



Assessment of the Carrying Capacity of Integrated Pond Aquaculture of *Portunus trituberculatus* at the Ecosystem Level

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In recent years, integrated pond aquaculture under controlled management has been crucial in improving the supply of aquatic products and ensuring food security. This study constructed two trophic models of integrated pond aquaculture ecosystems of *Portunus trituberculatus*–*Penaeus japonicus* (PP) and *P. trituberculatus*–*P. japonicus*–*Sinonovacula constricta* (PPS) using Ecopath with Ecosim software. The energy flows, ecosystem properties, and carrying capacities of the two ecosystems were analyzed and evaluated. The results showed that the ecotrophic efficiency values in the PP and PPS ecosystems were 0.962 and 0.954 for *P. trituberculatus* and *P. japonicus* and 0.952 for *S. constricta*. The effective trophic levels of *P. trituberculatus* and *P. japonicus* were 2.065 and 2.027 in the PP system, and those of *P. trituberculatus*, *P. japonicus*, and *S. constricta* were 2.057, 2.018, and 2.010 in the PPS system. The primary productivities of the PP and PPS ecosystems were 2623.79 and 2781.48 g/m²/240 days, with 2.13 and 37.83% of the energy flowing to trophic level II and 97.87 and 62.17% flowing to the detritus, respectively. The total energy of the detritus group was 2900.89 and 2372.98 g/m²/240 days, with 931.02 and 1505.35 g/m²/240 days flowing to trophic level II, respectively. The total primary production/total respiration ratio of the PPS ecosystem (1.632) was lower than that of the PP ecosystem (4.824), indicating that the former had a greater degree of exploitation. At the current feeding level, the carrying capacities of *P. trituberculatus* and *P. japonicus* were 65.15 and 47.62 g/m² in the PP ecosystem, and those of *P. trituberculatus*, *P. japonicus*, and *S. constricta* were 64.96, 48.06, and 100.79 g/m² in the PPS ecosystem, respectively. At adequate feeding levels, the carrying capacities of *P. trituberculatus* and *P. japonicus* were 83.76 and 48.52 g/m² in the PP ecosystem and 81.82 and 53.44 g/m² in the PPS ecosystem. The ecotrophic efficiency values and energy flow parameters of the two integrated pond aquaculture ecosystems indicated that *S. constricta* was a suitable collocation culture species for *P. trituberculatus* and *P. japonicus*, and there is room for further improvement in yields of this integrated aquaculture ecosystem.

Keywords: carrying capacity, energy flow, ecopath model, integrated pond aquaculture, trophic structure

INTRODUCTION

Due to the ongoing depletion of fishery resources, the control of the global marine catch, and an increase in fishing bans in China's inland waters, an increase in aquatic products will mainly rely on the development of aquaculture. However, against the background of the ocean's negative carbon emissions and strict environmental protection policy, the aquaculture area decreased from 8.465 million hectares in 2015 to 7.108 million hectares in 2019 (China Fishery Statistics Yearbook, 2016, 2020). The mariculture area decreased from 2.318 million hectares to 1.992 million hectares, showing a decreasing trend in the aquaculture area year-by-year in China (Jiao et al., 2018; China Fishery Statistics Yearbook, 2020). In this context, aquaculture pattern optimization and carrying capacity assessments have become the main focus to ensure sustainable aquaculture development.

Carrying capacity can be defined as the maximum biomass maintained by an ecosystem in a given period (Bacher et al., 1997). It has become a fundamental concept in aquaculture management and is considered the basis and a tool for sustainable development (Stigebrandt, 2011; Weitzman and Filgueira, 2020). Since carrying capacity was first applied in fish pond research in 1963, it has gradually developed from the individual level to the ecosystem level (Yashouv, 1963). In recent years, carrying capacity assessments based on ecosystem models have become a research hotspot in aquaculture. Currently, the most applied ecosystem models are the Ecopath model, farm model, and spatial model (Filgueira et al., 2015). The Ecopath model is based on trophic dynamics, focusing on energy transfer between trophic levels and assessing carrying capacity from the perspective of ecosystem food webs (Jiang and Gibbs, 2005; Byron et al., 2011a,b). The farm model restricts the model domain to the farm extent, combines a hydrodynamic model and individual growth model, and focuses on bivalve-phytoplankton interaction to assess the carrying capacity (Pilditch et al., 2001; Ferreira et al., 2007; Duarte et al., 2008; Rosland et al., 2011). The spatial model is classified into two main classes according to the spatial resolution, i.e., the box model and the full spatial model. The box model typically divides the sea area into several homogenized boxes according to different factors, such as the geographic environment and the population, whereas the full spatial model is typically based on the grid of a hydrodynamic model (Raillard and Ménesguen, 1994; Duarte et al., 2003; Filgueira et al., 2010, 2014). Ecosystem model studies have focused on bivalve culture systems (Ferreira et al., 2008; Silva et al., 2011; Gao et al., 2020). To date, no other ecosystem models have been developed for the carrying capacity assessment of pond aquaculture, except for two preliminary models to assess the carrying capacity of shrimp pond culture with integrated bioremediation techniques and intertidal mangrove planting-aquaculture (Xu et al., 2011; Song et al., 2020).

The Ecopath model was created by Polovina (1984) and was supplemented and refined by Christensen and Pauly (1992a,b). The model was developed into computer software based on

the analysis of the ecosystem characteristics and has been applied to investigate energy flows, ecosystem properties, and ecosystem carrying capacities. Currently, more than 500 models have been developed worldwide and were used to study a wide range of ecosystems, including marine, freshwater, and terrestrial systems (Colléter et al., 2015). In recent years, the model has also been gradually applied to high-density culture ponds and integrated pond aquaculture (Zhang, 2011; Zhou et al., 2015; Feng et al., 2018; Gamito et al., 2020; Hu, 2020). However, due to the limited use of highly anthropogenic control conditions, most of those studies focused on the energy flow and structural characteristics of ecosystems and lacked carrying capacity assessments.

Portunus trituberculatus is the first of the three major crab aquaculture species in China, with production reaching 113,810 tons in 2019 (China Fishery Statistics Yearbook, 2020). In order to improve various ecological and economic benefits of *P. trituberculatus* aquaculture pond, crabs are usually polyculture with kuruma shrimp *Penaeus japonicus*, Pacific white shrimp *Litopenaeus Vannamei*, razor clams *Sinonovacula constricta*, and Manila clams *Ruditapes philippinarum* (Wang, 2011). Therefore, we constructed two Ecopath models of integrated pond aquaculture ecosystems of *P. trituberculatus*–*Penaeus japonicus* (PP) and *P. trituberculatus*–*P. japonicus*–*S. constricta* (PPS) using data from a field survey and the literature. We analyzed and assessed energy flows, ecosystem properties, and carrying capacities of the two ecosystems. This study is important for the optimization of the pond culture pattern and the improvement of culture management techniques. It also provides a reference for carrying capacity assessments of integrated aquaculture systems.

MATERIALS AND METHODS

Study Areas

The experimental ponds used in the present study were located in Zhoushan City, Zhejiang Province, China (24°35'N, 112°7'E). The size of the two polyculture ponds was 1.33 ha, with an average water depth of 1.2 m during the study period. The stocking density of *P. trituberculatus*, *P. japonicus*, and *S. constricta* is shown in **Table 1**. The experiment lasted 240 days from June 2020 to January 2021.

Ecopath Modeling Approach

An ecosystem consists of several interrelated functional groups in the Ecopath model, each consisting of a species or many related species. During model construction, all functional groups should cover the energy flow of the ecosystem. The energy of each functional group needs to be balanced between the input and output, i.e., production – predation mortality – harvesting – net migration – biomass accumulation = 0.

The complete ecosystem model is represented by a linear system of joint cubic equations describing n biological functional groups:

$$\begin{aligned}
 &B_1 \cdot \left(\frac{P}{B}\right)_1 \cdot EE_1 - B_1 \cdot \left(\frac{Q}{B}\right)_1 \cdot DC_{11} - B_2 \cdot \left(\frac{Q}{B}\right)_2 \cdot DC_{21} \dots \\
 &\quad - B_n \cdot \left(\frac{Q}{B}\right)_n \cdot DC_{n1} - Y_1 - E_1 - BA_1 = 0 \\
 &B_2 \cdot \left(\frac{P}{B}\right)_2 \cdot EE_2 - B_1 \cdot \left(\frac{Q}{B}\right)_1 \cdot DC_{12} - B_2 \cdot \left(\frac{Q}{B}\right)_2 \cdot DC_{22} \dots \\
 &\quad - B_n \cdot \left(\frac{Q}{B}\right)_n \cdot DC_{n2} - Y_2 - E_2 - BA_2 = 0 \\
 &\quad \dots \dots \dots \\
 &B_n \cdot \left(\frac{P}{B}\right)_n \cdot EE_n - B_1 \cdot \left(\frac{Q}{B}\right)_1 \cdot DC_{1n} - B_2 \cdot \left(\frac{Q}{B}\right)_2 \cdot DC_{2n} \dots \\
 &\quad - B_n \cdot \left(\frac{Q}{B}\right)_n \cdot DC_{nn} - Y_n - E_n - BA_n = 0
 \end{aligned}$$

where, B_n is the biomass of group n , $\left(\frac{P}{B}\right)_n$ is the production biomass ratio of group n , EE_n is the ecotrophic efficiency of group n , B_n is the biomass of predator n , $\left(\frac{Q}{B}\right)_n$ is the consumption biomass ratio of predator n , DC_{nn} is the contribution of prey n in the diet of predator n , Y_n is the yield of fisheries, E_n is the migration of group n , and BA_n is the biomass accumulation of n during the study period.

Ecopath Model Parameterization and Data Collection

The PP and PPS integrated pond aquaculture ecosystems comprised 14 and 15 functional groups, respectively. In addition to aquaculture animals, both ecosystems contained 12 identical functional groups: benthos, macrozooplankton,

microzooplankton, benthic bacteria, bacterioplankton, micro-phytoplankton, nano-phytoplankton, pico-phytoplankton, crab feed, shrimp feed, detritus in the sediment, and detritus in water.

The two main inputs to the Ecopath model were biomass (B), production/biomass (P/B), and consumption/biomass (Q/B) (Table 2). Three replicate ponds were set up for both types of aquaculture ponds, and the survey data was compared to ensure the credibility of the model input data, and finally one of the replicate ponds was randomly selected to construct the ecosystem model. The biomass of all functional groups was determined by performing measurements every month, except for the biomass of *P. trituberculatu*, *P. japonicus*, and *S. constricta*, which was calculated from initial and harvesting weights. The P/B values of the aquaculture animals were calculated as the average value of the initial and harvesting weights. The P/B value of each phytoplankton group was obtained from experiments using the light and dark bottle oxygen method (Diana et al., 1991). The production of bacterioplankton was obtained according to Schwaerter et al. (1988). The P/B value of benthic bacteria was calculated from the measured respiration and P/Q value, which was 0.30 (Winberg, 1972). The Q/B values of *P. trituberculatu*, *P. japonicus*, and *S. constricta* were calculated from the feeding rates (Qi et al., 2010; Yang et al., 2010; He et al., 2017). The Q/B value of bacterioplankton was calculated based on field experiments (Williams, 1981). The Q/B value of benthic bacteria was calculated by measuring sediment respiration (Hagrave, 1972). The P/B and Q/B values of zooplankton were obtained from reported references (Feng et al., 2017). The amounts of crab and shrimp feed were recorded and entered into the system as the “detritus” group (Zhou et al., 2015).

The food composition of the consumers in the two integrated pond aquaculture ecosystems is shown in Table 3. The diets of *P. trituberculatus*, *P. japonicus*, *S. constricta*, benthos (Jin, 2010), macrozooplankton, and microzooplankton (Li and Lin, 1995) were analyzed using carbon stable-isotope analysis based on the related references (Craig, 1957; Anderson et al., 2007). The food composition of bacterioplankton and benthic bacteria was derived from available results of previous studies on shrimp ponds (Zhou, 2015).

The assimilation efficiency (AE) of consumers is highly variable (Blanchard et al., 2002). Here the proportion of unassimilated food (1 - AE) was 0.4 for zooplankton and 0.2 for most of other consumers (Feng et al., 2018).

Model Balancing and Uncertainty

Since the Ecopath model has to ensure the conservation of matter and energy among the functional groups, ecotrophic efficiency (EE) ≤ 1 is primarily used as the basic constraint during model debugging (Christensen and Pauly, 1992a). If the EE of a functional group in the output parameters is greater than 1, the food composition, P/B, or Q/B values need to be adjusted repeatedly until the output parameters are in a reasonable range. The P/Q value was maintained in the range of 0.1–0.3 to ensure that EE ≤ 1 (the P/Q value of some fast-growing animals may be greater than 0.3). The reliability and accuracy of the basic input data are the main factors affecting the quality of Ecopath models. Ecopath models are typically evaluated using the

TABLE 1 | Stocking density of *Portunus trituberculatus*, *Penaeus japonicus*, and *Sinonovacula constricta* in two integrated pond aquaculture ecosystems.

Aquaculture species	Stocking situation	Systems	
		PP	PPS
<i>Portunus trituberculatus</i>	Carapace length, mm	4.1 ± 0.2	4.1 ± 0.2
	Body weight, g	0.024	0.024
	Density, kg/ha	7.50	7.50
<i>Penaeus japonicus</i>	Body length, mm	10.2 ± 0.7	10.2 ± 0.7
	Body weight, g	0.0087	0.0087
	Density, kg/ha	1.96	1.96
<i>Sinonovacula constricta</i>	Shell length, mm	–	18.5 ± 1.4
	Body weight, g	–	0.32 ± 0.02
	Density, kg/ha	–	37.50

PP: The integrated pond aquaculture ecosystem of *Portunus trituberculatus* and *Penaeus japonicus*; PPS: The integrated pond aquaculture ecosystem of *Portunus trituberculatus*, *Penaeus japonicus*, and *Sinonovacula constricta*.

TABLE 2 | Basic input data and output parameters of Ecopath model for the two integrated pond aquaculture ecosystems.

Systems	Group name	Trophic level	B (g/m ²)	P/B (240 day ⁻¹)	Q/B (240 day ⁻¹)	EE	Detritus import (g/m ² /240day)
PP	<i>Portunus trituberculatus</i>	2.065	37.13	1.96	6.03	0.962	
	<i>Penaeus japonicus</i>	2.027	21.85	1.98	13.49	0.954	
	Benthos	2.650	1.98	9.23	30.76	0.221	
	Macrozooplankton	2.098	0.58	40.50	139.65	0.618	
	Microzooplankton	2.135	0.15	108.00	372.41	0.261	
	Benthic bacteria	2.000	0.74	84.67	281.72	0.630	
	Bacterioplankton	2.000	0.52	78.22	262.86	0.261	
	Micro-phytoplankton	1.000	6.98	154.80		0.019	
	Nano-phytoplankton	1.000	4.12	194.70		0.023	
	Ico-phytoplankton	1.000	3.20	231.60		0.023	
	Crab feeds	1.000	12.83			0.582	353.49
	Shrimp feeds	1.000	4.94			0.482	585.24
	Detritus in sediment	1.000	532.20			0.609	0.00
	Detritus in water	1.000	165.72			0.067	0.00
PPS	<i>Portunus trituberculatus</i>	2.057	40.88	1.96	6.03	0.962	
	<i>Penaeus japonicus</i>	2.018	24.85	1.98	13.49	0.954	
	<i>Sinonovacula constricta</i>	2.010	48.38	1.85	27.60	0.952	
	Benthos	2.650	1.96	9.23	30.76	0.246	
	Macrozooplankton	2.098	0.44	40.50	139.65	0.651	
	Microzooplankton	2.135	0.03	108.00	372.41	0.831	
	Benthic bacteria	2.000	0.84	81.00	270.00	0.575	
	Bacterioplankton	2.000	0.89	68.46	399.60	0.288	
	Micro-phytoplankton	1.000	6.30	154.80		0.418	
	Nano-phytoplankton	1.000	4.40	194.70		0.407	
	Pico-phytoplankton	1.000	4.10	231.60		0.311	
	Crab feeds	1.000	12.83			0.638	353.49
	Shrimp feeds	1.000	4.94			0.533	585.24
	Detritus in sediment	1.000	700.80			0.660	0.00
Detritus in water	1.000	185.04			0.310	0.00	

B is the biomass of functional group, *P/B* stands for production/biomass and *Q/B* is the consumption/biomass. *EE* is the ecotrophic efficiency of functional group. Values in bold are the parameters estimated by the model.

pedigree index (*P*), which refers to the quality and uncertainty of the input parameters. The higher the *P* value, the more credible the model is and the closer it is to actual ecosystem conditions. The Ecopath model balancing and the *P* are described in detail by Christensen et al. (2005).

Carrying Capacity Estimation

The carrying capacity assessment of the integrated pond aquaculture ecosystems was established according to existing studies on the carrying capacity assessment of bivalve aquaculture ecosystems based on the Ecopath model (Jiang and Gibbs, 2005; Byron et al., 2011a; Kluger et al., 2016). In this study, *P. trituberculatus* and *P. japonicus* were the artificial feeding animals, and thus the carrying capacity was estimated for both current and adequate feeding levels. The carrying capacity estimation of the integrated pond aquaculture ecosystems was similar to that of bivalve aquaculture ecosystems. We continuously increased the biomass of one of the three species (*P. trituberculatus*, *P. japonicus*, and *S. constricta*) (0.01 g/m² each time) until any of the functional groups in the system was unbalanced. The resulting biomass of the cultured organism was recorded as the carrying capacity at current feeding levels. Since the biomass of cultured organisms eventually reaches the carrying capacity, the amount of crab and shrimp feed may be the

limiting factor. Therefore, as the biomass of cultured organisms increased, the amount of feed was also increased until any of the functional groups was unbalanced (*EE* > 1), except for the feed functional group. The resulting biomass of cultured organisms was recorded at adequate feeding levels. The ratio of the biomass and the carrying capacity of cultured organisms is multiplied by current stocking density to obtain the stocking density at which the biomass reach the carrying capacity.

RESULTS

Ecotrophic Efficiency and Effective Trophic Level

The *EE* values and effective trophic level of the functional groups in the two integrated pond aquaculture ecosystems are listed in **Table 2**. Ecotrophic efficiency refers to the efficiency of production transfer from one trophic level of the food web to the next (a range of 0–1) affected by fishing and predation pressures. The *P. trituberculatus*, *P. japonicus*, and *S. constricta* showed high *EE* values in their respective systems. The *EE* values of *P. trituberculatus* and *P. japonicus* were 0.962 and 0.954 in both systems, and that of *S. constricta* was 0.952 in the PPS system. The *EE* values of micro-phytoplankton, nano-phytoplankton,

TABLE 3 | Diet matrix of the two integrated pond aquaculture ecosystems.

Systems	Prey/predator	1	2	3	4	5	6	7	8
PP	(1) <i>Portunus trituberculatus</i>								
	(2) <i>Penaeus japonicus</i>								
	(3) Benthos	0.018							
	(4) Macrozooplankton	0.032	0.025						
	(5) Microzooplankton				0.050				
	(6) Benthic bacteria			0.650					
	(7) Bacterioplankton				0.041	0.135			
	(8) Micro-phytoplankton	0.018	0.020		0.066	0.090			
	(9) Nano-phytoplankton	0.018	0.015		0.066	0.090			
	(10) Pico-phytoplankton	0.019	0.012		0.062	0.080			
	(11) Crab feeds	0.875		0.100	0.045				
	(12) Shrimp feeds		0.871		0.315				
	(13) Detritus in sediment	0.020	0.057	0.250	0.260	0.300	0.950	0.050	
	(14) Detritus in water				0.095	0.305	0.050	0.950	
		1	2	3	4	5	6	7	8
PPS	(1) <i>Portunus trituberculatus</i>								
	(2) <i>Penaeus japonicus</i>								
	(3) <i>Sinonovacula constricta</i>								
	(4) Benthos	0.018							
	(5) Macrozooplankton	0.025	0.016						
	(6) Microzooplankton					0.050			
	(7) Benthic bacteria				0.650				
	(8) Bacterioplankton			0.010		0.041	0.135		
	(9) Micro-phytoplankton	0.018	0.028	0.291		0.066	0.090		
	(10) Nano-phytoplankton	0.018	0.013	0.251		0.066	0.090		
	(11) Pico-phytoplankton	0.019	0.013	0.211		0.062	0.080		
	(12) Crab feeds	0.880			0.100	0.045			
	(13) Shrimp feeds		0.873			0.315			
	(14) Detritus in sediment	0.022	0.057	0.110	0.250	0.260	0.300	0.950	0.050
	(15) Detritus in water			0.127	0.000	0.095	0.305	0.050	0.950

pico-phytoplankton, and bacterioplankton were 0.019, 0.023, 0.023, and 0.067 in the PP system and 0.418, 0.407, 0.311, and 0.310 in the PPS system, respectively. The EE value of the microzooplankton in the PP system (0.261) was lower than that in the PPS system (0.831). The EE values of crab feed in the PP and PPS systems were 0.582 and 0.638, respectively, and those of the shrimp feed were 0.482 and 0.533. The EE values of benthic bacteria in the two systems were 0.630 and 0.575, and those of bacterioplankton were 0.261 and 0.288, respectively. The EE values for each functional group were less than 1, which was within the range required by the Ecopath model. The effective trophic level is the trophic level at which each organism feeds in proportion to the predator's food composition (Odum, 1971). In the two integrated pond aquaculture ecosystems, the highest effective trophic level was benthos with 2.650. The effective trophic levels of *P. trituberculatus* and *P. japonicus* were 2.065 and 2.027 in the PP system, and those of *P. trituberculatus*, *P. japonicus*, and *S. constricta* were 2.057, 2.018, and 2.010 in the PPS system. The effective trophic levels of the other functional groups were equal in the two systems.

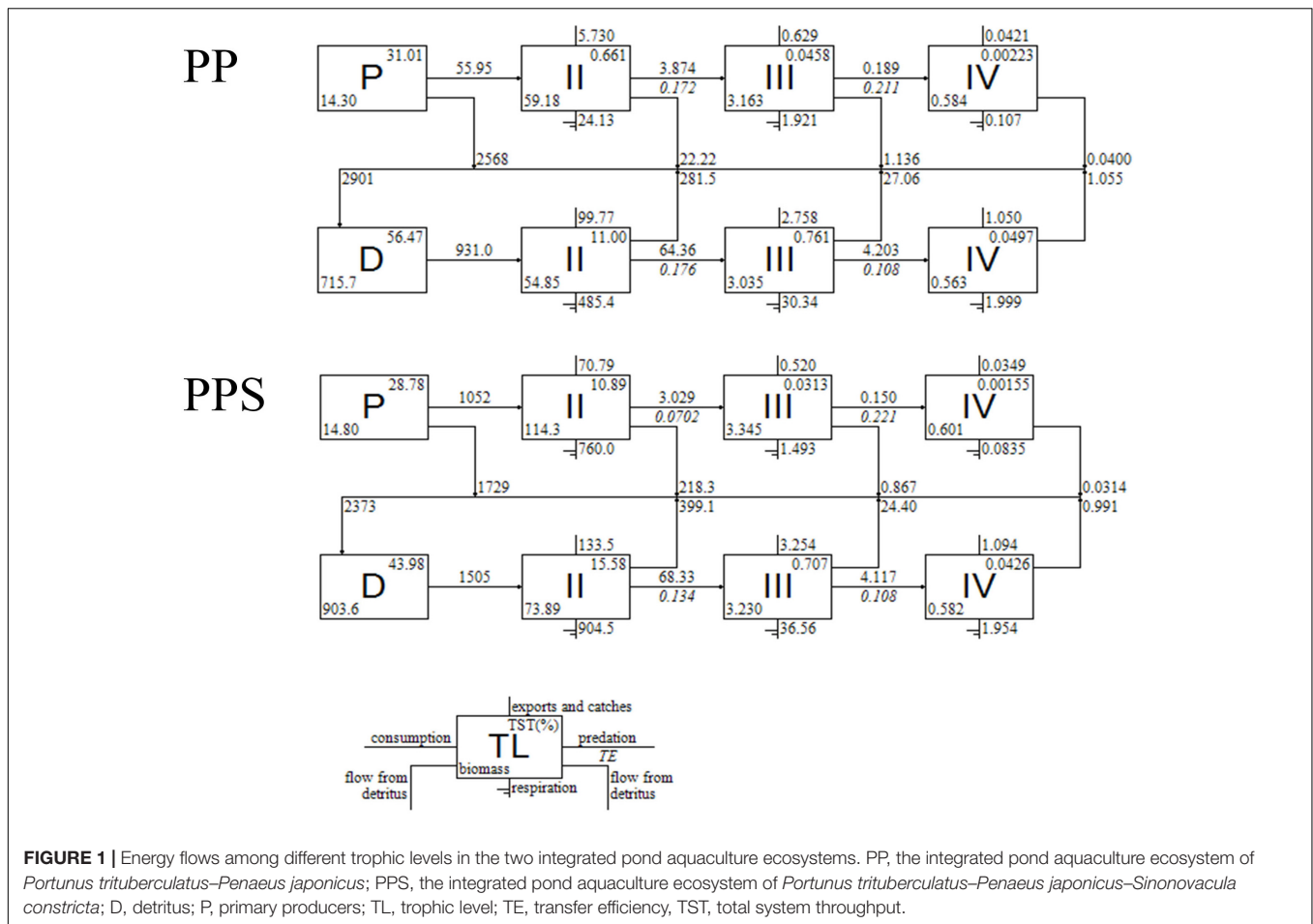
Energy Flows Between Trophic Levels

The energy flows between the trophic levels in the two integrated pond aquaculture ecosystems are shown in **Figure 1**. The

energy flows occurred mainly within four trophic levels. The total biomass of the primary producers in the PP system was 14.30 g/m², and the primary production was 2623.79 g/m²/240 days, of which 55.95 g/m²/240 days flowed to trophic level II and 2568.84 g/m²/240 days flowed to detritus, with 2.13 and 97.87% of the energy flowing to trophic level II and the detritus. The total biomass of the primary producers in the PPS system was 14.80 g/m², and the primary production was 2781.48 g/m²/240 days, of which 1052.16 g/m²/240 days flowed to trophic level II, and 1729.32 g/m²/240 days flowed to detritus, with 37.83 and 62.17% of the energy flowing to trophic level II and detritus. The total energy of the detritus group was 2900.89 and 2372.98 g/m²/240 days, with 931.02 and 1505.35 g/m²/240 days flowing to trophic level II, respectively. In the two integrated pond aquaculture ecosystems, the system energy circulation was mainly distributed in trophic levels I and II. In addition, the transfer efficiency of trophic level II was 17.16% from primary producers and 17.63% from detritus in the PP system and 7.02 and 13.41% in the PPS system, respectively.

Ecosystem Properties

The values of the main energy flow parameters and characteristic parameters of the Ecopath model for the two integrated pond aquaculture ecosystems are shown in **Table 4**. The total



system throughput (TST) was 8461.70 g/m²/240 days and 9665.06 g/m²/240 days in the PP and PPS systems, respectively. In the PP and PPS systems, total consumption accounted for 12.52 and 27.24%, total respiration (TR) accounted for 6.43 and 17.64%, total output accounted for 34.28 and 32.78%, and total flow to detritus accounted for 45.38 and 34.26% of the TST, respectively. The values of the energy flow parameters, such as total system flow, total consumption, TR, total productivity, and total primary production (TPP), were higher in the PPS system than the PP system, and the value of total flow to detritus was higher in the PP system than the PPS system. The TPP/TB and TPP/TR ratios describe the activity, extent, and potential of ecosystem development. The TPP/TB values of the PP and PPS systems were 33.969 and 20.903, respectively. The TPP/TR value of the PP system (4.824) was higher than that of the PPS system (1.632). The connectance index (CI) and system omnivory index (SOI) are correlated with ecosystem complexity, indicating whether the food chain is web-like or linear (Odum, 1971; Christensen et al., 2000). The CI values of the PP and PPS systems were 0.350 and 0.339, and the SOI values were 0.040 and 0.041, respectively. Finn's cycling index (FCI) is the ratio of the amount of material or energy flowing into the debris in the system required to re-enter the system circulation to the total system flow. It characterizes the maturity, stability, and degree of external disturbance of the

system. Finn's mean path length (FML) is the average length of each cycle flowing through the food chain in the system. The FCI values of the PP and PPS systems were 27.217 and 3.933%, and the FML were 2.375 and 2.598, respectively.

Carrying Capacity Estimation

The estimation results of the carrying capacity of *P. trituberculatus*, *P. japonicus*, and *S. constricta* in the two integrated pond aquaculture ecosystems are shown in **Figure 2**. At the current feeding level, the carrying capacities of *P. trituberculatus* and *P. japonicus* were 65.15 and 47.62 g/m² in the PP ecosystem, and those of *P. trituberculatus*, *P. japonicus*, and *S. constricta* were 64.96, 48.06, and 100.79 g/m² in the PPS ecosystem, respectively. After the biomass of *P. trituberculatus* and *P. japonicus* in the two ecosystems exceeded the carrying capacity, the first imbalanced functional group was the feed group, indicating that the biomass of crab and shrimp could be increased by increasing the amount of aquatic animal feed. At adequate feeding levels, the carrying capacities of *P. trituberculatus* and *P. japonicus* were 83.76 and 48.52 g/m² in the PP ecosystem and 81.82 and 53.44 g/m² in the PPS ecosystem, respectively. After the biomass of each aquaculture animal in the two ecosystems exceeded the carrying capacity, the first imbalanced functional group was the microzooplankton. When

TABLE 4 | Comparison of energy flow parameters and characteristic parameters of the two integrated pond aquaculture ecosystems.

Attribute parameters	Systems		Units
	PP	PPS	
Total system throughput (TST)	8,461.70	9,665.06	g/m ² /240 days
Sum of all production (TP)	2,900.60	3,168.67	g/m ² /240 days
Sum of all consumption (TC)	1,059.63	2,633.14	g/m ² /240 days
Sum of all respiratory flows (TR)	543.86	1,704.59	g/m ² /240 days
Calculated total net primary production (TPP)	2,623.79	2,781.48	g/m ² /240 days
Sum of all flows into detritus (TD)	3,839.59	3,311.71	g/m ² /240 days
Total biomass (excluding detritus) (TB)	77.24	133.06	g/m ²
Total catch	110.00	209.20	
Total primary production/total biomass (TPP/TB)	33.969	20.903	
Total primary production/total respiration (TPP/TR)	4.824	1.632	
Connectance Index (CI)	0.350	0.339	
System Omnivory Index (SOI)	0.040	0.041	
Finn's mean path length (FML)	2.375	2.598	
Finn's cycling index (FCI)	2.544	3.933	% of total throughput
Ecopath pedigree index	0.556	0.561	

the biomass of the cultured organisms reached the carrying capacity at adequate feeding levels, the minimum amounts of crab and shrimp feed were 451.67 and 595.66 g/m²/240 days in the PP system and 442.94 and 648.58 g/m²/240 days in the PPS system. The results showed that when the biomass of the cultured organisms reached the carrying capacity, the stocking density of *P. trituberculatus* and *P. japonicus* in the PP system was increased to 13.16 and 4.21 kg/ha, and the stocking density of *P. trituberculatus*, *P. japonicus*, and *S. constricta* in the PPS system was increased to 11.92, 3.73, and 78.13 kg/ha in the current aquaculture environment with artificial feeding. After increasing the feeding amount to ensure that the feed was not a limiting factor, the stocking densities of *P. trituberculatus* and *P. japonicus* in the PP system were increased to 16.92 and 4.29 kg/ha and those were increased to 15.01 and 4.15 kg/ha in the PPS system, respectively.

Ecosystem Pedigree Index

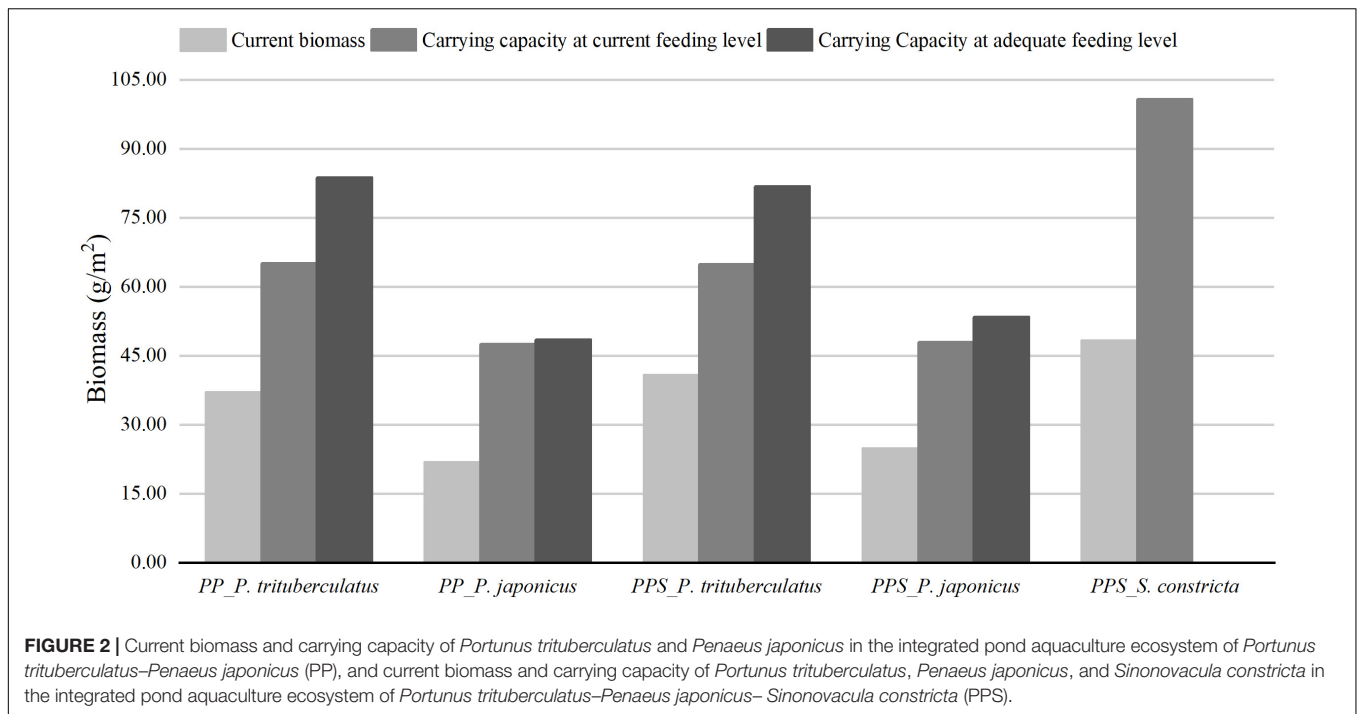
The Ecopath pedigree indices of the PP and PPS systems were 0.556 and 0.561, respectively. The indices were in the upper levels compared to those of 50 ecosystems and 393 Ecopath models evaluated by Morissette et al. (2006) (0.164–0.676).

DISCUSSION

The Ecopath model has been mostly used in studies of large water bodies but has also been increasingly used for analyzing pond culture ecosystems in China. Unlike large water body ecosystems, pond ecosystems are relatively small water bodies, have short food chains, and contain a relatively homogeneous number of species; thus, the biological populations in the functional groups have a finer classification. In this study, zooplankton was classified into macrozooplankton and microzooplankton according to size; phytoplankton was classified into micro-

nano-, and pico-phytoplankton according to the particle size. Bacteria were classified into detritus in the sediment and the water according to the habitat. In terms of system material flow, a higher degree of refinement of each functional group allows for a more accurate description of the model results, facilitating precise regulation in a relatively semi-closed pond system. Ecopath model construction requires a large number of parameters, and the parameters in this study were mainly obtained from pond sampling surveys and field experiments. The P/B values and Q/B values of some parameters were difficult to obtain from the experiment; thus, the research data of similar ecosystems were used as input parameters for the two food web models. Ecopath pedigree indice of the Ecopath model shows the uncertainty of the input data. Based on Ecopath pedigree indices of other Ecopath models, the parameter values of the two models were reliable, and the results of the two models in this study were acceptable (Christensen and Walters, 2004; Christensen et al., 2005).

In ecosystems, species and biomass differences and food composition changes are the main reasons for differences in ecosystem properties, such as trophic structure and energy flow (Christensen and Walters, 2004). In the two integrated pond aquaculture ecosystems, *P. trituberculatus*, *P. japonicus*, and *S. constricta* showed higher EE values owing to greater harvesting pressure. The EE values of phytoplankton (micro-, nano-, and pico-) and detritus in water in the PPS system were significantly higher than those in the PP system; the main reason for this difference in EE values was the feeding pressure of *S. constricta*. The EE values of microzooplankton in the PPS system were significantly lower than that in the PP system due to the lower biomass of microzooplankton in the PPS system, which may be related to feeding competition between *S. constricta* and microzooplankton due to the similar food composition (Table 3). In this study, the effective trophic levels of *P. trituberculatus* and *P. japonicus* in the PPS system were slightly lower than those in the PP system due to differences in the biomass of the natural



food at higher trophic levels (benthos and macrozooplankton). Another reason may be spatial and food competition pressures between *S. constricta* and the biological feed. Unlike the higher EE values of the “feed group” in previous studies of the pond Ecopath model, the EE values of the crab feed and shrimp feed in this study were between 0.4 and 0.7, indicating that the feed amount in both systems was sufficient, and the utilization of artificial feed requires improvements (Feng et al., 2017, 2018). In addition, the microbial environment is an important reason for the outbreak of biological diseases (Ren et al., 2013). In the two ecosystems, the EE values of detritus in the sediment and in water were not significantly different, indicating that the current stocking density of *S. constricta* culture did not significantly impact the microbial environment.

Unlike natural ecosystems, the integrated pond aquaculture ecosystem is a closed or semi-closed ecosystem under highly artificial control. Artificial feeding and mechanical oxygen enrichment significantly affect the internal structure of the ecosystem and the relationship between organisms (Zhang, 2011). In previous ecosystem studies based on the Ecopath model, researchers tended to focus on the system characteristics, such as ecosystem complexity, maturity, and stability (Cruz-Escalona et al., 2007; Anh et al., 2015; Rehren et al., 2018). However, research on artificial culture systems should focus on improving the energy utilization and output of the aquatic animals while ensuring the stability of the system (Hu, 2020). The results of the ecosystem energy flow analysis showed that the proportion of primary productivity flow to trophic level II was 2.13 and 37.83% in the PP and PPS systems, and the proportion of total energy flow to trophic level II was 32.09 and 63.44% in the detritus group, respectively, indicating that *S. constricta* could improve the utilization of primary productivity

and detritus in the PPS system. In addition, the transfer efficiency of trophic level II from the primary producers and the detritus in the PPS system was significantly smaller than that in the PP system, suggesting that the energy used by *S. constricta* was left in trophic level II, ensuring that this part of the energy flowed directly to the output. According to the theory of ecosystem balance, when the production of an ecosystem is higher than the respiration ($TPP/TR > 1$), the development potential of the ecosystem is greater, and the development degree is lower (Odum, 1969; Dong et al., 2021). Therefore, the development degree of the PPS ecosystem was greater than that of the PP ecosystem. It is important to note that this variation in TPP/TR values was not found in the Ecopath model of four other integrated pond aquaculture ecosystems with *P. trituberculatus* because the “feed group” was a producer in the ecosystem (Feng et al., 2018). Thus, *S. constricta*, as an economically relevant shellfish that is commonly farmed, is a good species for integrated pond aquaculture of *P. trituberculatus* and *P. japonicus*.

There is no uniform indicator of carrying capacity. In this study, carrying capacity was evaluated using Ecopath models of two integrated pond aquaculture ecosystems based on ecosystem stability ($EE \leq 1$) combined with artificial feeding. In existing pond carrying capacity assessment studies, the individual biological parameters, the water environment, and economic profit are the main indicators of carrying capacity (Dai et al., 2019; Song et al., 2020). In integrated pond aquaculture ecosystems with small water bodies, the carrying capacity is related to various factors, such as the aquaculture animal species, pond facilities, and aquaculture technology. The consideration of multiple limiting indicators represents a problem in carrying capacity assessments. In future studies, we plan to combine the carbon-nitrogen-phosphorus cycle with a food web model to

optimize the assessment indicators and improve the accuracy and universality of carrying capacity assessments of integrated pond aquaculture ecosystems. The evaluation results can assist farm operators with possible management strategies for high-yield aquaculture and government with some practical policy for environmental protection.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

REFERENCES

- Anderson, R. K., Parker, P. L., and Lawrence, A. (2007). A 13C/12C tracer study of the utilization of presented feed by a commercially important shrimp *penaeus vannamei* in a pond growout system. *J. World Aquacult. Soc.* 18, 148–155. doi: 10.1111/j.1749-7345.1987.tb00433.x
- Anh, V. P., Everaert, G., Goethals, P., Vinh, T. C., and Laender, D. F. (2015). Production and food web efficiency decrease as fishing activity increases in a coastal ecosystem. *Estuar. Coast. Shelf. Sci.* 65, 226–236. doi: 10.1016/j.ecss.2015.05.019
- Bacher, C., Duarte, P., Ferreira, J. G., Heral, M., and Raillard, O. (1997). Assessment and comparison of the Marennes Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. *Aquat. Ecol.* 31, 379–394. doi: 10.1023/a:1009925228308
- Blanchard, J. L., Pinnegar, J. K., and Mackinson, S. (2002). Exploring marine mammal-fishery interactions using ‘Ecopath with Ecosim’: modelling the Barents Sea ecosystem. *Sci. Ser. Tech. Rep.* 117:52.
- Byron, C., Link, J., Costa-Pierce, B., and Bengtson, D. (2011b). Modeling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. *Aquaculture* 314, 87–99. doi: 10.1016/j.aquaculture.2011.02.019
- Byron, C., Link, J., Costa-Pierce, B., and Bengtson, D. (2011a). Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modeling: narragansett Bay, Rhode Island. *Ecol. Model.* 222, 1743–1755. doi: 10.1016/j.ecolmodel.2011.03.010
- China Fishery Statistics Yearbook (2016). *Department of Agriculture, Fisheries Bureau. China Fishery Statistics Yearbook*. Beijing: China Agricultural Press.
- China Fishery Statistics Yearbook (2020). *Department of Agriculture, Fisheries Bureau. China Fishery Statistics Yearbook*. Beijing: China Agricultural Press.
- Christensen, V., and Pauly, D. (1992a). *A Guide to the Ecopath ii Software System (Version 2.1)*. Penang: International Center for Living Aquatic Resources Management.
- Christensen, V., and Pauly, D. (1992b). Ecopath ii — a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* 61, 169–185. doi: 10.1016/0304-3800(92)90016-8
- Christensen, V., and Walters, C. J. (2004). Ecopath with ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003
- Christensen, V., Walters, C. J., and Pauly, D. (2000). *Ecopath with Ecosim, Version 5, Help system* ©. Vancouver, BC: University of British Columbia.
- Christensen, V., Walters, C. J., and Pauly, D. (2005). *Ecopath with Ecosim: A User's Guide*. Vancouver, BC: University of British Columbia.
- Colléter, M., Valls, A., Guitton, J., Pauly, D., and Christensen, V. (2015). Global overview of the applications of the ecopath with ecosim modeling approach using the EcoBase models repository. *Ecol. Model.* 302, 42–53. doi: 10.1016/j.ecolmodel.2015.01.025
- Craig, H. (1957). Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Acta* 12, 133–149. doi: 10.1016/0016-7037(57)90024-8
- Cruz-Escalona, V. H., Arreguin-Sanchez, F., and Zetina-Rejon, M. (2007). Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. *Estuar. Coast. Shelf. Sci.* 72, 155–167. doi: 10.1016/j.ecss.2006.10.013
- Dai, D. C., Ma, X. Z., Zhang, Y., and Zhou, Z. (2019). Impact of Eriocheir sinensis ecological culture ponds on water environment in Gehu Lake area of Yixing City. *Environ. Chem.* 38, 2573–2582. doi: 10.7524/j.issn.0254-6108.2018122004
- Diana, J. S., Lin, C. K., and Schneeberger, P. J. (1991). Relationships among nutrient inputs, water nutrient concentrations, primary production, and yield of *Oreochromis niloticus* in ponds. *Aquaculture* 92, 323–341. doi: 10.1016/0044-8486(91)90038-9
- Dong, S. P., Gao, Y. F., Gao, Y. P., He, M. D., Liu, F., Yan, F. J., et al. (2021). Evaluation of the trophic structure and energy flow of a rice-crayfish integrated farming ecosystem based on the ecopath model. *Aquaculture* 539:736626. doi: 10.1016/j.aquaculture.2021.736626
- Duarte, P., Labarta, U., and Fernández-Reiriz, M. J. (2008). Modelling local food depletion effects in mussel rafts of Galician Rias. *Aquaculture* 274, 300–312. doi: 10.1016/j.aquaculture.2007.11.025
- Duarte, P., Meneses, R., Hawkins, A. J. S., Zhu, M., Fang, J., and Grant, J. (2003). Mathematical modelling to assess the carrying capacity for multi-species culture within coastal waters. *Ecol. Model.* 168, 109–143. doi: 10.1016/S0304-3800(03)00205-9
- Feng, J., Tian, X. L., Dong, S. L., He, R. P., Zhang, K., Zhang, D. X., et al. (2018). Comparative analysis of the energy fluxes and trophic structure of polyculture ecosystems of *Portunus trituberculatus* based on ecopath model. *Aquaculture* 496, 185–196. doi: 10.1016/j.aquaculture.2018.07.020
- Feng, J., Tian, X. L., Dong, S. L., He, R. P., and Zhang, Q. Q. (2017). Model-based analysis of the energy fluxes and trophic structure of a *Portunus trituberculatus* polyculture ecosystem. *Aquacult. Environ. Interact.* 9, 479–490. doi: 10.3354/aei00247
- Ferreira, J. G., Hawkins, A. J. S., and Bricker, S. B. (2007). Management of productivity, environmental effects and profitability of shellfish aquaculture – the farm aquaculture resource management (FARM) model. *Aquaculture* 264, 160–174. doi: 10.1016/j.aquaculture.2006.12.017
- Ferreira, J. G., Hawkins, A. J. S., Monteiro, P., Moore, H., Service, M., Pascoe, P. L., et al. (2008). Integrated assessment of ecosystem scale carrying capacity in shellfish growing areas. *Aquaculture* 275, 138–151. doi: 10.1016/j.aquaculture.2007.12.018
- Filgueira, R., Comeau, L. A., Guyondet, T., Mckindsey, C. W., and Byron, C. J. (2015). *Modelling Carrying Capacity of Bivalve Aquaculture: A Review of Definitions and Methods*. New York, NY: Springer.
- Filgueira, R., Grant, J., Strand, O., Asplin, L., and Aure, J. (2010). A simulation model of carrying capacity for mussel culture in a Norwegian fjord: role of induced upwelling. *Aquaculture* 308, 20–27. doi: 10.1016/j.aquaculture.2010.08.005
- Filgueira, R., Guyondet, T., Comeau, L. A., and Grant, J. (2014). A fully-spatial ecosystem-DEB model of oyster (*Crassostrea virginica*) carrying capacity in the Richibucto Estuary, Eastern Canada. *J. Mar. Syst.* 136, 42–54. doi: 10.1016/j.jmarsys.2014.03.015
- Gamito, S., Ferreira, H. Q., Parejo, A., Aubin, J., and Cunha, E. (2020). Integrated multi-trophic aquaculture systems: energy transfers and food web organization

AUTHOR CONTRIBUTIONS

SD, DZ, and FW designed the experiments and wrote the manuscript. LY, WP, and XX performed the experiments. FW supervised and validated the manuscript. All authors contributed to the article and approved the submitted version.

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- in coastal earthen ponds. *Aquac. Environ. Interact.* 12, 457–470. doi: 10.3354/aei00375
- Gao, Y. P., Fang, J. G., Lin, F., Li, F. X., Li, W. H., Wang, X. Q., et al. (2020). Simulation of oyster ecological carrying capacity in Sanggou Bay in the ecosystem context. *Aquac. Int.* 285, 2059–2079. doi: 10.1007/s10499-020-00576-3
- Haggrave, B. T. (1972). Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnol. Oceanogr.* 17, 583–586. doi: 10.4319/lo.1972.17.4.0583
- He, M., Lai, Q. F., Me, Z. L., Sui, Y. M., Lu, J. X., Gao, P. C., et al. (2017). Effects of pH and temperature on carbon budget of *Sinonovacula constricta*. *Chin. J. Plant Ecol* 36, 1014–1019.
- Hu, G. Y. (2020). *Research on Integrated Aquaculture Mode of Shrimp and Shellfish Pond Based on Ecopath mode*. Ph.D. Dissertation. Shanghai: Shanghai Ocean University.
- Jiang, W., and Gibbs, M. T. (2005). Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture* 244, 171–185. doi: 10.1016/j.aquaculture.2004.11.050
- Jiao, N. Z., Wang, H., Xu, G. H., and Aricò, S. (2018). Blue carbon on the rise: challenges and opportunities. *Natl. Sci. Rev.* 5, 464–468. doi: 10.1093/nsr/nwy030
- Jin, B. C. (2010). *Using Stable Isotope to Evaluate Food Sources of Pond-Cultured Sea Cucumber (*Apostichopus japonicus*)*. Ph.D. Dissertation. Qingdao: Ocean University of China.
- Kluger, L., Taylor, M., Mendo, J., Tam, J., and Wolff, M. (2016). Carrying capacity simulations as a tool for ecosystem-based management of a scallop aquaculture system. *Ecol. Model.* 331, 45–55. doi: 10.1016/j.ecolmodel.2015.09.002
- Li, C. H., and Lin, W. L. (1995). Grazing rate of zooplankton on bacterioplankton in Donghu Wuhan. *Acta Ecol. Sin.* 15, 142–147.
- Morissette, L., Hammill, M. O., and Savenkoff, C. (2006). The trophic role of marine mammals in the northern Gulf of St. Lawrence. *Mar. Mammal Sci.* 22, 74–103. doi: 10.1111/j.1748-7692.2006.0.0007.x
- Odum, E. P. (1969). The strategy of ecosystem development. *Science* 164, 262–270. doi: 10.1126/science.164.3877.262
- Odum, E. P. (1971). *Fundamental of Ecology*. Philadelphia, PA: Wiley, doi: 10.2307/3564656
- Pilditch, C. A., Grant, J., and Bryan, K. R. (2001). Seston supply to sea scallops (*Placopecten magellanicus*) in suspended culture. *Can. J. Fish. Aquat. Sci.* 58, 214–253. doi: 10.1139/cjfas-58-2-241
- Polovina, J. J. (1984). An overview of the ecopath model. *Fishbyte* 2, 5–7.
- Qi, M., Shen, Y. H., and Zhu, C. H. (2010). A primary study on conversion efficiency of *Litopenaeus vannamei* feed on artificial diets. *Fish. Modern.* 37, 34–37.
- Raillard, O., and Ménesguen, A. (1994). An ecosystem box model for estimating the carrying capacity of a macrotidal shellfish system. *Mar. Ecol. Prog. Ser.* 115, 117–130. doi: 10.3354/meps115117
- Rehren, J., Wolff, M., and Jiddawi, N. (2018). Holistic assessment of Chwaka Bay's multi-gear fishery – using a trophic modeling approach. *J. Mar. Syst.* 180, 265–278. doi: 10.1016/j.jmarsys.2018.01.002
- Ren, C. H., Hu, C. Q., Jiang, X., Sun, H. Y., Zhao, Z., Chen, C., et al. (2013). Distribution and pathogenic relationship of virulence associated genes among *Vibrio alginolyticus* from the mariculture systems. *Mol. Cell. Probe.* 27, 164–168. doi: 10.1016/j.mcp.2013.01.004
- Rosland, R., Bacher, C., Strand, Ø., Aure, J., and Strohmeier, T. (2011). Modelling growth variability in longline mussel farms as a function of stocking density and farm design. *J. Sea Res.* 66, 318–330. doi: 10.1016/j.seares.2011.04.009
- Schwaerter, S., Søndergaard, M., Bo, R., and Jensen, L. M. (1988). Respiration in eutrophic lakes: the contribution of bacterioplankton and bacterial growth yield. *J. Plankton. Res.* 10, 515–531. doi: 10.1093/plankt/10.3.515
- Silva, C., Ferreira, J. G., Bricker, S. B., DelValls, T. A., Martín-Díaz, M. L., and Yanez, E. (2011). Site selection for shellfish aquaculture by means of GIS and farm-scale models, with an emphasis on data-poor environments. *Aquaculture* 318, 444–457. doi: 10.1016/j.aquaculture.2011.05.033
- Song, X. L., Pang, S. N., Guo, P. P., and Sun, Y. (2020). Evaluation of carrying capacity for shrimp pond culture with integrated bioremediation techniques. *Aquac. Res.* 51, 761–769. doi: 10.1111/are.14426
- Stigebrandt, A. (2011). Carrying capacity: general principles of model construction. *Aquac. Res.* 42, 41–50. doi: 10.1111/j.1365-2109.2010.02674.x
- Wang, Y. Q. (2011). *Integrated Mariculture with Multi-Trophic Levels*. Beijing: Ocean Press.
- Weitzman, J., and Filgueira, R. (2020). The evolution and application of carrying capacity in aquaculture: towards a research agenda. *Rev. Aquacult.* 3, 1297–1322. doi: 10.1111/raq.12383
- Williams, P. J. L. B. (1981). Microbial contribution to overall marine plankton metabolism: direct measurements of respiration. *Oceanol. Acta* 4, 359–364.
- Winberg, G. G. (1972). “Some interim results of soviet IBP investigations on lakes,” in *Proceedings of the Productivity Problems of Freshwaters*, (Poland), 363–381.
- Xu, S. N., Chen, Z. Z., Li, C. H., Huang, X. P., and Li, S. Y. (2011). Assessing the carrying capacity of tilapia in an intertidal mangrove-based polyculture system of Pearl River Delta, China. *Ecol. Model.* 222, 846–856. doi: 10.1016/j.ecolmodel.2010.11.014
- Yang, H., Ma, S., and Su, Y. P. (2010). Differences of food consumption, metabolism and growth of the crab (*Portunus trituberculatus*) fed fresh, frozen and oven-dried clam (*Ruditapes philippinarum*) meat. *J. Ocean Univ. China* 40, 65–70.
- Yashouv, A. (1963). Increasing fish production in ponds. *Transc. Am. Fish. Soc.* 92, 292–297. doi: 10.1577/1548-8659(1963)92[292:ifpip]2.0.co;2
- Zhang, T. W. (2011). *The Model of Carbon Flux in Intensive Penaeid Shrimp Culture and Ecological Cultivation*. Ph.D. Dissertation. Qingdao: Ocean University of China.
- Zhou, B. (2015). *Research on Grass Carp (*Ctenopharyngodon idella*) Integrated Aquaculture Pond Ecosystem: Based on EwE Model*. Ph.D. Dissertation. Qingdao: Ocean University of China.
- Zhou, B., Dong, S. L., and Wang, F. (2015). Trophic structure and energy fluxes in a grass carp (*Ctenopharyngodon idellus*) cultured pond ecosystem. *Aquacult. Int.* 23, 1313–1324. doi: 10.1007/s10499-015-9886-7

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