Assessment of bivalve carrying capacities and seeding densities in aquaculture areas of Jiaozhou Bay, China, using ecological modeling and the food balance

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Abstract
The increasing growth of the bivalve-culture industry necessitates a scientific assessment of the carrying capacity (CC) of this aquaculture system, in order to ensure sustainability. Here, using a marine plankton ecological model and the food balance, bivalve CCs were estimated for aquaculture zones in Jiaozhou Bay (JZB), an important aquaculture center in China. The results indicated that CCs mainly depended on bivalve filtration rates, which were in turn regulated by temperature. The CCs of Manila clams, razor clams, and scallops were lowest in August–September, while the CCs of oysters and mussels were lowest in October. For all taxa, CCs were higher in areas with higher primary production. Further evaluation indicated that present cultures were saturated, with high mortality rates. To improve culture quality and efficiency, the seeding density of the Manila clam, the most widely farmed species in the JZB, should be reduced to ~700 individuals (ind.)/m². We also recommend reducing the seeding densities of razor clams, oysters, and mussels to 345, 60, and 165 ind. /m², and reducing scallop seeding density to 280 ind./cage. Our methods and results provide a basis for further
assessments of stocking capacities and the promotion of sustainable, healthy aquaculture in other bays.

**KEYWORDS**

aquaculture, bivalve, carrying capacity, Jiaozhou Bay, model estimation, seeding densities

## 1 | INTRODUCTION

In recent decades, Chinese mariculture has developed rapidly. The area devoted to mariculture increased from $\approx 4.5 \times 10^5$ ha ($1 \text{ ha} = 10^4 \text{ m}^2$) in 1991 to $\approx 2.1 \times 10^6$ ha in 2010, while Chinese production increased from $1.9 \times 10^6$ t to $1.5 \times 10^7$ t over the same period (Jiang, Mu, & Yao, 2013). At present, 84.5% of all mariculture production worldwide originates from China (Food and Agriculture Organization, 2018). However, intensive aquaculture has had a negative impact on the ecological environments of many Chinese bays, leading to increased mortality rates, intensified disease outbreaks, and reduced condition among the cultured organisms (Ma et al., 2013). To maintain aquaculture health and sustainability, aquaculture scale and density must be within the carrying capacity (CC) of a given ecosystem. CC is defined as the yield or density at which production is maximized without negative ecological impacts (Duarte et al., 2003).

Previous studies have calculated bivalve CCs using several different methods. First, some authors have determined CC based on historical statistics. That is, culture density is equivalent to CC when production is maximized; above this CC, bivalve growth decreases, and mortality increases (Filgueira, Comeau, Guyondet, Mckindsey, & Byron, 2015). Second, bivalve CC has been estimated based on hydrographic conditions, food availability, and feeding characteristics (Garen, Robert, & Bougrier, 2004). Third, bivalve CC has been determined based on a material equilibrium, in which food supply is exactly sufficient for bivalve growth (Byron, Link, Costa-Pierce, & Bengtson, 2011). Fourth, bivalve CC has been computed using an ecological modeling approach, integrating the biochemical processes of nutrients, plankton, and bivalves (Guyondet, Roy, Koutitonsky, Grant, & Tita, 2010). The first three of these methods depend on measured data, which may be limited, and they often lack timeliness, which inhibits the assessment of dynamic CCs that vary temporally (Filgueira et al., 2015; Ibarra, Fennel, & Cullen, 2014). Use of the fourth method poses different challenges, including defining acceptable ecological impacts, identifying tipping points associated with ecological resilience, and parameterizing bivalve biological processes (Ibarra et al., 2014). For an aquaculture area, determining a reasonable method is the prerequisite for assessment of CC.

The culturing stocks in Jiaozhou Bay (JZB), an important center of bivalve aquaculture in China, have become saturated as culture scale and seeding density have increased, which caused poor growth and heavy mortality (N. Yu, Wang, Lu, Li, & Zhang, 2013). As a result, bivalve production has decreased or even halted (N. Yu et al., 2013; M. Zhang, 2008). For an example, under a seedling density of 2,500 ind./m², the mortality rate for 2–3-year-old Manila clams reached 47% because of deficiency in food and oxygen (M. Zhang, 2008). In this paper, we estimated bivalve CCs of aquaculture zones (HD, JZ, HW, HS, and HE) in JZB by using the marine plankton ecological model in conjunction with food-balance relationships. This joint approach avoids the data shortages associated with assessments based purely on the material equilibrium, and it also overcomes the difficulties associated with assessments based purely on models. Firstly, the ecological model was used to determine spatiotemporal biomass and primary production of aquaculture zones. Then, these model results were used to compute dynamic CCs of bivalves (Manila clams, razor clams, scallops, Pacific oysters, and mussels) based on the food-balance relationships. At last, seedling densities of these bivalves were investigated with respect to bivalve mortality rates and the estimated CCs, in order to identify optimal densities and ultimately make recommendations.
2 | MATERIALS AND METHODS

2.1 | The ecological model

We selected model variables according to the principle that key biochemical processes should be reflected, but the model should not be too complicated (Chen, 2003; X. Liu, Li, & Yuan, 2010). First, for the purposes of estimating bivalve CCs based on the food-balance relationship, the ultimate bivalve food source was considered equivalent to primary production. Second, because detritus is not the primary food source for bivalves, detritus was not measured in our survey nor considered in our model. Third, because our aim was to estimate CCs rather than residual capacities by using the modeled biomass and primary production in aquaculture zones, the model did not consider the biological processes of the bivalves. Thus, we adopted a nutrient-phytoplankton-zooplankton (NPZ) model. The biochemical processes and parameterization of the model are shown in Appendix A.

2.2 | Model configuration and data usage

Hydrodynamic modeling was performed using the Princeton Ocean Model (Mellor, 2004). Only tidal forces were considered because tidal currents are the prominent physical processes in the JZB (X. Liu et al., 2010). The model domain covered the entire bay (Figure 1). The open boundary was at the bay mouth, where the water-level forcing was calculated as follows:

\[ H = \sum A_i \cos(w_i t - \theta_i + \phi_i) \]

where \( A_i, \theta_i, \) and \( \phi_i \) represented the amplitude, phase lag, and initial phase, respectively, of \( M_2, S_2, O_1, \) and \( K_1 \) component tides. These values were obtained based on harmonic analysis (Huang & Huang, 2007) of observed water levels at Site 1 shown in Figure 1. Biochemical processes were simulated using a plankton ecological model that has been used in previous studies of coastal seas (H. Hu, Wang, Liu, & Goes, 2016; X. Liu et al., 2010; X. Liu, Pu, Luo, Lu, & Liu, 2019; Wan, Yuan, & Wang, 2001). The model was started from May 15, 2006 and repeated for 2006 until June 30, 2007, so the model time covered all of the field survey time. The calculation step was set to 300 s. The grid distances in horizontal directions of east-west and south-north were 599 and 740 m, respectively, while the vertical model space was evenly split into 5 layers. Observations of biological and chemical variables in May 2006 were used as initial values in each grid following spatial Kriging interpolation. The linear time interpolations of observations at Site 1 were used as the open-boundary values.

The model was designed based on the observations at 17 sites (Figure 1) between March 2006 and May 2007. The observed variables included water temperature, DIN, DIP, silicate, Chl-a, and zooplankton. They were sampled in the surface and bottom layers when site depth was \( \geq 5 \) m, and only surface samples were taken when site depth was < 5 m. Sites 1–11 were surveyed monthly, while sites 12–17 were surveyed in February, May, August, and October only. Water temperature was observed by reversing thermometers with a resolution of 0.02 °C; DIN involved nitrate (\( NO_3^- \)), nitrite (\( NO_2^- \)), and ammonium (\( NH_4^+ \)) nitrogen, which were detected by zinc cadmium reduction method, diazo-coupling method, and sodium hypobromite oxidation method, respectively; DIP was measured by phospho-molybdenum blue method; silicates were determined by silico-molybdenum blue method; Chl-a concentration was recorded by spectrophotometric method; and zooplankton was measured using the gravimetric method. The methods accorded to the standard (Standardization Administration of China [SAC], 2008). Besides, water levels were continuously measured using an Aanderaa recorder at Site 1 between September 21 and October 31, 2006.

Terrestrial nutrients enter the JZB via six rivers (Figure 1); the associated nutrient input data were obtained from K. Li, Zhang, Li, Zhang, and Wang (2015).
The primary bivalve species cultured in the JZB are Manila clams, *Ruditapes philippinarum*; razor clams, *Sinonovacula constricta*; scallops, *Chlamys farreri*; Pacific oysters, *Crassostrea gigas* and mussels (*Mytilus edulis*). Of these, the two clams are bottom cultured, while the oysters, scallops, and mussels are suspension cultured. Our survey divided the aquaculture area into five zones: HE, HS, HW, JZ, and HD (Figure 1). All five species are cultivated in zones HE, HS, and HW; only Manila clams, razor clams, and oysters are cultivated in zone JZ; and only Manila clams and razor clams are cultivated in zone HD.

**Figure 1** Configurations of the model domain, observation sites, benthic sampling sites, and aquaculture zones. HE, HS, HW, JZ, and HD represent Hongdao East, Hongdao South, Hongdao West, Jiaozhou, and Huangdao culture zones, respectively; DX and DY are benthic sampled sites.

### 2.3 The food-balance relationship used to estimate CCs

The primary bivalve species cultured in the JZB are Manila clams, *Ruditapes philippinarum*; razor clams, *Sinonovacula constricta*; scallops, *Chlamys farreri*; Pacific oysters, *Crassostrea gigas* and mussels (*Mytilus edulis*). Of these, the two clams are bottom cultured, while the oysters, scallops, and mussels are suspension cultured. Our survey divided the aquaculture area into five zones: HE, HS, HW, JZ, and HD (Figure 1). All five species are cultivated in zones HE, HS, and HW; only Manila clams, razor clams, and oysters are cultivated in zone JZ; and only Manila clams and razor clams are cultivated in zone HD.
With a known feeding rate and food supply, the maximum number of bivalves supported by the food supply (i.e., the CC) at any given time can be estimated based on the food balance, which assumes an equilibrium between food consumption and supply (Byron et al., 2011). Given primary production PP (representing food supply, unit: mgC/[m² hr]) and ingestion rate IR of individual bivalve, the CC, represented with the number of individuals per area, in a given zone was calculated as

\[
CC = \frac{PP}{IR}
\]

where \( IR = FR \cdot k \cdot P \), \( P \) was the algal concentration, \( k (=45) \) was the mass ratio of carbon to Chl-a in algae, and filtration rate (FR) was the volume of water filtered by the bivalve per unit time (Ehrich & Harris, 2015).

For the suspension-cultured bivalves, PP was equal to algal primary production (PP1). The bottom-cultured bivalves, however, are supplied with food by both algae and microphytobenthos. Therefore, the PP of these bivalves was PP1 plus benthic primary production (PP2).

With the above formula, modeled results (primary production and algal concentration), and observed data (benthic primary production and filtration rates), we computed CCs of aquaculture zones for five species in different sizes in 1 year. Based on the estimated CCs and the mortality rates of bivalves, the stocking densities were evaluated so as to present the suggested seeding densities.

2.4 | Observations of benthic primary production

By using \(^{14}\)C isotope tracer method according the specification for oceanographic survey (SAC, 2008), benthic primary production was measured in seabed samples (0–1 cm columns) taken at sites DX and DY (Figure 1) in February, April, August, and October in 2000. Benthic primary production in February, April, August, and October was 4.06, 19.77, 8.33, and 47.88 mgC/[m² hr], respectively, at site DX, and was 4.45, 9.87, 7.02, and 8.65 mgC/[m² hr], respectively, at site DY. Monthly production was estimated by the linear interpolation of the observations, and the contribution of an observed site to a zone was estimated based on the inverse proportion of the distance between the site and the zone.

2.5 | FRs of Manila clams

Manila clams are classified into size groups based on size: shell lengths of 2–2.6, 2.6–3.3, and 3.3–4 cm (J. Zhang, Fang, Sun, & Zhao, 2005). The clearance rate (CR), which corresponds to the volume of water filtered per unit time in which food particles are completely ingested, has been studied in Manila clams. J. Zhang et al. (2005) reported the CRs of Manila clams at 21°C while Dong, Xue, and Li (2000) investigated the effects of temperature on CR. J. Wang et al. (2006) reported the FRs of Manila clams at 15.4°C (seen in Table S1). By extending the results of Dong et al. (2000) (Table S1) in a linear fashion, we estimated that CRs at 4 and 28°C were 0.03 and 0.58 L/hr, respectively. Then, the average CR at 21°C and FR at 15.4°C were obtained. Assuming that the effects of temperature on CR and FR are identical, we combined the results of J. Wang et al. (2006) and Dong et al. (2000) to determine the average FR at 21°C and the ratio of average FR to average CR at 21°C. The ratio was multiplied by CR to yield the FR at 21°C. Finally, FRs at various temperatures were obtained using linear interpolation based on the effects of temperature on FR.

2.6 | FRs of razor clams

Pan et al. (2002) classified razor clams into three groups based on shell size (3.9 ± 0.27, 5.4 ± 0.24, and 6.3 ± 0.48 cm) and measured FRs at 4, 15, 20, 25, and 30°C (Table S2). FR was lowest at 4°C and the highest at 20°C. The FRs were linearly interpolated to predict FRs at other temperatures.
2.7 FRs of scallops

Fang et al. (1996) divided scallops into three groups based on shell size (3–4, 4–5, and 5–6 cm) and measured the FRs of scallops from Sungo Bay, China, a bay near the JZB. We estimated FRs for the scallops in the JZB taking into account the temperature difference between the JZB and Sungo Bay (Table S3).

2.8 FRs of oysters

Kuang et al. (1996) classified Pacific oysters into six size groups based on dry weight (0.12, 0.21, 0.42, 0.66, 1.1, and 1.39 g) and measured the FRs at different temperatures (Table S4). We used linear interpolation based on these results to estimate FRs for different size oysters at different temperatures.

2.9 FRs of mussels

J. Wang et al. (2006) classified mussels into three size groups based on shell length (3.9, 4.8, and 6.5 cm) and measured FRs for three sizes at \(17.79 \pm 0.87\) °C (Table S5). However, as FRs were not measured at different temperatures, we were unable to estimate the effects of temperature on mussels based on this previous study. However, as mussels and oysters have similar habits, we assumed that the relationship between oyster FR and temperature was identical to that between mussel FR and temperature. We then estimated mussel FRs at various temperatures by the linear-interpolation of the measured values.

3 RESULTS

3.1 Simulated phytoplankton biomass

Figure 2 shows the modeled and observed monthly Chl-a levels at each site, while Figure 3 shows the monthly variations in average temperature in the bay and the average primary productions in each zone. From winter to spring, as temperature and solar radiation increased, phytoplankton biomass gradually increased. After May, Chl-a levels and primary production decreased slightly as algal metabolism and ingestion by zooplankton increased. During the summer, Chl-a levels and primary production increased continuously because of favorable nutrient, temperature, and solar radiation conditions. Phytoplankton biomass and primary production decreased in autumn. In all seasons, Chl-a levels in the northern area of the bay were higher than those in the central part of the bay and at the bay mouth.

The modeled Chl-a levels were generally consistent with observed values in the bay. However, annual average observed Chl-a (4.08 mg/m³) was higher than that predicted by the model (3.35 mg/m³). This discrepancy was mainly attributed to the maximums recorded in February. Excluding the values measured in February, the annual average observed Chl-a (3.3 mg/m³) was consistent with the modeled value (3.5 mg/m³). In addition, the maximum Chl-a levels in the bay were predicted by the model in August (in the south) and September (in the north). In contrast, excluding February, measured Chl-a levels were highest in June at Sites 3 and 11, in October at Sites 8–10, and in August at all other sites. Overall, measured Chl-a levels were highest in August–October.

Deviations between measured and simulated data are common, and may be because of a number of factors, including survey time and test method. Notably, at northern sites, observed Chl-a levels were highest in February (while quite low in January and March), even significantly greater than those in the summer. Wu, Sun, Zhang, and Zhang (2004) and Sun et al. (2005) reported that, in February, Chl-a peaked, but primary production remained low. To date, the underlying biological causes of these observations have not been clarified. For a mid-latitude bay, at very low temperature in the JZB, algae grow very slowly, so the biomass and the primary production should not be high. The model here presents this regular pattern and cannot reproduce the maximal phenomenon in February. So
so far, no ecological model described this phenomenon in the JZB. As bivalve CC is greatest in the winter, our model accurately estimated bivalve CC and assessed bivalve stocking despite not reproducing these February maxima, under the premise that the model objectively reflected the spatiotemporal characteristics of algae in the other seasons.

**FIGURE 2** Modeled (connected dots) and observed (individual squares) concentrations of Chl-a

**FIGURE 3** The monthly average water temperatures in the bay, and the monthly primary production in the aquaculture zones. Green bars show the temperature ranges among the observation sites shown in Figure 1
3.2 | Manila clam CCs

Large monthly variations in CCs of Manila clams were estimated (Figure 4). The CC of large clams was lower than that of small clams, but the CCs of clams of different sizes varied similarly in response to seasonal changes in temperature. At higher temperatures, FRs were higher, and CC was lower. CCs for all sizes of Manila clams were higher in the winter and lower in the summer. In winter, maximum CC for clams of 2–2.6, 2.6–3.3, and 3.3–4 cm were 4,534, 3,364, and 2,744 individuals/m², respectively, in the JZB. As temperatures increased in the spring, CC continued to decline, even though primary production increased, because clam metabolism improved significantly. CC was lowest from August to September, with CCs of 630, 468, and 382 ind./m² for clams of 2–2.6, 2.6–3.3, and 3.3–4 cm, respectively. As temperatures decreased in autumn, CC gradually increased. It is thus clear that the dominant environmental factor affecting CC was temperature. Throughout 1 year, the highest is ~7 times greater than the minimum.

Figure 4 shows the CCs of five culture zones in May–November (CCs in the other months were not presented because they were significantly high and not used in assessing stocking densities). In zones HE, HS, HW, JZ, and HD, the minimum CC for 2–2.6 cm clams was 669, 657, 535, 628, and 744 ind./m², respectively; the minimum CC for 2.6–3.3 cm clams was 497, 488, 396, 466, and 552 ind./m², respectively; and the minimum CC for 3.3–4 cm clams was 405, 398, 323, 380, and 450 ind./m², respectively. In the summer, zone HD had the highest CCs and primary production, while zone HW had the lowest CCs and primary production.

3.3 | Razor clam CCs

Because razor clam CCs are highest in the winter, CCs between May and November are shown (Figure 5). CC varied significantly among months and clams of different sizes. However, in general, larger clams had lower CCs. Seasonal variations in CC followed similar patterns in clams of different sizes. Because filtration is affected by temperature, CCs decreased gradually through the spring and summer, and CCs increased gradually through the autumn and winter. In zone JZ, CCs were lowest in August–September: for 3.9, 5.4, and 6.3 cm
clams, CCs were 279, 111, and 82 ind./m², respectively, in August, and 274, 109, and 80 ind./m², respectively, in September. In zone HD, CCs were lowest in September: for 3.9, 5.4, and 6.3 cm clams, CCs were 278, 114, and 86 ind./m² in August. The average CCs of two zones were 276, 112, and 83 ind./m² for 3.9, 5.4, and 6.3 cm clams, respectively.

3.4 | Scallop CCs

Figure 6 shows seasonal variations in scallop CCs. It was evident that scallop CCs varied with size and season. Larger scallops, with higher FRs, had lower CCs. Seasonal variations in CC followed similar patterns in scallops of different sizes, with high CCs in winter and low CCs in summer. The CCs of 3–4 and 4–5 cm scallops peaked in December, and the CCs of 5–6 cm scallops peaked in January. In zones HE, HS, and HW, the maximum CCs of 3–4 cm scallops were 305, 327, and 265 ind./m², respectively; the maximum CCs of 4–5 cm scallops were 189, 202, and 163 ind./m², respectively; and the maximum CCs of 5–6 cm scallops were 88, 89, and 74 ind./m², respectively. The minimum CCs for 3–4 cm, 4–5 cm, and 5–6 cm scallops were 74, 50, and 39 ind./m², respectively, in zone HE; 76, 52, and 41 ind./m², respectively, in zone HS; and 61, 41, and 32 ind./m², respectively, in zone HW. Across all sizes of scallop, CC was highest in zone HS and lowest in zone HW.

3.5 | Oyster CCs

Oyster CCs varied with size and month. Because larger oysters have lower FRs, the CC of larger oysters is lower than the CC of smaller oysters at any given time point. Seasonal variations in CC were consistent among oysters of different sizes: CCs were higher in the winter and lower in the summer and autumn. Figure 7 shows CCs between May and November, when CCs were significantly lower than those in other months. In zone HE, CCs were lowest in October: the minimum CCs for oysters of 0.12, 0.21, 0.42, 0.66, 1.1, and 1.39 g were 108, 79, 51, 36, 28, and 23 ind./m². In other zones, CCs were lowest in September. Minimum CCs for oysters of 0.12, 0.21, 0.42, 0.66, 1.1, and 1.39 g were 120, 87, 56, 39, 31, and 25 ind./m², respectively, in zone HS; 96, 70, 45, 32, 25, and 20 ind./m², respectively, in zone HW; and 106, 77, 49, 34, 27, and 22 ind./m², respectively, in zone JZ.

3.6 | Mussel CCs

Mussel CCs varied with size and month. In general, bigger mussels had lower FRs and lower CCs. Seasonal variations in CC were consistent among mussels of different sizes: CCs were higher in the winter and lower in the summer and autumn. The maximum CC was observed in February and was ~11 times greater than the minimum
CC. Figure 8 shows the CCs of mussels of different sizes between May and November. Similar to oysters, mussel CC was lowest in zone HE in October, but lowest in September in all other zones. Minimum CCs for 3.9, 4.8, and 6.5 cm mussels were 142, 115, and 108 ind./m², respectively, in zone HE; 157, 128, and 120 ind./m², respectively, in zone HS; and 126, 103, and 96 ind./m², respectively, in zone HW.

FIGURE 6  Carrying capacities of scallops of different sizes

FIGURE 7  Carrying capacities of oysters of different sizes

CC. Figure 8 shows the CCs of mussels of different sizes between May and November. Similar to oysters, mussel CC was lowest in zone HE in October, but lowest in September in all other zones. Minimum CCs for 3.9, 4.8, and 6.5 cm mussels were 142, 115, and 108 ind./m², respectively, in zone HE; 157, 128, and 120 ind./m², respectively, in zone HS; and 126, 103, and 96 ind./m², respectively, in zone HW.

4  |  DISCUSSION

4.1  |  Culture densities of Manila clams

Manila clams of 2–2.6, 2.6–3.3, and 3.3–4 cm are 1, 2, and 3 years old, respectively; Manila clams are harvested at 2–3 years old (dry weights of 6–10 g) (Ren, Xu, Guo, & Yang, 2006). Based on the estimated CCs, if 2-year-old
Manila clams are harvested, the maximum production in zones HE, HS, HW, JZ, and HD is predicted to be 29,820, 29,280, 23,760, 27,960, and 33,120 kg/ha, respectively (an average of 28,080 kg/ha). If 3-year-old Manila clams are harvested instead, the maximum production in zones HE, HS, HW, JZ, and HD is predicted to be 40,500, 39,800, 32,300, 38,000, and 45,000 kg/ha, respectively (an average of 38,200 kg/ha). Given the 9,600 ha in the JZB devoted to Manila clam cultivation (Ren et al., 2006), the maximum production of 2- and 3-year-old clams is estimated to be 269,570 and 366,720 t/year, respectively. In recent years, Manila clam production in the JZB has averaged 33,750 kg/ha (a total of 324,970 t) (M. Zhang, 2008), which is in the range for 2–3-year-old clams calculated above. Therefore, if only 3-year-old clams were harvested, output and income might both increase. That is, the selective harvest of 3-year-old clams might both reduce culture costs and increase economic benefits.

In the JZB, Manila clams are seeded at density of 2,500 ind./m²; the mortality rate for 1–2-year-old clams is 35%, and that of 2–3-year-old clams is 47% (Guo, Ren, & Yang, 2005). Based these data, 411 ind./m² remained 2 years after sowing, which was less than the CC of 2-year-old clams (468 ind./m²) but more than the CC of 3-year-old clams (382 ind./m²). It is thus evident that seeding clams at a density 2,500 ind./m² does not significantly improve output, but instead increases mortality while decreasing individual quality and fatness, ultimately increasing culture costs. Thus, seeding densities should be appropriately reduced. According to expected survival rates (80% at 2-years-old and 70% at 3-years-old; Guo et al., 2005), we recommend seeding densities (shown in Table 1) in zones HE, HS, HW, JZ, and HD of 723, 710, 576, 678, and 804 ind./m², respectively (an average of 700 ind./m²).

### 4.2 Culture densities of razor clams

Juvenile razor clams (shell length ~ 1.5 cm) are typically sown in April. After more than 1 year, razor clams reach the required size for harvest (5–6 cm). In August–September, when shell size is ~4 cm, the CC is low. Therefore, based on the lowest CC of the 3.9 cm clams, the theoretical maximum average stocking density is 276 ind./m² in the JZB. Previous authors have proposed a variety of suitable stocking densities in northern China: 150–230 ind./m² (B. Wang & Wang, 2001), 300–375 ind./m² (H. Wang, Zhou, Xing, & Yu, 2002), 360–750 ind./m² (W. Hu & Ji, 2003), and 300–450 ind./m² (Zhou, Wang, & Xing, 2003). However, no previous studies have assessed razor clam mortality at these densities. We predicted that razor clam mortality rates were similar to those of Manila clams: 20% at 2-years-old. Thus, we recommend a razor clam seeding density (shown in Table 1) of 345 ind./m² in the JZB (343 ind./m² in JZ, 348 ind./m² in HD).

### 4.3 Culture densities of scallops

A scallop cage (5.5 m²) has 8 layers with ~120 ind./layer; thus, scallop culture density in the JZB is 960 ind./cage (mortality >50%) and the total output is 5,782 t. However, based on the estimated CC of 5–6 cm scallops, we...
predicted a yield of 4,883 t in the JZB. Because scallop density exceeds the supported CC, mortality is high. Therefore, scallop culture density should be reduced. M. Zhang (2008) reported that scallop mortality was only 5% if seeded at a density of ≤50 ind./layer, and that mortality increased significantly above this threshold density. C. Li et al. (2011) reported that the seedling density in the JZB and nearby bays was ~30 ind./layer in the early 1980s and increased to 50 or even >100 ind./layer in the 1990s, leading to a decrease in algal abundance: algal abundance was 1,000–2,000 × 10^4 cell/m^3 in 1988, but only ~400 × 10^4 cell/m^3 after 1995. In 2006, we collected an average of 405 × 10^4 phytoplankton cells/m^3 in the JZB. Overstocking leads to decreased individual quality and high mortality. In some years, mortality rates reached 90% (C. Li et al., 2011). Y. Wang, Li, Qiu, Zhang, and Wang (2001) reported that mortality rates in these bays were 50–95% between 1995 and 2001, with deaths mainly occurring in the summer. Accordingly, Y. Wang et al. (2001) recommended seeding densities of <40–50 ind./layer, and showed that when seeding density in nearby Sungo Bay decreased to 20 ind./layer, both the ecological environment and the culture efficiency were improved. R. Yu, Lin, and Bi (1994) and Z. Yu et al. (2010) recommended a seeding density of 25–30 ind./layer in a cage.

In the aquaculture zone of the JZB, scallop spats are placed in cages in March and harvested in December as 5–6 cm adults. Therefore, 4–5 cm scallops (September growth) were chosen to determine reasonable seeding densities. The estimated CC of 4–5 cm scallops in zones HE, HS, and HW was 275, 286, and 226 ind./cage, respectively, equivalent to 34, 36, and 28 ind./layer, respectively. Given a 5% mortality rate, the suggested seedling density (shown in Table 1) in zones HE, HS, and HW is therefore 289, 301, and 238 ind./cage, respectively, equivalent to 36, 38, and 30 ind./layer, respectively. Thus, we recommend an average of 280 ind./cage and 35 ind./layer across the JZB.

### 4.4 Culture densities of oysters

In the JZB, oysters are normally sown in late October and are harvested after 2–2.5 years. Because oyster CC was lowest in September–October, and because oysters are harvested at dry weights >1.1 g, we used the CCs of 0.66 g oysters (36, 39, 32, and 34 ind./m^2 in zones HE, HS, HW, and JZ, respectively) to determine reasonable culture densities. In nearby Sungo Bay, oyster mortality was ~10% per year at a culture density of 59 ind./m^2 (Nunes et al., 2003). Gong (1995) reported that the temporary survival rate of seedlings was 75%. Based on these data, we calculated that the survival rate from seeding to harvest was 58%. Thus, the recommended seeding densities (shown in Table 1) in zones HE, HS, HW, and JZ are 62, 68, 55, and 59 ind./m^2, respectively. The average recommended density across the bay is thus 59 ind./m^2, consistent with that reported by Nunes et al. (2003) in Sungo Bay.

### 4.5 Culture densities of mussels

In the JZB, mussels are seeded around November and are cultured more than 1 year; the best harvest time is January–March. Our survey indicated that mussels are usually harvested after reaching a shell length of ~6 cm.
because mussel farmers emphasize economic value and fatness. As CC was lowest in September–October, when mussels are growing rapidly but are not yet ready for harvest, we used the CCs of 4.8 cm mussels to calculate optimal seeding densities. The calculated densities were 115, 128, and 103 ind./m² for zones HE, HS, and HW, respectively (115 ind./m² on average). Q. Liu (1993) reported that high seeding densities may lead to mortality rates of 60–70% and may significantly reduce individual size and weight; it was suggested that the seeding density should be limited to ≤166 ind./m². Given that 30% of all mussels may die between seeding time and harvest time, we recommend mussel seeding densities (shown in Table 1) of 165, 179, and 147 ind./m² in zones HE, HS, and HW, respectively (an average of 165 ind./m²).

4.6 Culturing arrangement

To maintain the ecological balance and promote healthy aquaculture, rational arrangement in aquaculture systems is prerequisite, so as to increase organismal reproduction and enrich the aquatic food chain (Powers, Peterson, Summerson, & Powers, 2007). In most of the aquaculture zones of the JZB, the water is shallow and the sediment type is of a sandy one, which is advantageous to benthic primary production. This good condition satisfies bottom culture in a large scale with relatively high density. At present, Manila clams occupy 93.8% of the total aquaculture area and represent 95.8% of the total production. This arrangement generally accorded with the condition. Only in the deeper water, scallop, oyster, and mussel are suspended cultured. Besides, culture structures may be adjusted by introducing polyculture (such as kelp and bivalve), choice seafood culture, or fish-cage culture.

5 CONCLUSIONS

Here, we presented a method of CC estimation that can be used to assess the sustainability of a mariculture system. Our approach reflected spatiotemporal variations in bivalve CCs by combining an ecological model and food-balance relationships. We estimated bivalve CCs and evaluated seeding densities in aquaculture zones in the JZB. Our results indicated that CCs were lower in the summer and autumn because of high FRs and high temperatures; areas with high primary production had higher CCs; and bivalve stocks in the JZB exceeded maximal CC. We recommend reductions in average seeding densities to ~700 ind./m² for Manila clams, 345 ind./m² for razor clams, 60 ind./m² for oysters, 165 ind./m² for mussels, and 280 ind./cage for scallops. Our study provides references for future estimations of aquaculture CCs and reasonable seeding densities in other bays.

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SUPPORTING INFORMATION
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APPENDIX

The biochemical processes and parameterization

In our NPZ model, \( N \) (mg/L) included dissolved inorganic nitrogen (DIN), phosphate (DIP), and silicate (Si); algal biomass \( P \) was expressed as chlorophyll a (Chl-a) (mg/m\(^3\)); and the net weight of \( Z \) was expressed in mg/m\(^3\). The associated equations were

\[
\begin{align*}
\left( \frac{\partial}{\partial t} - \text{diff + adv} \right) P & = (\text{Grow} - \text{Rsp} - \text{Mort}) P - \text{Up} Z \\
\left( \frac{\partial}{\partial t} - \text{diff + adv} \right) Z & = (\text{Grow} - \text{Excr} - \text{Mort}) Z \\
\left( \frac{\partial}{\partial t} - \text{diff + adv} \right) N & = -(\text{Grow} - \text{Rsp} - \text{Mort}) P + (\text{Up} - \text{Grow}) Z + (\text{Excr} + \text{Mort}) Z
\end{align*}
\]

where the terms on left represent time variation, diffusion, and convection, respectively. The biochemical processes are:

- Algal growth was calculated as \( \text{Grow} P = g_P e^{\mu P T} \min \left( \frac{\text{DIN}}{K_N}, \frac{\text{DIP}}{K_P}, \frac{\text{Si}}{K_S} \right) \frac{1}{I_{\text{opt}}} e^{\left(1-I_{\text{opt}}/I_0\right)} P \), where the maximum growth rate at 0°C (\( g_P \)) was 0.029/hr, the exponent coefficient (\( \mu_P \)) was 0.0633/°C, and the half-saturation constants (\( K_N, K_P, K_S \)) were 2.4, 0.15, and 2.6 μmol/L, respectively (Hu et al., 2016; Liu et al., 2010; this study). The optimum radiation for photosynthesis (\( I_{\text{opt}} \)) was 66.1 W/m\(^2\) (this study). Light intensity (\( I \)) at depth \( z \) was equivalent to \( I_0 P_a(1 - R_a) e^{-kz} \), where \( I_0 \) was the sea-surface solar radiation, \( k \) was max (1.4–0.08 \( z \), 0.2), the penetration ratio through cloud (\( P_a \)) was 0.8, the sea surface reflection coefficient \( R_a \) was 0.04, and the light ratio for photosynthesis (\( E \)) was 0.43 (Liu et al., 2010).

- Algal respiration was calculated as \( \text{Rsp} P = m_P e^{\gamma_P T} P \), where the maximum respiration rate at 0°C (\( m_P \)) was 0.0015/hr and \( \gamma_P \) was 0.0633/°C (Liu et al., 2010; this study).

- Algal mortality was calculated as \( \text{Mort} P = d_P P \), where \( d_P \) was 0.0042/hr (Liu et al., 2010; Onitsuka, Yanagi, & Yoon, 2007).

- Zooplankton grazing was calculated as \( \text{Up} Z = g_Z e^{\mu Z T} (1 - e^{-\lambda Z}) Z \), where the maximum zooplankton growth rate at 0°C (\( g_Z \)) was 0.017/hr, \( \mu_Z \) was 0.06/°C, and the Ivlev constant (\( \lambda \)) was 0.6 m\(^3\)/mg (Hu et al., 2016; Liu et al., 2010).

- Zooplankton growth was calculated as \( \text{Grow} Z = \beta UpZ \), where the assimilation ratio (\( \beta \)) was 0.4 (Hu et al., 2016; Liu et al., 2010).

- Zooplankton metabolism was calculated as \( \text{Excr} Z = m_Z e^{\gamma Z T} Z \), where the maximum metabolic rate at 0°C (\( m_Z \)) was 0.042/hr and \( \gamma_Z \) was 0.06/°C (Liu et al., 2010).

- Zooplankton mortality was calculated as \( \text{Die} Z = d_Z Z \), where \( d_Z \) was 0.0042/hr (Liu et al., 2010; Onitsuka et al., 2007).

The nitrogen content in Chl-a is 0.3 mmol/mg, and the molar ratios N:P and N:Si in plankton were set at 16 and 1.39, respectively (Liu et al., 2010). The above functions and parameters were determined based on the literature and on model calibrations.