration and optimal species selection across diverse habitats.

## 1. Introduction

Oysters are ecosystem engineers in coastal habitats, forming biogenic reefs that provide vital ecosystem services, including habitat provisioning, shoreline stabilization, and

biodiversity enhancement [1]. The dominant species in China comprise the Suminoe oyster (*Crassostrea ariakensis*), the Pacific oyster (*Crassostrea gigas*), and the Portuguese oyster (*Crassostrea angulata*). *C. ariakensis* spans from the Yalu River in the north to Hainan Island in the south [2]; *C. gigas* is predominantly located in the coastal waters north of the Yangtze River Estuary, mainly in the Yellow Sea and Bohai Sea [3,4]. In contrast, *C. angulata* inhabits the coasts south of the Yangtze River Estuary, along the coastal waters of the East China Sea [5]. The distributions of these species overlap in certain transitional zones. In Qianhu Bay (southern China), both *C. ariakensis* and *C. angulata* are native, while *C. gigas* is largely introduced through farming activities. The Yangtze River Estuary is the convergence zone where both *C. ariakensis* and *C. gigas* are native. In Jiaozhou Bay (Yellow Sea), *C. gigas* is the native and predominant species, whereas *C. ariakensis* was historically present but is now scarce [2–7]. Oysters are highly sensitive to changes in external environmental conditions, including temperature and food availability, attributable to their sedentary nature [8]. Natural fluctuations in these factors impact oysters' physiological processes, such as feeding, development, and reproduction. This may cause regional population declines, significantly constraining the sustainability of oyster aquaculture and the ecological restoration effectiveness of oyster reefs [9–11].

The dynamic energy budget (DEB) model, introduced by Kooijman in 1986 [12], has seen remarkable development in energetics research of various organisms, including algae, shellfish, and fish. It has emerged as a valuable approach for evaluating the environmental adaptations of aquatic species [13–17]. The model has been effectively applied in species including *C. gigas*, Eastern oyster (*Crassostrea virginica*), Hooded oyster (*Saccostrea cucullata*), and *C. angulata* [4,8,18–23]. Current studies on *C. ariakensis* focus solely on its physiological and metabolic features, as well as energy balance, leaving a gap in DEB modeling that restricts comprehensive knowledge of its growth dynamics and environmental adaptations.

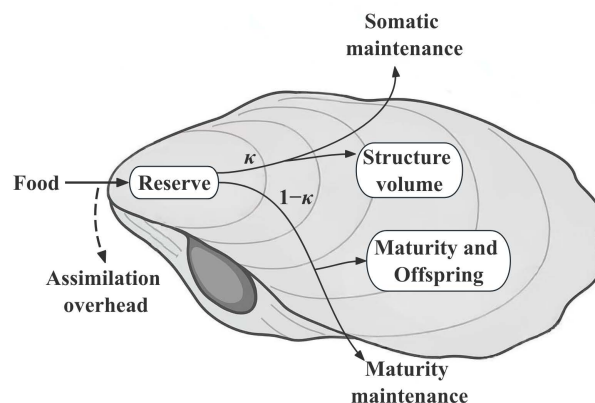
This study developed a numerical model for *C. ariakensis* utilizing DEB theory, estimated critical parameters through linear and nonlinear regression methods, and optimized the current model parameters for *C. gigas* and *C. angulata*. The accuracy of models was validated by comparing the simulated and observed values of shell height and wet weight for the three species of oyster, respectively. Furthermore, the models were applied to three representative habitats: Qianhu Bay, the Yangtze River Estuary, and Jiaozhou Bay, to simulate the dynamic growth process of the oysters. The aim of the study is to investigate the adaptive variations among the three oyster species under temperature and food-related conditions, ultimately supporting the informed selection of species, particularly for ecological restoration using oyster reefs. While previous studies have reported species-specific thermal tolerances and growth patterns based on empirical observations, these findings remain largely qualitative and site-specific and do not allow direct comparison across species or habitats within a unified quantitative framework. To address this gap, we apply the DEB models for the three oyster species to simulate growth dynamics under the contrasting environmental conditions of three representative habitats. This approach enables us to move beyond descriptive accounts of species performance, providing quantitative, directly comparable predictions of growth trajectories and mortality timing that can inform science-based species selection for oyster reef restoration.

## 2. Materials and Methods

### 2.1. Model Construction

The DEB model simulates an organism's energy metabolism by tracking the dynamics of reserve, structure, and either maturity (before puberty) or reproduction buffer (after puberty) via differential equations. The underlying theory proposes that the energy assimilated by an organism is stored in reserve and proportionately distributed to metabolic

processes, including growth, maintenance, maturation, and reproduction [24]. Energy distribution adheres to the  $\kappa$ -principle, wherein a fraction ( $\kappa$ ) of the reserve energy is allocated for somatic maintenance and growth, while the residual ( $1 - \kappa$ ) is designated for maturity maintenance, maturation and reproduction (Figure 1) [15,25]. The model's key drivers, food availability and water temperature, regulate *C. ariakensis* growth dynamics, leading to either growth restrictions or even death when tolerance thresholds are breached [18,23].



**Figure 1.** Schematic diagram of the dynamic energy budget model of *C. ariakensis*.

Based on the DEB theory and its parameter estimation method [14,24–29], a DEB model for *C. ariakensis* is developed in this study. The model's governing equations are presented in Table 1.  $E$  is reserve energy (J),  $E_R$  is reproduction buffer energy (J),  $E_H$  is maturation energy (J),  $E_H^P$  is maturation energy at puberty (J),  $V$  is structural volume ( $\text{cm}^3$ ),  $\kappa$  is allocation fraction to somatic growth and maintenance (–),  $\kappa_R$  is reproduction efficiency (–),  $d_v$  is specific density of structural volume ( $\text{g}/\text{cm}^3$ ),  $\mu_E$  is energy content of reserve (J/g),  $X$  is food concentration ( $\text{mg}/\text{m}^3$ ),  $F_k$  is half-saturation coefficient ( $\mu\text{g}/\text{L}$ ),  $k(T)$  is temperature correction factor (–),  $T_1$  is reference temperature (K),  $T_H$  is upper boundary temperature of the tolerance range (K),  $T_L$  is lower boundary temperature of the tolerance range (K),  $T_{AH}$  is Arrhenius temperature for the rate of decrease at upper boundary (K),  $T_{AL}$  is Arrhenius temperature for the rate of decrease at lower boundary (K),  $[E_G]$  is volume-specific cost for structure ( $\text{J}/\text{cm}^3$ ),  $[E_M]$  is maximum reserve density ( $\text{J}/\text{cm}^3$ ),  $\{\dot{p}_{Am}\}$  is maximum surface-area specific assimilation rate ( $\text{J cm}^{-2} \text{d}^{-1}$ ),  $[\dot{p}_M]$  is volume-specific somatic maintenance costs ( $\text{J cm}^{-3} \text{d}^{-1}$ ),  $W$  is total wet weight (g),  $IR_{max}$  is maximum ingestion rate ( $10^6 \text{ cell} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ),  $P$  is energy content per food cell (J/cell),  $AE$  is assimilation efficiency (%),  $V_P$  is structural volume at puberty,  $T_n$  is temperature on day  $n$  (K),  $96 \text{ hLT}_{50}$  refers to the median lethal temperature causing 50% mortality of oysters within a 96 h exposure period (K),  $S_n$  is mortality factor (–), was applied to simulate mortality under continuous stress.

**Table 1.** The main governing equations in the dynamic energy budget model of oysters.

| Description            | Governing Equation                                                                                                                                                                                                                                                       |
|------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Total wet weight       | $W = \frac{E}{\mu_E} + \frac{\kappa_R \cdot E_R}{\mu_E} + V \cdot d_v$ [27]                                                                                                                                                                                              |
| Structure length       | $L = V^{1/3}$ [24]                                                                                                                                                                                                                                                       |
| Temperature dependence | $k(T) = (1 + \exp(\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T_L})) + \exp(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_L}) \cdot (1 + \exp(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}) + \exp(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}))^{-1} \cdot \exp(\frac{T_A}{T_1} - \frac{T_A}{T})$ [28] |

Table 1. Cont.

| Description                                                   | Governing Equation                                                                                                                                                     |
|---------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| The functional response of assimilation to food concentration | $f = \frac{X}{X + F_k}$ [27]                                                                                                                                           |
| Energy assimilation rate                                      | $\dot{p}_A = k(T) \cdot f \cdot \{\dot{p}_{Am}\} \cdot V^{2/3}$ [27]                                                                                                   |
| Energy utilization rate                                       | $\dot{p}_C = k(T) \cdot \frac{[E]}{\kappa \cdot [E] + [E_G]} \cdot \left( \frac{[E_G] \cdot \{\dot{p}_{Am}\} \cdot V^{2/3}}{[E_M]} + [\dot{p}_M] \cdot V \right)$ [27] |
| Reserve dynamic                                               | $\frac{d}{dt} E = \dot{p}_A - \dot{p}_C$ [27]                                                                                                                          |
| Energy density                                                | $[E] = \frac{E}{V}$ [24]                                                                                                                                               |
| Maximum surface-area-specific assimilation rate               | $\{\dot{p}_{Am}\} = IR_{max} PW / (L^2) \cdot AE$ [29]                                                                                                                 |
| Structural maintenance rate                                   | $\dot{p}_M = k(T) \cdot [\dot{p}_M] \cdot V$ [27]                                                                                                                      |
| Maturity maintenance rate                                     | $\dot{p}_J = k(T) \cdot [\dot{p}_M] \cdot \min(V, V_P) \cdot \frac{1-\kappa}{\kappa}$ [27]                                                                             |
| Reproductive reserve dynamic                                  | $\frac{d}{dt} E_R = (1 - \kappa) \cdot \dot{p}_C - \dot{p}_J$ if $E_H > E_H^P$ , else $\frac{d}{dt} E_R = 0$ [27]                                                      |
| Biovolume growth                                              | $\frac{d}{dt} V = \frac{\kappa \cdot \dot{p}_C - \dot{p}_M}{[E_G]}$ [27]                                                                                               |
| Mortality factor                                              | $S_n = 0$ if $T_n < 96 \text{ h } LT_{50}$ , else $S_n = S_{n-1} + 1$<br>oysters died on Day n when $S_n = 4$                                                          |

## 2.2. Parameter Estimation and Model Validation

### 2.2.1. Estimation of Model Parameters

The parameters used in this study are derived from three sources, according to the DEB parameter estimation approach [24,25]. The first category comprises parameters directly estimated in this study, including the shape coefficient ( $\delta_m$ ), the Arrhenius temperature ( $T_A$ ), and the maximum surface-area specific assimilation rate ( $\{\dot{p}_{Am}\}$  for *C. ariakensis*)—all based on experimental or literature data for the respective species. The second category includes parameters adopted from published DEB studies for the same species, such as  $[\dot{p}_M]$  for *C. gigas* from Ren & Schiel (2008) [27] and for *C. angulata* from Jiang et al. (2022) [23] after re-optimisation. The third category includes parameters transferred from closely related species only when no data existed for the target species (e.g.,  $[E_G]$  and  $[E_M]$ ), following the synergistic agreement principle [25]. All parameters are explicitly indicated in Table 2.

Table 2. Parameter values of the dynamic energy budget model in *C. ariakensis*, *C. gigas* and *C. angulata*.

| Parameters                                            | Symbol             | Unit                               | Value for <i>C. ariakensis</i> , <i>C. gigas</i> and <i>C. angulata</i>            | Source             |
|-------------------------------------------------------|--------------------|------------------------------------|------------------------------------------------------------------------------------|--------------------|
| Volume-specific cost for structure                    | $[E_G]$            | J/cm <sup>3</sup>                  | <i>C. ariakensis</i><br><i>C. gigas</i> 2900<br><i>C. angulata</i>                 | [27]               |
| Allocation fraction to somatic growth and maintenance | $\kappa$           | —                                  | <i>C. ariakensis</i> 0.6<br><i>C. gigas</i> 0.43<br><i>C. angulata</i> 0.725       | [27]<br>This study |
| Reproduction efficiency                               | $\kappa_R$         | —                                  | <i>C. ariakensis</i> 0.95<br><i>C. gigas</i> 0.89<br><i>C. angulata</i> 0.95       | [28]               |
| Shape coefficient                                     | $\delta_m$         | —                                  | <i>C. ariakensis</i> 0.5002<br><i>C. gigas</i> 0.2974<br><i>C. angulata</i> 0.3769 | This study         |
| Maximum surface-area-specific assimilation rate       | $\{\dot{p}_{Am}\}$ | J cm <sup>−2</sup> d <sup>−1</sup> | <i>C. ariakensis</i> 800<br><i>C. gigas</i> 952<br><i>C. angulata</i> 1018         | This study         |

Table 2. Cont.

| Parameters                                                       | Symbol                   | Unit                              | Value for <i>C. ariakensis</i> , <i>C. gigas</i> and <i>C. angulata</i> |        | Source     |
|------------------------------------------------------------------|--------------------------|-----------------------------------|-------------------------------------------------------------------------|--------|------------|
| Volume-specific somatic maintenance costs                        | $\left[\dot{p}_M\right]$ | $\text{J cm}^{-3} \text{ d}^{-1}$ | <i>C. ariakensis</i>                                                    | 18.5   | [27]       |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 4.9    | This study |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 5.45   | This study |
| Maximum reserve density                                          | $[E_M]$                  | $\text{J/cm}^3$                   | <i>C. ariakensis</i>                                                    |        |            |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 5900   | [27]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      |        |            |
| Half-saturation coefficient                                      | $F_k$                    | $\mu\text{g/L}$                   | <i>C. ariakensis</i>                                                    | 0.8    | [19]       |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 1.8    | [23]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 4      | [23]       |
| Arrhenius temperature                                            | $T_A$                    | K                                 | <i>C. ariakensis</i>                                                    | 4444   | This study |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 5900   | [27]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 5900   | [27]       |
| Upper boundary temperature of the tolerance range                | $T_H$                    | K                                 | <i>C. ariakensis</i>                                                    | 307    | [30,31]    |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 297    | [32]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 303    | [33]       |
| Lower boundary temperature of the tolerance range                | $T_L$                    | K                                 | <i>C. ariakensis</i>                                                    | 279    | [30,31]    |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 285    | [32]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 291    | [33]       |
| Arrhenius temperature for the rate of decrease at upper boundary | $T_{AH}$                 | K                                 | <i>C. ariakensis</i>                                                    | 30,000 | [26]       |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 85,000 | [32]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 98,321 | [33]       |
| Arrhenius temperature for the rate of decrease at lower boundary | $T_{AL}$                 | K                                 | <i>C. ariakensis</i>                                                    | 75,000 | [26]       |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 38,092 | [32]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 60,274 | [33]       |
| Reference temperature                                            | $T_1$                    | K                                 | <i>C. ariakensis</i>                                                    | 299    | [30,31]    |
|                                                                  |                          |                                   | <i>C. gigas</i>                                                         | 291    | [27]       |
|                                                                  |                          |                                   | <i>C. angulata</i>                                                      | 291    | [27]       |

This study estimated the significant physiological parameters (the shape coefficient and the Arrhenius temperature) of the DEB model for *C. ariakensis* using linear and nonlinear regression methods. The shape coefficient ( $\delta_m$ ) was estimated from shell height and total wet weight. The Arrhenius temperature ( $T_A$ ) was derived from oxygen consumption rates ( $R$ ,  $\text{mg g}^{-1} \text{ h}^{-1}$ ) measured across a temperature gradient for five shell height classes. The oxygen consumption data used to calculate the Arrhenius temperature were taken from Li et al. (2011) [34], which reported oxygen consumption rates for *Crassostrea rivularis*. *C. rivularis* is a taxonomic synonym of *C. ariakensis* (the species name has been revised in recent taxonomic treatments [5]), and the experimental methods (static respirometry at controlled temperatures) are the standard approach for estimating thermal dependence of metabolic rate in oysters. The maximum surface-area-specific assimilation rate  $\{\dot{p}_{Am}\}$  was calculated based on published experimental datasets. According to the equation  $\{\dot{p}_{Am}\} = IR_{max}PW/(L^2) \cdot AE$  in Table 1,  $\{\dot{p}_{Am}\}$  of *C. ariakensis* was estimated by the feeding rate under different chlorophyll concentrations [35,36]. Additional parameters were sourced from the literature, and for some parameters, values of analogous species were adopted based on the principle of synergistic agreement [26].

The DEB model developed by Jiang et al. (2022) [23] was applied to *C. gigas* and *C. angulata*, with certain parameters optimized. The shape coefficients of *C. gigas* and *C. angulata* were estimated from the wet weight of soft tissues in Jiang et al. (2022) [23]. To ensure consistency for interspecific comparisons, we re-estimated the shape coefficients using the shell height and total wet weight data and proportionally adjusted the values of maximum surface-area specific assimilation rate  $\{\dot{p}_{Am}\}$  and the volume-specific mainte-

nance rate  $\left[\dot{p}_M\right]$  accordingly. The datasets for parameter estimation and optimization were kept entirely independent of the validation dataset described in Section 2.2.2.

### 2.2.2. Model Validation

Model performance was evaluated by linear regression of simulated values against observed values. The coefficient of determination ( $R^2$ ) was computed to assess the proportion of variance in observed values explained by the model. Additionally, the normalized root mean square error (NRMSE) was calculated to quantify the relative prediction error and expressed as a percentage; lower NRMSE values indicate better model performance and smaller relative deviations from the observed data.

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^N (M_i - S_i)^2}{N}}$$

$$\text{NRMSE} = \frac{\text{RMSE}}{\bar{M}}$$

$$R = \frac{\sum_{i=1}^N (M_i - \bar{M})(S_i - \bar{S})}{\sqrt{\sum_{i=1}^N (M_i - \bar{M})^2 \sum_{i=1}^N (S_i - \bar{S})^2}}$$

where  $M_i$  is observed values,  $S_i$  is simulated values,  $\bar{M}$  and  $\bar{S}$  are the mean of observed and simulated values, respectively, and  $N$  is the number of observations [37,38].

Validation data for the DEB model were obtained from the independent sampling designs of the original studies cited. The model validation data for *C. gigas* were collected from Sanggou Bay (lat 37°08′16.80″ N, long 122°35′36.10″ E) in the Yellow Sea, with 20 oysters randomly selected at 15–30 day intervals from August 2016 to February 2017 to measure the shell height and the wet weight of the soft tissue [23]. Validation data for *C. angulata* were collected from the shellfish cultivation region of Shenhui Bay (lat 24°39′18.30″ N, long 118°38′55.00″ E) in the East China Sea, where 50 oysters were randomly sampled at 30-day intervals from August 2018 to March 2019 to measure the shell height and the wet weight of soft tissue [23]. The Dafeng River (lat 21°39′36″ N, long 108°49′48″ E) and Zhulin Pond (lat 21°27′00″ N, long 109°18′00″ E) in the South China Sea provided *C. ariakensis* model validation data [39], with the shell height measured on Day 90, 180, 270, 390 as well as 510 and the total wet weight measured on Day 270, 390, and 510 (60 individuals randomly sampled at each time point per site). The shell height (the distance from the apex to the base of the shell) was measured using a vernier caliper with an accuracy of 0.01 cm. The wet weights of total and soft tissues were quantified using a scale with an accuracy of 0.01 g.

According to E.U. Copernicus Marine Service Information (CMEMS) from 2017 to 2019 [40–42] (Table S1), model-driven daily data for water temperature and chlorophyll concentration were shown in Figure 2. The data, with a spatial resolution of  $1/4^\circ \times 1/4^\circ$  (approximately 28 km) and a temporal resolution of 1 day, were extracted for the surface layer (0–0.51 m depth) at the study sites. The initial shell heights of *C. gigas* and *C. angulata* were 6.01 cm and 1.94 cm, respectively, while the wet weights of their soft tissues were 1.97 g and 0.20 g. The initial shell heights of *C. ariakensis* in the Zhulin Pond and Dafeng River were 2.89 cm and 2.93 cm, with their corresponding total wet weights as 3.46 g and 3.59 g, respectively.

### 2.3. Conditions Set for Different Simulation Scenarios

The validated models were used to simulate the growth of three oysters in Qianhu Bay (a small coastal bay), the Yangtze River Estuary (open, large-scale), and Jiaozhou Bay (semi-enclosed) (Figure 3a) from September 2021 to September 2022, October 2021 to October 2022, and April 2021 to April 2022, respectively. The simulation periods were determined by the

availability of continuous environmental data (temperature and chlorophyll) from CMEMS for each specific location; the start and end dates vary because the data coverage for each site differed. According to CMEMS (2021–2022) [40,42] (Table S1), the model-driven data for water temperature and chlorophyll concentration were presented in Figure 3b,c. The data have a spatial resolution of  $0.25^\circ \times 0.25^\circ$  and a temporal resolution of 1 day, representing conditions in the surface water layer. The initial shell height of *C. gigas*, *C. angulata* and *C. ariakensis* was 3.28 cm, 3.27 cm and 3.31 cm, while the wet weight of the soft tissue was 0.81 g, 0.60 g and 0.91 g, respectively.

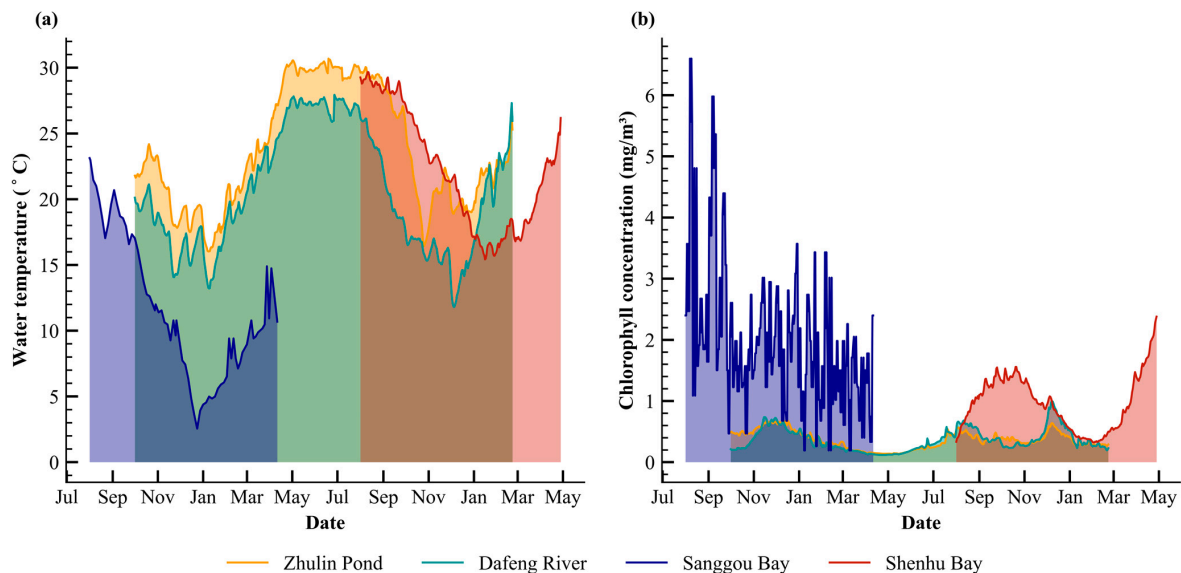


Figure 2. Water temperature (a) and chlorophyll concentration (b) trends.

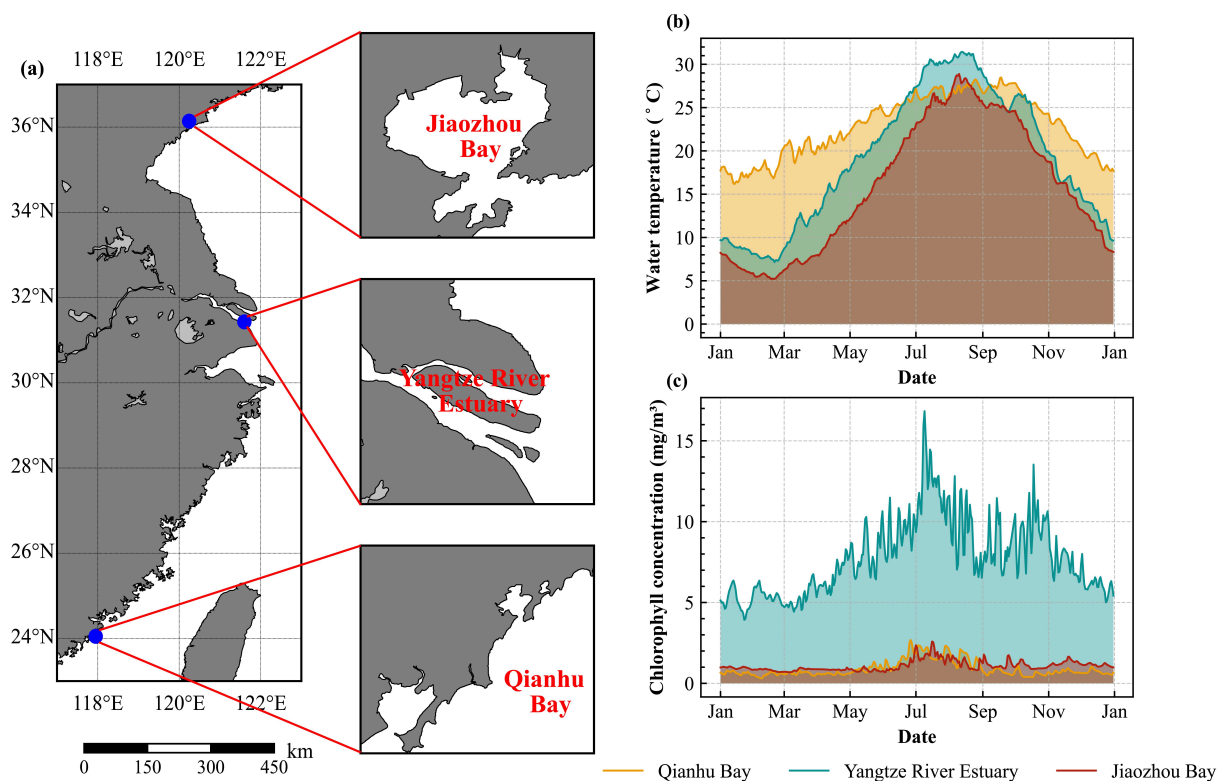


Figure 3. Geographical distribution map (a), water temperature (b) and chlorophyll concentration (c) trends of Qianhu Bay, the Yangtze River Estuary and Jiaozhou Bay.

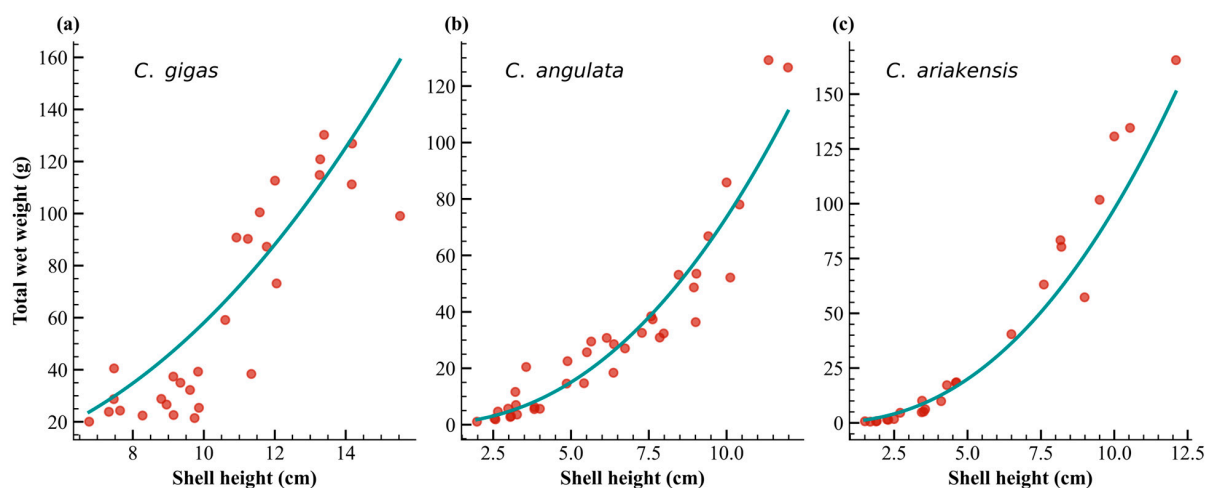
### 3. Results

#### 3.1. Model Parameters for Three Oyster Species

The model parameters for three species are shown in Table 2. The key parameters, such as shape coefficient and maximum surface-area specific assimilation rate, were estimated, and other parameters were adopted from existing literature [19,23,26–28,30–33].

##### 3.1.1. Model Parameters of *C. gigas* and *C. angulata*

The shape coefficients of *C. gigas* and *C. angulata* were re-estimated based on the shell height and total wet weight, which were 0.2974 and 0.3769, respectively (Figure 4a,b), and the associated  $\{\dot{p}_{Am}\}$  and  $[\dot{p}_M]$  were adjusted accordingly, as shown in Table 2 [7,43,44].



**Figure 4.** The relationship between shell height and total wet weight for *C. gigas* (a), *C. angulata* (b) and *C. ariakensis* (c).

##### 3.1.2. Model Parameters of *C. ariakensis*

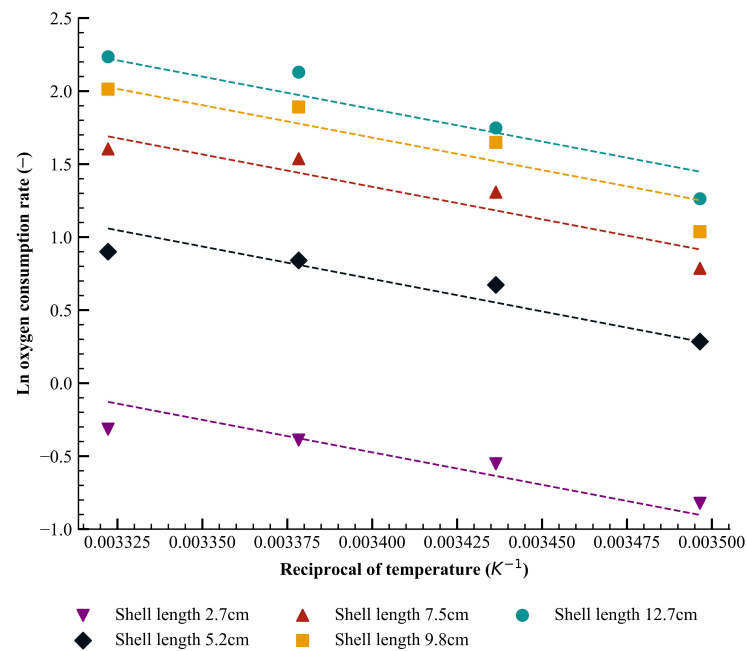
The shape coefficient ( $\delta_m$ ) was estimated from shell height and total wet weight [2,9,45–48]. The regression of shell height and total wet weight of *C. ariakensis* was carried out, and the shape coefficient was 0.5002, as shown in Figure 4c.

The Arrhenius temperature  $T_A$  was calculated based on the relationship between the oxygen consumption rate ( $R$ ,  $\text{mg g}^{-1} \text{h}^{-1}$ ) and water temperature ( $T$ , thermodynamic temperature  $K$ ) of *C. ariakensis*. The logarithm of the oxygen consumption rate of *C. ariakensis* in five different size groups [34] and the reciprocal of the thermodynamic temperature were linearly regressed. The absolute value of the slope obtained was the Arrhenius temperature ( $\pm \text{SE}$ ), and the result was  $4444 \pm 482 \text{ K}$  (Figure 5).

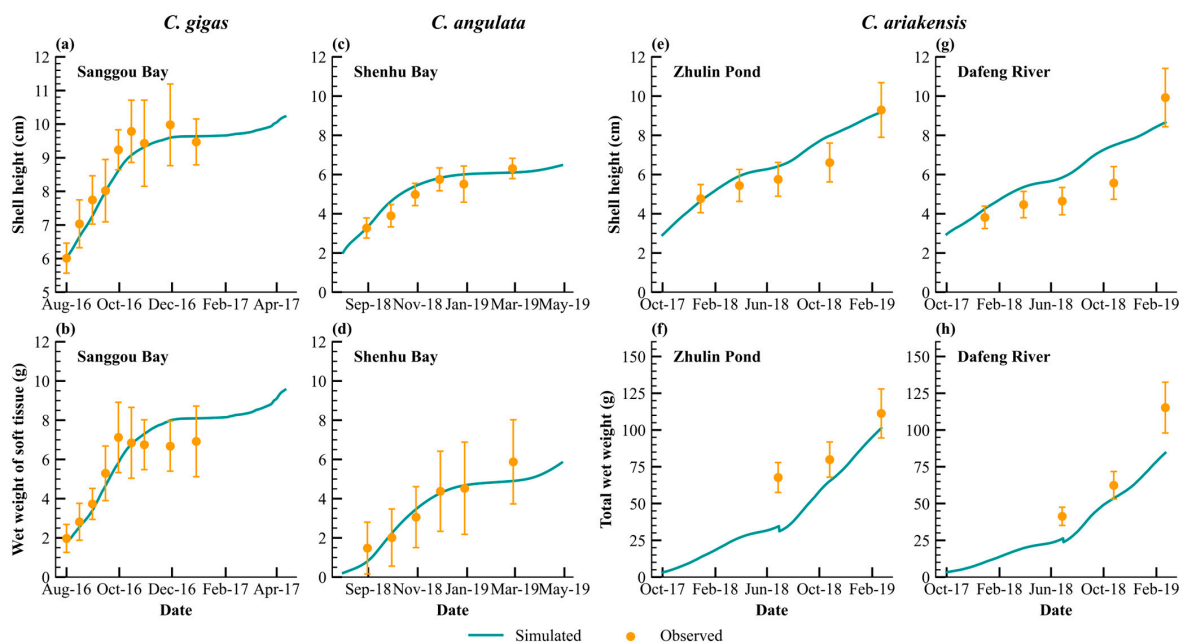
The temperature range for survival of *C. ariakensis* is 18 to 30 °C, with an upper tolerance limit  $T_H$  of 34 °C, a lower tolerance limit  $T_L$  of 6 °C, and a reference temperature  $T_1$  of 26 °C [30,31]. The maximum surface-area-specific assimilation rate  $\{\dot{p}_{Am}\}$  of *C. ariakensis* calculated from published experimental datasets was  $800 \text{ J cm}^{-2} \text{d}^{-1}$  [35,36].

#### 3.2. Model Validation Results for Three Oyster Species

The comparison of both observed and simulated growth data for *C. gigas* in Sanggou Bay is shown in Figure 6a,b. The  $R^2$  values for the simulated and observed shell height and wet weight of the soft tissue were 0.9989 and 0.9816, while the slopes of the linear regression were 0.9665 and 1.0178, respectively. The normalized root mean square error (NRMSE) values were 4.7% and 14.9%, indicating that the model accurately captures the dynamic growth performance of *C. ariakensis*.



**Figure 5.** The relationship between the logarithm of oxygen consumption rate and the reciprocal of thermodynamic temperature of *C. ariakensis* with different sizes.



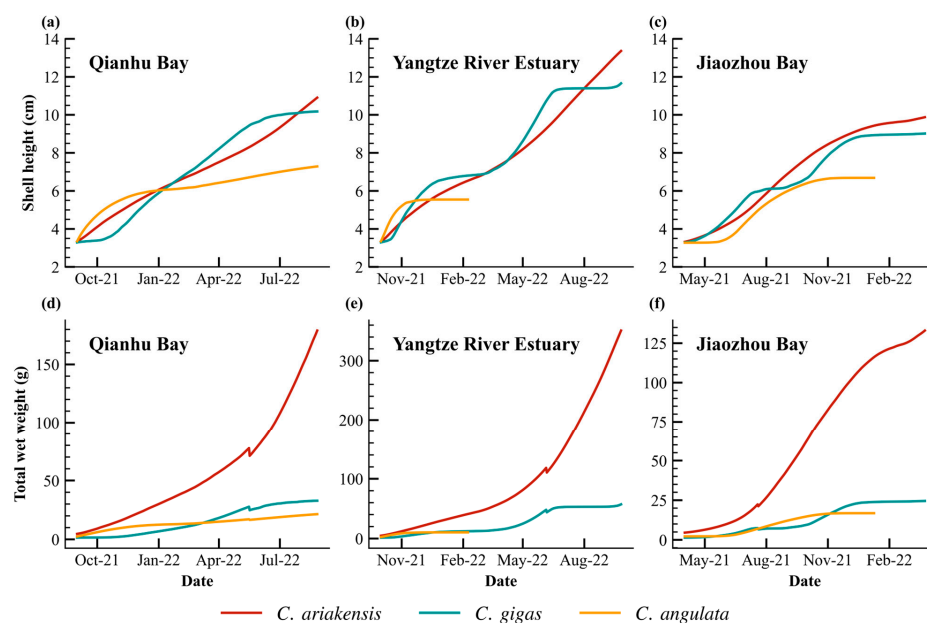
**Figure 6.** Comparison chart of measured data and simulated data for three oyster species. (a) Shell height of *C. gigas* in Sanggou Bay; (b) Wet weight of soft tissue of *C. gigas* in Sanggou Bay; (c) Shell height of *C. angulata* in Shenhui Bay; (d) Wet weight of soft tissue of *C. angulata* in Shenhui Bay; (e) Shell height of *C. ariakensis* in Zhuolin Pond; (f) Total wet weight of *C. ariakensis* in Zhuolin Pond; (g) Shell height of *C. ariakensis* in Dafeng River; (h) Total wet weight of *C. ariakensis* in Dafeng River.

The  $R^2$  values for the observed and simulated shell height and wet weight of the soft tissue of *C. angulata* were 0.9956 and 0.9466, with linear regression slopes of 1.0469 and 0.9830, and NRMSE values of 8.6% and 14.7%, respectively. The model effectively replicated the temporal variations in shell height and wet weight of the soft tissue of *C. angulata* in Shenhui Bay (Figure 6c,d).

In Zhulin Pond (Figure 6e,f), the  $R^2$  values between the measured and modeled data for shell height and total wet weight of *C. ariakensis* in the adjacent river were 0.9933 and 0.9654, with linear regression slopes of 1.0645 and 0.8054, and NRMSE values of 11.2% and 25.3%, respectively. In the Dafeng River (Figure 6g,h), the  $R^2$  values were 0.9658 and 0.9930, with linear regression slopes being 1.0501 and 0.7498, and NRMSE values of 21.9% and 28.1%, respectively. The results of the growth simulation of *C. ariakensis* in the two areas above were consistent with the actual data.

### 3.3. Dynamic Growth Simulation in Different Scenarios

Figure 7 illustrates the simulation results for shell height and total wet weight of three oyster species across three habitats: Qianhu Bay, the Yangtze River Estuary, and Jiaozhou Bay. The data are provided in Supplementary Table S1. In Qianhu Bay (Figure 7a,d), *C. ariakensis* exhibited the most rapid growth, achieving a maximum shell height of nearly 11 cm. *C. gigas*, with a maximum shell height of 10 cm, outpaced the other two oysters in growth during February and August, attaining 10 cm in June, while it showed slower growth from June to September. *C. angulata* exhibited superior growth compared to the other two oysters from September to January, reaching a shell height of 6 cm by January, after which its growth decelerated, with a maximum shell height of 7 cm by September. All three oysters experienced a reduction in their total wet weights in May, and the trend in the alteration of total wet weight corresponded with that of their shell heights.

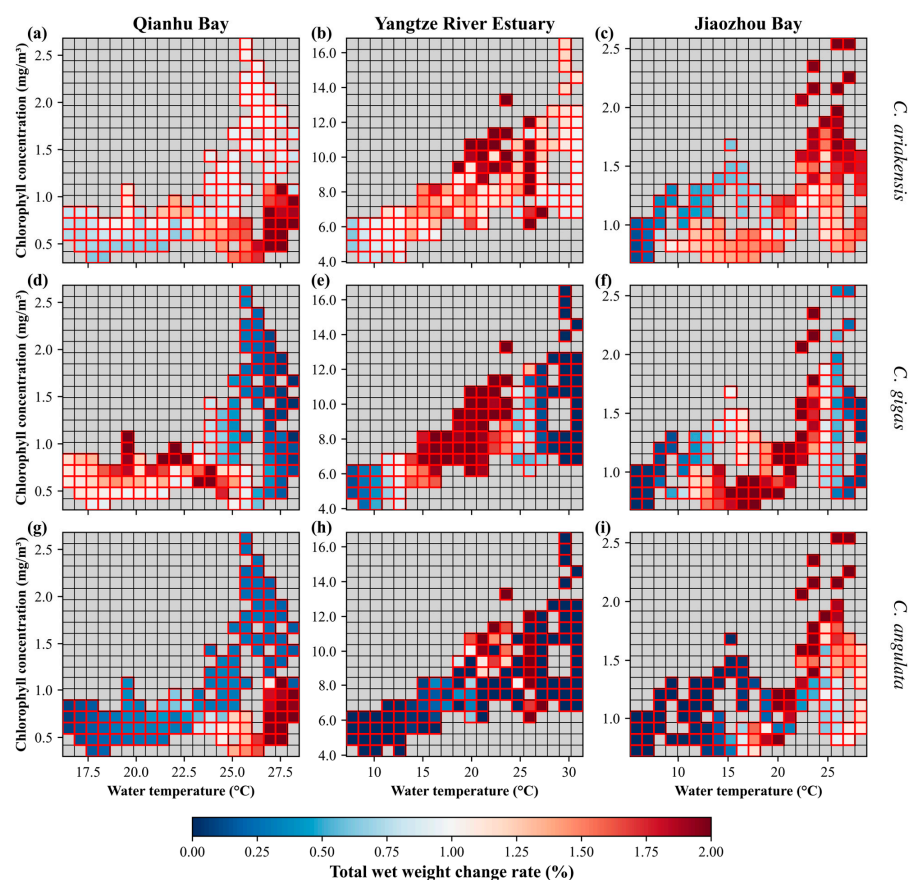


**Figure 7.** The simulated growth results of three oyster species in Qianhu Bay, the Yangtze River Estuary and Jiaozhou Bay. The panels (a–f) show shell height and total wet weight dynamics of *C. ariakensis*, *C. angulata*, and *C. gigas* in Qianhu Bay, Yangtze River Estuary, and Jiaozhou Bay, respectively.

In the Yangtze River Estuary (Figure 7b,e), *C. ariakensis* showed the highest growth rate, achieving a maximum shell height of 13 cm, surpassing the other oysters. *C. gigas* reached a shell height of 7 cm in March, followed by a rapid increase from May to June, when the shell height rose from 8 to 11 cm, before entering a phase of stagnant growth from July to September. *C. angulata* showed the most significant rise in its shell height from October to November, reaching 5 cm in November, followed by growth cessation and mortality in the next February. Regarding the total wet weight, both *C. ariakensis* and *C. gigas* exhibited a decline in June.

In Jiaozhou Bay (Figure 7c,f), *C. ariakensis* achieved a maximum shell height of approximately 10 cm. *C. gigas* showed a notably elevated growth rate from May, attaining a shell height of 6 cm by July. Its growth then decelerated, with stagnant growth found from August to September. *C. angulata* exhibited the slowest growth, with stagnation from April to June, a deceleration in September upon reaching a height of 6 cm, further stagnation in November, and death in the next January. The three oyster species showed a decline in total wet weight from mid to late July.

Figure 8 illustrates the total wet weight change rates of the three oyster species across varying temperatures and chlorophyll concentrations according to the model simulations. In Qianhu Bay (Figure 8a,d,g), the growth rates of total wet weight for the oyster species *C. ariakensis* and *C. angulata* were considerably elevated at temperatures of 25–28.5 °C and at chlorophyll concentrations below 1.1 mg/m<sup>3</sup>, but those of *C. gigas* were enhanced at temperatures of 18–25 °C and chlorophyll concentrations of 0.5–1.1 mg/m<sup>3</sup>. In the Yangtze River Estuary (Figure 8b,e,h), the change ranges of total wet weight for the three species have been elevated at higher temperatures and increased chlorophyll concentrations. *C. ariakensis* and *C. angulata* exhibited peak growth at 18–26.5 °C and 6–13.5 mg/m<sup>3</sup>, while *C. gigas* achieved enhanced growth at 14–24 °C and 5.5–13.5 mg/m<sup>3</sup>. In Jiaozhou Bay (Figure 8c,f,i), *C. ariakensis* grew fast at temperatures between 21.5 and 28 °C and chlorophyll concentrations above 1.3 mg/m<sup>3</sup>. *C. gigas* exhibited enhanced growth at temperatures ranging from 13 to 24.5 °C with chlorophyll concentrations between 0.4 and 2.4 mg/m<sup>3</sup>, whereas *C. angulata* showed superior growth at temperatures from 17.5 to 27 °C and chlorophyll concentrations ranging from 0.5 to 2.6 mg/m<sup>3</sup>.



**Figure 8.** Total wet weight change rate distribution of three oyster species in Qianhu Bay, the Yangtze River Estuary and Jiaozhou Bay. (a–c) Total wet weight change rate distribution for *C. ariakensis* in Qianhu Bay, Yangtze River Estuary, and Jiaozhou Bay, respectively; (d–f) for *C. gigas*; (g–i) for *C. angulata*.

#### 4. Discussion

The shape coefficients  $\delta_m$  were estimated to be 0.5002 for *C. ariakensis*, 0.2974 for *C. gigas*, and 0.3769 for *C. angulata*, exceeding the coefficients reported for the same species in previous studies: 0.175 for *C. gigas* [26] and 0.23 for *C. angulata* [23]. As a crucial parameter in the DEB model of shellfish, the shape coefficient is derived from either the total wet weight or the wet weight of the soft tissue, with the latter method better approximating biomass in certain contexts [14].

The estimated Arrhenius temperature for *C. ariakensis* (4444 K) in this study is lower than the value reported for *C. gigas* (5900 K) [26], due to variations in optimal growth temperatures among different oyster species.  $T_L$  of *C. ariakensis* (279 K) is lower than those of *C. gigas* (285 K) and *C. angulata* (291 K), whereas its  $T_H$  (307 K) exceeds those of *C. gigas* (297 K) and *C. angulata* (303 K). This thermal adaptation pattern corresponds to their ecological distributions: *C. angulata* thrives in high-temperature environments and exhibits low tolerance to cold; conversely, *C. gigas* is better adapted to cool climates and is relatively intolerant of high temperatures. In contrast, *C. ariakensis* is a eurythermal species capable of enduring broader temperature ranges than the other two oysters [30,32,33].

The slopes of linear regression,  $R^2$ , and NRMSE of simulated and observed values serve as critical validation indexes for models [37,38]. The mean  $R^2$  values for shell height and weight, as predicted by the models for *C. gigas*, *C. angulata*, and *C. ariakensis*, all exceeded 0.97; the average slopes of the linear regression varied from 0.91 to 1.02, and the average NRMSE values ranged from 9.8% to 21.62%. These suggest that the three models effectively replicate the dynamic growth process of oysters in marine environments.

Beyond validation, however, the models offer practical value for species selection. They predict site-specific mortality timing, February for *C. angulata* in the Yangtze River Estuary and January in Jiaozhou Bay, providing quantitative exclusion criteria rather than relying on qualitative statements of cold intolerance. Furthermore, the unified framework enables direct comparison of growth curves across three species and three habitats (Figure 7), allowing restoration practitioners to identify both the fastest-growing species and the timing of growth stagnation or mortality risk at a given site. These predictions inform species selection in ways that simple application of known thermal tolerances cannot.

Temperature is a critical environmental variable influencing oyster growth and survival [8,49], and the simulation results suggest distinct species-specific responses to thermal variation. *C. angulata* died when water temperatures fell below 8 °C during the low winter temperatures in Jiaozhou Bay in January and the Yangtze River Estuary in February, according to its physiological threshold of 96 h  $LT_{50}$  ( $7.83 \pm 0.45$  °C) [50], thereby accounting for the absence of wild populations north of the Yangtze River Estuary. In contrast, *C. gigas* was predicted to exhibit greater low-temperature tolerance, maintaining a mean daily shell-height growth rate of 0.64% in Jiaozhou Bay from April to November, which outperformed *C. angulata*. This is consistent with comparative growth patterns reported by Qin et al. (2023) [51] in Laizhou Bay and with *C. gigas* growth data in Jiaozhou Bay from Su and Shao (2007) [52]. In Qianhu Bay during July–August, higher temperatures severely constrained the growth of *C. gigas*, resulting in a mean daily shell height increment of merely 0.004 cm, despite an abundant food supply. Conversely, *C. angulata*, which favored elevated water temperatures, exhibited superior growth (mean daily shell height growth of 0.028 cm) from September to December. The observed growth responses of *C. angulata* and *C. gigas* at high temperatures align with the findings of Qin (2013) [7] and Zeng et al. (1999) [53]. The elevated chlorophyll concentration in the Yangtze River Estuary provided favorable growth conditions for all three oyster species. *C. gigas* achieved 0.89% mean daily shell-height growth from October 2021 to June 2022 under these conditions, consistent with the findings of Wang et al. (2023) in Xiangshan Harbor [54], Zhejiang Province. This confirms that

sufficient food availability within optimal temperature ranges substantially enhances oyster growth. Temperature influences the timing of oyster spawning, which occurs only when the requisite spawning temperature and energy thresholds are attained. As documented by Pouvreau et al. (2006) [55], spawning of oysters is triggered at 20 °C, accompanied by a significant decline in soft-tissue wet weight. Across all three habitats, a reduction in the wet weight of soft tissue was observed from May to July, with spawning occurring earliest in Qianhu Bay (May) and latest in Jiaozhou Bay (July), probably attributable to the earlier warming of water temperatures at lower latitudes [56]. In the Yangtze River Estuary, water temperatures exceeding 20 °C in June triggered a reduction in soft-tissue wet weight across all three oyster species, corresponding to Jiang's (2021) [57] findings of higher gonadal cross-section index values for *C. ariakensis* during the same period.

Oyster reef construction, a key approach for ecological restoration, has been effectively implemented both domestically and internationally. China has progressively developed *C. ariakensis* oyster reef ecosystems in the Yangtze River Estuary, the Yellow Sea and Bohai Sea, and the intertidal zone of the Yellow River Delta, improving the environmental quality of near-shore estuarine waters and increasing fishery resources [58–61]. Restoration projects for oyster reefs in the United States, Australia, and New Zealand predominantly utilize their native species *C. virginica* and its shells as the primary substrate, with successful outcomes achieved in the Chesapeake Bay, Port Phillip Bay, and Gulf of St. Vincent [61–63].

The primary determinant of the ecological restoration effectiveness of oyster reefs is the choice of reef-building species. This study examined the growth adaptations of the three oysters across three different habitats, revealing considerable disparities in their temperature adaptation strategies. Despite the robust cold tolerance of *C. gigas*, its growth was impeded by higher summer temperatures in Jiaozhou Bay. *C. angulata* adapted to elevated water temperatures but could not endure the low winter temperatures in the Yangtze River Estuary and Jiaozhou Bay. *C. ariakensis* exhibited a broader range of temperature adaptability and thrived in all three scenarios, particularly in the Yangtze River estuary, where it predicted a notable growth advantage. This suggests that variations in species adaptation can directly influence the efficacy of restoration efforts. Moreover, oyster reefs and their associated reef-building species typically encounter several environmental pressures, including climate change, hurricanes, and river management policies [11,64,65]. Substantial changes in environmental circumstances might result in restoration failures, even for native or introduced species in a specific region. Research conducted by Green et al. (2019) [66] indicated that the mortality of *C. gigas* reached 77.4% when temperatures abruptly rose from 20 °C to 25 °C. Efforts to introduce the non-native species *C. gigas* into the Chesapeake Bay, prompted by the significant decline of the native oyster, ultimately failed due to high local water temperatures and inadequate food availability, resulting in substantial mortality of *C. gigas* [67,68]. Consequently, selection assessments based on biological modeling of locally appropriate reef-building species prior to oyster reef restoration are essential, providing a fundamental method for enhancing the efficacy of oyster reef ecological restoration in the context of climate change [69].

One limitation of this study is that some parameters were transferred from closely related species, which may introduce uncertainty. Future studies should estimate these parameters through independent experiments and conduct global sensitivity analyses to quantify the influence of parameter uncertainty on model predictions.

Current DEB modeling of *C. ariakensis* fails to fully capture key physiological processes, such as food filtration efficiency, and oversimplifies nutrition by considering only chlorophyll a without accounting for the intake of other nutrients [23], which may explain the minor observed-simulated data mismatches. Future modeling should parameterize filtration, ingestion, and absorption processes while incorporating diverse nutritional sources

to optimize model performance. Additionally, salinity, stocking density, and other environmental factors should also be incorporated to enable cross-habitat analysis of oyster growth dynamics, providing scientific foundations for assessing aquaculture carrying capacity and selecting optimal reef-building species across diverse marine ecosystems.

## 5. Conclusions

In summary, the DEB models applied in this study reliably simulate the growth dynamics of the three oyster species. Beyond reproducing previously documented interspecific differences, which serve as essential validation, the models provide quantitative predictions directly applicable to restoration species selection. Specifically, the models predict mortality months for *C. angulata* (February in the Yangtze River Estuary, January in Jiaozhou Bay), offering a quantitative basis for excluding this species from these sites. They also enable, for the first time, direct comparison of growth curves across three species and three habitats within a unified framework. The results suggested that *C. ariakensis* grows fastest in the Yangtze River Estuary and Qianhu Bay, while *C. gigas* performs well in the Yangtze River Estuary but experiences summer growth suppression in Qianhu Bay. These findings suggest that DEB modelling translates qualitative knowledge of thermal tolerances into site-specific, quantitative criteria for species selection, providing scientific support for oyster reef restoration. It should be noted that the model predictions address the suitability dimension of species selection; actual restoration decisions should also consider the native distribution of the species, their genetic diversity, and relevant regulatory requirements.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fishes11070391/s1>; Table S1: Supplementary data.

**Author Contributions:** J.L.: Writing—original draft, Methodology, Software, Data curation, Validation, Formal analysis; Z.Y.: Visualization, Writing—review & editing, Formal analysis, Investigation; H.L.: Methodology, Software, Investigation; C.Y.: Writing—original draft, Writing—review & editing, Conceptualization, Methodology, Funding acquisition, Supervision; R.W.: Supervision, Conceptualization, Resources. All authors have read and agreed to the published version of the manuscript.

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