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Temporal Dynamics in Energy Fluxes and Trophic Structure of a Portunus trituberculatus Polyculture Ecosystem During Different Culture Periods

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Swimming crab (*Portunus trituberculatus*) are an important aquaculture species in eastern coastal areas of China. To improve the understanding of *P. trituberculatus* culture ecosystem functioning, the dynamics of energy flow and trophic structure of a *P. trituberculatus* polyculture system (co-culture with white shrimp *Litopenaeus vannamei* and short-necked clam *Ruditapes philippinarum*) were investigated in this study. Three Ecopath models representing the early, middle, and late culture periods of a *P. trituberculatus* polyculture ecosystem, respectively, were constructed to compare ecosystem traits at different culture periods. The results demonstrated that detritus was the main energy source in this polyculture ecosystem, and most of the total system throughput occurred at trophic levels I and II. Artificial food input and consumption by the culture organisms increased from early to middle and late periods, which produced marked impacts on biomass structure and primary production. *R. philippinarum* was considered to have a dominant influence on phytoplankton community dynamics which changed from nano- to pico-phytoplankton predominance, from the middle to the late period. Considering the low utilization efficiency of pico-phytoplankton production, large amounts of detritus accumulated in the sediment in the late period, which may constitute a potential risk for the ecosystem. Ecological network analyses indicated that the total energy flow and level of system organization increased from the early to the middle and late periods, whereas food web complexity and system resilience decreased from early to middle and late periods, which may indicate a trend of decreasing ecosystem stability. The system may be further optimized by increased stocking density of *R. philippinarum* and by introducing macro-algae at a suitable biomass to increase ecosystem stability, energy utilization efficiency, and aquaculture production.

Keywords: *Portunus trituberculatus*, polyculture, trophic structure, dynamics, Ecopath, ecological network analysis

1 INTRODUCTION

Most of the world's fishing areas have reached their maximal potential for capture fishery production, while demand for seafood worldwide is steadily increasing (Pauly et al., 2002; FAO, 2014). Global production from aquaculture has been increasing steadily over the past decade (Soto-Zarazúa et al., 2014), and the constantly increasing demand for seafood can only be met by aquaculturing (Troell et al., 2003). However, potential increase in aquaculture production is limited by environmental challenges and resource constraints (Klinger and Naylor, 2012; FAO, 2020). Integrated multi-trophic aquaculture, which involves the cultivation of fed species (e.g., finfish or shrimps fed sustainable commercial diets) with extractive species (e.g., suspension- and deposit-feeders, or seaweeds or other aquatic vegetation), is considered an effective solution to meet the demands of aquaculture production and achieve sustainable aquaculture development (Chopin et al., 2001; Abreu et al., 2011; Dong et al., 2022).

The swimming crab *Portunus trituberculatus* is an important marine-culture species in China (Song et al., 2006), with a production of 100,895 tons in 2020 [FDAMC (Fisheries Department of Agriculture Ministry of China), 2021]. This species was typically cultured in ponds by small-holders or family farms in eastern coastal areas of China. Polyculture of *P. trituberculatus*, with shrimp (e. g. white shrimp *Litopenaeus vannamei*) and clam (e. g. short-necked clam *Ruditapes philippinarum*) in ponds is considered effective integrated multi-trophic aquaculture of this species (Zhang et al., 2016). *P. trituberculatus* consume large particles of food input (e.g., residue of imported fish and shellfish), and considerable amounts of small particles are not consumed; however, such small particles are a good food source for shrimps. Moreover, clams in polyculture systems inhabit the bottom of ponds and feed on phytoplankton and detritus (Xu et al., 1987; Zhang et al., 2016). Polyculture of these three organisms at suitable farming densities may thus constitute an effective use of food and space resources in *P. trituberculatus* polyculture pond systems.

Aquaculture ponds are simple yet fragile ecosystems (Zhai, 2012; Feng et al., 2017), and system stability is susceptible to organic pollution, eutrophication, and emergence of diseases (Cai, 2006). Culture management and associated technologies (e.g., water and sediment quality regulation, feed management, and co-cultured species) are important for avoiding such threats, however, high-level culture management depends on a profound understanding of the respective aquaculture ecosystem. Various aspects of the *P. trituberculatus* pond ecosystem during the whole culture period have been investigated, including variations in biomass structure of phytoplankton (Mao et al., 2013), zooplankton (Mao et al., 2014), microbial communities (Zhang et al., 2015), variations in size-fractioned chlorophyll a concentration (Sun et al., 2012), and water quality (Zhang et al., 2015; Ban et al., 2015). Most of these studies concentrated on individual processes, which helped understand the *P. trituberculatus* pond ecosystems at population level. However, as ecosystems comprise numerous interacting factors, examination of any such factor in isolation cannot comprehensively explain ecosystem functioning (Likens, 1985; Allen, 1988; Patrício and Marques, 2006). The food web in a *P. trituberculatus* polyculture pond ecosystem was reconstructed in a previous study (Feng et al., 2018b), and energy flow and trophic structures of different *P. trituberculatus* pond culture ecosystems at ecosystem level were previously analyzed (Feng et al., 2017, Feng et al., 2018a). These studies improved our understanding of the structural and functional characteristics of *P. trituberculatus* pond culture ecosystems. However, the temporal dynamics of energy fluxes and trophic structures of *P. trituberculatus* pond ecosystems throughout the culture period remained unclear. This may hamper efforts to determine the impact of *P. trituberculatus* culture activities on pond ecosystems, and this lack precludes science-based management of *P. trituberculatus* pond culturing at ecosystem level.

Here, Ecopath modeling in combination with ecological network analyses was used to investigate temporal dynamics of energy fluxes and the trophic structure of a *P. trituberculatus* polyculture pond ecosystem. Ecopath is a mass-balanced ecosystem model, which presents a "snapshot" of the trophic flows between species in an ecosystem (Christensen et al., 2005). Ecological network analysis is a useful and efficient tool for quantifying the condition of an ecosystem, and to systematically analyze each defined ecosystem period (Dubois et al., 2012; Akoglu et al., 2014; Tecchio et al., 2015). The Ecopath model can be used in combination with ecological network analysis to analyze energy flow and trophic structures of aquaculture ecosystems (Ulanowicz, 2004; Zhou et al., 2015; Kluger et al., 2016b; Feng et al., 2017; Aubin et al., 2021; Dong et al., 2021a; Mayekar et al., 2022). Ecopath models also facilitate comparisons between different aquaculture ecosystems or within an ecosystem during different periods (Christensen and Pauly, 1992a; Días López et al., 2008; Feng et al., 2018a). In addition, this model was used to evaluate the carrying capacity of cultured species in aquaculture ecosystems (Jiang and Gibbs, 2005; Byron et al., 2011a; Byron et al., 2011b; Xu et al., 2011; Kluger et al., 2016a; Dong et al., 2021b). In this study, we used Ecopath to model energy flow in a *P. trituberculatus* polyculture pond ecosystem (co-cultured species included *L. vannamei* and *R. philippinarum*) during various culture periods (early, middle, and late). The produced insights may improve our understanding of temporal dynamics of biomass structure and system functioning in *P. trituberculatus* polyculture ecosystems.

2 MATERIAL AND METHODS

2.1 Pond and Enclosures

The *P. trituberculatus* polyculture experiment was conducted using the land-based experimental enclosures in a pond. Enclosure is an efficient tool to investigate aquatic ecosystem, which establishes a relatively closed ecosystem by enclosing the

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Abbreviations: Pot, P. trituberculatus; Liv, Litopenaeus vannamei; Rup, Ruditapes philippinarum; Mab, macrobenthos; Mib, microbenthos; Maz, macrozooplankton; Miz, microzooplankton; Beb, benthic bacteria; Bap, bacterioplankton; Mip, micro-phytoplankton; Nap, nano-phytoplankton; Pip, pico-phytoplankton; Pep, periphyton; All, Aloidis laevis; Shf, shrimp feeds; Des, detritus in sediment; Dew, detritus in water.

water body, and there is no water exchange with the surrounding water (Sun et al., 2011). Land-based enclosure in this study means the enclosure built on the bottom of the pond to simulate pond ecosystem (Li et al., 1998b), which was different from the floating enclosure (Li et al., 1993). The experimental pond located in Ganyu County, Jiangsu Province, China (34°58′17.30″ N, 119°11′53.70″ E), covered 2 ha, with a water column depth of 1.6–1.7 m at the study site. Four land-based enclosures, representing four replicates of the same size (length × width × depth = 5 × 5 × 2 m), were constructed in the pond, which were lined with polyethylene (water-proof) and supported with wood poles. The structure of the enclosures was previously described in detail (Wang et al., 1998; Tian et al., 2001). At the bottom of the enclosure, the walls were covered with mud from the same pond, and supported by posts at 2.5-m intervals. An aeration system consisting of a blower, PVC tubes, gas tubes, and air stones was used for aeration and water circulation. Five air stones connected by a gas tube were suspended approximately 20 cm from the bottom in each enclosure. The land-based enclosure can satisfactorily simulate a pond and be suitably used for aquacultural and ecological experiments (Li et al., 1998). The entire experiment was carried out for 90 days from July 13 to October 13, 2014. Detailed descriptions of the enclosure are provided in the **Supplementary Material** (part 1. Location and layout of the experiment).

2.2 Cultured Animals and Aquaculture Management

Juvenile swimming crabs (*P. trituberculatus*) were cultured with white shrimp *L. vannamei* and short-necked clam *R. philippinarum* in the four enclosures in the pond. All animals were purchased from Ganyu Jiaxin Aquatic Food Co., Ltd. (Ganyu, Jiangsu, China). The stocking densities of swimming crabs, white shrimps, and short-necked clams used in the four enclosures were 6 individuals/m^2, 45 individuals/m^2, and 30 individuals/m^2, respectively. Swimming crabs, white shrimps, and short-necked clams were stocked with an initial individual wet weight of 0.58 ± 0.10 g, 0.05 ± 0.01 g, and 0.91 ± 0.10 g, respectively.

Crabs cultured in the four enclosures were fed with chilled blue clam (*Aloidis laevis*) twice per day (06:00 and 18:00). The amounts of *A. laevis* supplied to the crabs were adjusted according to Zhou et al. (2010). Shrimps were fed a commercial pellet diet (Lianyungang Chia Tai Feed Co., Ltd., Lianyungang, Jiangsu, China), the amount of which was determined according to the product specifications. To assess growth and health condition of crabs and shrimps, 15–20 individuals per enclosure were sampled every ten days using a cage net (0.60 × 0.40 × 0.15 m) designed to trap crabs and shrimps in each enclosure; individuals were returned to the enclosure when sampling was completed.

2.3 Model Construction

The early, middle, and late periods of *P. trituberculatus* polyculturing were at 0–30, 31–60, and 61–90 d of the 90-d culture period, respectively. Three mass-balanced Ecopath models representing early, middle, and late culture periods of the *P. trituberculatus* polyculture ecosystem were constructed.

Ecopath models were constructed according to two master equations (Christensen and Pauly, 1992a; Christensen and Pauly, 1992b). The first equation represents the production of each functional group utilized in the ecosystem. Production is divided into predation, migration, biomass accumulation, exports, and other mortality, and is expressed as follows (Christensen et al., 2005):

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i - \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}\right) - Y_i - BA_i - E_i = 0$$

where B_i represents prey biomass (i), B_j represents predator biomass (j), $(P/B)_i$ represents the ratio of production to prey biomass (i), EE_i is ecotrophic efficiency, Y_i is catch biomass, $(Q/B)_j$ is the ratio of food consumption to predator biomass (j), DC_{ij} is the ratio of biomass (i) being consumed by (j) to the total consumption of (j), BA_i is the prey biomass accumulation rate (i), and E_i is the difference between immigration and emigration of prey (i).

The second equation describes the consumption of a consumer group which is constituted by production, respiration, and unassimilated food:

$$B_i \times \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i$$

where R_i is respiration and U_i is food which cannot be assimilated by consumers. The Ecopath model requires that at least three of the four parameters B, P/B, Q/B and EE are imported for each functional group. Because EE is difficult to obtain for each functional group, the EE value is typically estimated through the input of the other three parameters. Detailed descriptions of limitations, applicability, and methods of this model were published previously (Christensen and Walters, 2004).

We choose to simulate the dynamics of the polyculture ecosystem by constructing Ecopath steady-state models, rather than using dynamic simulation models such as an Ecosim model (Christensen et al., 2005). This is because aquaculture pond ecosystems are vulnerable to external disturbances such as weather changes. External disturbances may prevent Ecosims from accurate and comprehensive simulation of dynamic processes. With Ecopath, most of the model inputs can be obtained by field experiments directly. The modeled results may thus be more reliable than those of Ecosim models.

2.3.1 Functional Groups

According to the definition of the functional group and setting principles of the Ecopath model, 17 functional groups were used in the three Ecopath models. Phytoplankton was divided into three groups: pico-phytoplankton (< 10 μm), nano-phytoplankton (10–38 μm), and micro-phytoplankton (> 38 μm).

Zooplankton were divided into macrozooplankton (copepods and planktonic mollusks, > 150 μm) and microzooplankton (copepodites and rotifers,< 150 μm). The zoobenthos was divided into macrobenthos (polychetes, > 500 μm) and microbenthos (polychetes and nematodes,< 500 μm). Bacteria were divided into benthic bacteria and bacterioplankton. Detritus was divided into detritus in sediment and detritus in water. The imported artificial food of *A. laevis* and shrimp feed were also set as the functional group, both were categorized as detritus groups. The other functional groups included *P. trituberculatus*, *L. vannamei*, *R. philippinarum*, and periphyton (**Table 1**).

2.3.2 Field Data

During the experiment, data on parameters for the models were determined and collected. Input data for each model were the average values of sampling results collected during each culture period. These data were collected as follows:

The input data of biomass, P/B ratio, Q/B ratio, and diet composition of each group were estimated using data derived from field experiments and literature (**Table 2**). The biomass of each functional group, expressed as kJ m^{-2}. The energy content of *P. trituberculatus*, *L. vannamei*, *R. philippinarum*, periphyton, macrobenthos, shrimp feed, blue clam *A. laevis*, and detritus of sediment were measured by an oxygen bomb calorimeter (PARR-1281, America). The energy content of microbenthos, micro-, nano-, and pico- phytoplankton, macro- and micro-zooplankton, bacterioplankton, benthic bacteria, and detritus in water were determined by measuring the organic carbon content first, then converted to energy content. The relation between organic carbon (g) and energy (kJ) was obtained from Salonen et al. (1976) (1g C = 46 kJ).

The unassimilated ratio of consumption of macrozooplankton, and microzooplankton were set at 0.40 (Winberg, 1960), those of macrobenthos and microbenthos were set at 0.4 and 0.30, respectively (Bradford-Grieve et al., 2003), and all other consumers were set at 0.20 (Winberg, 1960). Biomass accumulation of *P. trituberculatus*, *L. vannamei*, and *R. philippinarum* were obtained through field experiments. The detritus input of artificial feeds of shrimp feed and blue clam *A. laevis* were recorded every day by the pond manager.

Detritus fate: according to Heymans et al. (2016), if more than one detritus group is defined, the detritus fate must be described in the model. In this study, it was set that the production, which was not used by the ecosystem (energy of flow to detritus) from the groups of *P. trituberculatus*, *R. philippinarum*, macrobenthos, microbenthos, benthic bacteria, *A. laevis*, and shrimp feed flowed into the detritus group of detritus in sediment; energy from detritus of the groups of macrozooplankton, microzooplankton, bacterioplankton, micro-phytoplankton, nano-phytoplankton, pico-phytoplankton, and periphyton flowed into the detritus group of detritus in water. Moreover, half of the energy of flow to detritus from the group of *L. vannamei* was set to flow into the detritus groups of detritus in sediment and detritus in water, respectively. The energy of detritus in water, which was not used by recycling, ultimately flowed to detritus in the sediment. This assumption was implemented because our field observations showed almost no biomass accumulation for detritus in water at the end of the experiment in the four ecosystems.

The methods of obtaining data of biomass, P/B ratios, Q/B ratios, unassimilated consumption rates, biomass accumulation, and detritus imports of the related functional groups are described in detail in the **Supplementary Material** (part 2. Input data of B, P/B, Q/B, unassimilated consumption rate, biomass accumulation, detritus import, and detritus fate); the diet matrix of the polyculture ecosystem in the early, middle, and late periods is also provided in the **Supplementary Material** (part 3. Diet composition).

TABLE 1 | Functional groups and main species included in models of polyculture ecosystem.

Functional groups	Main species or organic material
Portunus trituberculatus	*P. trituberculatus*
Litopenaeus vannamei	*L. vannamei*
Ruditapes philippinarum	*R. philippinarum*
Macrobenthos	Polychaetes, particle size > 500 μm
Microbenthos	Polychetes and nematodes, particle size< 500 μm
Macrozooplankton	Copepods and planktonic mollusks, particle size > 150 μm
Microzooplankton	Copepod larvae and rotifers, particle size< 150 μm
Benthic bacteria	Heterotrophic bacteria in sediment
Bacterioplankton	Heterotrophic bacteria in water column
Micro-phytoplankton	Phytoplankton, particle size > 38.00 μm
Nano-phytoplankton	Phytoplankton, particle size 10–38 μm
Pico-phytoplankton	Phytoplankton, particle size< 10 μm
Periphyton	Hydrophyte, grown on the polyvinyl plastic of the experimental enclosure
Aloidis laevis	Chilled blue clam *A. laevis*
Shrimp feeds	Shrimp feeds
Detritus in sediment	Detritus in sediment
Detritus in water	Detritus in water column

2.3.3 Model Balancing and Uncertainties

We used EE values< 1 as the first criterion to balance the model; EE values > 1 indicated that the consumed biomass was larger than the produced biomass. Where this occurred, we modified the diet composition of each consumer group, which was expressed as a proportion; such changes in diet proportions never exceeded 0.05. This method was chosen because the diet composition of each consumer was the input data, which was associated with high uncertainty. Some other criteria were also considered, including that the respiration:assimilation ratios should be< 1, and the ratio of respiration:biomass should be higher for mobile consumer groups than for sedentary consumer groups. Moreover, we also ensured that the P/Q values of most of the functional groups were in the range of 0.10–0.30 (Christensen et al., 2005).

2.3.4 Ecological Network Analysis Indicators

Ecological network analysis is a system-oriented method for analyses of within-system interactions used for identifying holistic properties of ecosystems (Fath et al., 2007), which is considered an effective tool for assessing the attributes of system structure and function and to compare ecosystems. Ecopath models use a series of ecological network analysis indicators to assess ecosystem attributes (Christensen et al., 2005). Holistic

TABLE 2 | Data sources of B, P/B, Q/B, and diet composition of each group in the *Portunus trituberculatus* polyculture ecosystem.

Groups	Biomass	P/B	Q/B	Diet composition
Pot	Calculated according to field survey and mortality estimation[1]	Field experiment[1]	Yang et al. (2010)	Feng et al. (2018b)
Liv	Calculated according to field survey and mortality estimation[1]	Field experiment[1]	Qi et al. (2010)	Feng et al. (2018b)
Rup	Calculated according to field survey and mortality estimation[1]	Field experiment[1]	Zhang and Yan (2010)	Wetzel (1983); Feng et al. (2018b), and Zhang et al. (2005)
Mab	Field survey[1]	Zhou and Xie (1995)	Lin (2012)	Wang and Zhang et al. (1998); Feng et al. (2017), and Tsuchiya and Kuhihara (1979)
Mib	Field survey[1]	Schwinghamer et al. (1986)	Lin (2012)	Jin (2010)
Maz	Field survey[1]	calculated according to: $P/B=Q/B*(P/Q)$. The P/Q was obtained from Straile (1997)	by measuring the respiration[5] first, then the Q/B was calculated according to: $Q/B = P/B + R/B + U/B$. $U = 0.4Q$ (Winberg, 1960), $U/B = 0.4Q/B$.	Feng et al. (2018b) and Li and Lin (1995)
Miz	Field survey[1]	calculated according to: $P/B=Q/B*(P/Q)$. The P/Q was obtained from Straile (1997)	by measuring the respiration[5] first, then the Q/B was calculated according to: $Q/B = P/B + R/B + U/B$. $U = 0.4Q$ (Winberg, 1960), $U/B = 0.4Q/B$.	Feng et al. (2018b) and Li and Lin (1995)
Beb	Field survey[1]	calculated according to: $P/B=Q/B*(P/Q)$. The P/Q was obtained from Moriarty (1986)	by measuring the sediment respiration[6] first, assuming the respiration of benthic bacteria accounts for 0.64 of sediment respiration (Hargrave, 1972), then the Q/B was calculated according to: $Q/B = Q/B*(P/Q) + R/B + U/B$. The P/Q was obtained from Moriarty (1986), $U = 0.2Q$ (Winberg, 1960), $U/B=0.2Q/B$.	Zhou (2015)
Bap	Field survey[1]	Field experiment[2]	by measuring the respiration[7] first, then the Q/B was calculated according to: $Q/B = P/B + R/B + U/B$. $U = 0.4Q$ (Winberg, 1960), $U/B = 0.4Q/B$.	Zhou (2015)
Mip	Field survey[1]	Field experiment[3]	/	
Nap	Field survey[1]	Field experiment[3]	/	
Pip	Field survey[1]	Field experiment[3]	/	
Pep	Field survey[1]	Field experiment[4]	/	
All	Daily record[1]	/	/	
Shf	Daily record[1]	/	/	
Des	Field survey[1]	/	/	
Dew	Field survey[1]	/	/	

Pot, P. trituberculatus; Liv, Litopenaeus vannamei; Rup, Ruditapes philippinarum; Mab, macrobenthos; Mib, microbenthos; Maz, macrozooplankton; Miz, microzooplankton; Beb, benthic bacteria; Bap, bacterioplankton; Mip, micro-phytoplankton; Nap, nano-phytoplankton; Pip, pico-phytoplankton; Pep, periphyton; All, Aloidis laevis; Shf, shrimp feeds; Des, detritus in sediment; Dew, detritus in water. B, biomass; U, unassimilated consumption; Q, consumption; P/B, production/biomass; Q/B, consumption/biomass; P/Q, production/consumption; R/B, respiration/biomass; U/B, unassimilated consumption/biomass. [1]: the detailed method was described in the ***Supplementary Material****; [2]: method obtained from Schwaerter et al. (1988); [3]: method obtained from Diana et al. (1991); [4]: method obtained from Zhang (2011); [5]: respiration was measured according to Williams (1981); [6]: respiration was measured according to Li et. al., (1998a); [7]: respiration was measured according to Schwaerter et al. (1988).*

ecological network analysis indices typically include total system throughput (TST), EE, Finn's cycling index (FCI), Finn's mean path length (FML), connectance index (CI), system omnivory index (SOI), average mutual information (AMI), flow diversity (H), relative ascendancy(A/C), etc. (Heymans et al., 2007).

TST is the sum of all flows in an ecosystem. It is estimated as the sum of four flow components: total consumption, total export, total respiration, and total flows to detritus. This index represents the size of the entire ecosystem in terms of flow (Ulanowicz, 1986). The *EE* value is calculated as the part of production that is used within or exported out of the system. Transfer efficiency is calculated as the ratio between the sum of exports from a given trophic level (TL) plus the flow that is transferred from one TL to the next and the throughput on the TL (Christensen et al., 2005). The FCI is the fraction of an ecosystem's throughput that is recycled. FML represents the average number of compartments that a unit of energy passes through from its entry into the ecosystem until its leave (Christensen et al., 2005). The CI is the ratio of the number of actual links between functional groups to the number of theoretically possible links. The SOI is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake, which measures the diversity of consumer–prey relationships in an ecosystem (Christensen et al., 2005).

AMI, H, ascendancy, total development capacity (C), and overhead (O) are indicators built on the foundation of information-theory concepts in ecological networks (Ulanowicz, 1986). H measures both the number of interactions and the evenness of flows in the food web, and the AMI measures the degree of specialization of flows in the food web (Ulanowicz, 1986). Ascendancy is a measure of the average mutual information in an ecosystem, scaled by TST (Ulanowicz and Norden, 1990) (ascendancy (A) = AMI × TST). C measures the potential for a system to develop and is the natural upper limit of ascendancy (C = H × TST) (Ulanowicz, 1986). O measures the uncertainty of energy flow of the network (Ulanowicz and Norden, 1990), and represents the unorganized part of C in an ecosystem (Bodini and Bondavalli, 2002) (O = C-A). The ascendency, O, and C can be split into contributions from imports, internal flow, exports and respiration. The relative overhead (O/C) is calculated as O to C. The A/C is calculated as ascendancy to C. A/C is the fraction of a potential food-web organization that is actually realized, and the O/C is the fraction of a potential food-web organization that is not realized (Ulanowicz, 1986).

3 RESULTS

3.1 Parameters of Each Group of the Three Models

The basic input data and the estimated EE values of the three models are presented in **Tables 3–5**. The biomass of *P. trituberculatus*, *L. vannamei*, *R. philippinarum*, and benthic bacteria increased from the early to the middle and late period, while macro- and micro-benthos biomass showed a decreasing trend over these periods. The biomass of macro- and micro-zooplankton, bacterioplankton, and micro- and nano-phytoplankton increased from the early to the middle period, and then decreased from the middle to the late period. The biomass of pico-phytoplankton showed a marked increase from the middle to the late period. The groups of microbenthos and benthic bacteria had the lowest EE values in models of all three periods owing to the lack of consumers. The EE values of these two groups were all< 0.10. The periphyton also had low EE values in models of the early, middle, and late periods, with the values of 0.12, 0.11, and 0.04, respectively. Moreover, the EE value of pico-phytoplankton was also low in the model of the late period (0.24). The groups of *P. trituberculatus*, *L. vannamei* and *R. philippinarum* all had high EE values in the three models, and the EE values were higher than 0.90 in models of the middle and late period. The groups of blue clam *A. laevis* and shrimp feed also had high EE values (> 0.80, each) in models of all three periods. The detritus in sediment had high EE values in the early and middle periods (0.95 and 0.99, respectively). Other groups including microzooplankton and bacterioplankton had high EE values in the model of the late period (0.86 and 0.85, respectively).

Consumption by various groups in models of the three periods is presented in **Figure 1**. The total consumption increased from the early to the middle and late period. Benthic bacteria were the dominant consumers in all three culture periods, followed by *L. vannamei*. Bacterioplankton and macrozooplankton had the third and fourth largest consumption, respectively, in the early period, whereas bacterioplankton and *P. trituberculatus* had the third- and fourth-largest consumption, respectively, in both middle and late periods. Macrobenthos had the least consumption in all three culture periods, followed by microbenthos and microzooplankton.

3.2 Energy Flow Structure of the Modeled Ecosystem

Aggregating the three modeled ecosystems into discrete TLs led to the identification of five integer trophic levels in the early, middle, and late periods (**Tables 6–8**). TL I in the three modeled ecosystems was composed of primary producers, including micro-, nano-, and pico-phytoplankton; periphyton; and the detritus groups of *A. laevis*, shrimp feed, detritus in sediment, and detritus in water. 75.76%, 82.17%, and 76.77% of the energy on TL I originated from detritus groups in the early, middle and late periods, respectively, whereas the remaining 24.24%, 17.83%, and 23.23% originated from the primary producers in the early, middle and late periods, respectively. Energy flows at TL II encompassed almost all the consumer groups in the early, middle and late periods in this ecosystem, except microbenthos, which was more relevant at TL III in this ecosystem during all three periods. Most of the energy flow of the 17 groups in the early, middle, and late periods in this ecosystem was distributed at TLs I and II. Energy flow at TLs IV and V during the three culture periods was negligible. Benthic bacteria had the highest energy of flow to detritus in the early and middle periods (1493.45 and 1703.20 kJ m^{-2}, respectively), whereas in the late period, the highest energy flow to detritus was pico-phytoplankton (1950.37 kJ m^{-2}). The second-highest energy flow to detritus was pico-phytoplankton (532.80 kJ m^{-2}), macrozooplankton (638.61 kJ m^{-2}), and benthic bacteria (1914.31 kJ m^{-2}) in the early, middle, and late periods, respectively.

A Lindeman spine plot was constructed to represent flow and biomass for the models of the early, middle, and late culture periods (**Figure 2**). Primary production was calculated as 40.66, 60.38, and 54.84 kJ m^{-2} for the models of the early, middle, and late periods, respectively, which contributed approximately 11.92%, 8.78%, and 11.13%, respectively to the TST. In the early, middles, and late periods, 891.60, 1001.00, and 1180.00 kJ m^{-2} 30 $days^{-1}$, respectively, of primary production were consumed by its consumers, whereas 1156.00, 1213.00 and 2582.00 kJ m^{-2} 30 $days^{-1}$, respectively, of primary production flowed to the detritus groups. In the early, middle, and late periods, 5,683.00, 8,857.00, and 10,843.00 kJ m^{-2} 30 $days^{-1}$, respectively, of total energy flow to detritus was consumed by primary consumers, whereas 150.55, 28.63, and 750.11 kJ m^{-2} 30 $days^{-1}$, respectively, of the total energy flow to detritus was accumulated in the group of detritus in sediment. The energy transfer efficiencies from TL II to III in the early, middle, and late periods was 4%, 4%, and 2%, respectively. The transfer efficiencies were lower than the 10% energy transfer efficiency of typical natural ecosystems (Lindeman, 1942). Most of the TST was distributed at TLs I and II in all three models.

3.3 System Attributes of the Modeled Ecosystem

The system attributes of the three models are described in **Table 9**. The TST in this ecosystem comprised total respiration, total consumption, and total energy flow to detritus; TST increased

TABLE 3 | Ecopath inputs and outputs for a *Portunus trituberculatus* polyculture ecosystem model during the early period.

Groups	Biomass (kJ m^{-2})	*P/B* (30 d^{-1})	*Q/B* (30 d^{-1})	*EE*	*P/Q*	Biomass accumulation (kJ m^{-2} 30 d^{-1})	Detritus import (kJ m^{-2} 30 d^{-1})
Pot	106.80	1.94	4.73	**0.81**	**0.41**	166.85	
Liv	159.07	1.85	7.70	**0.85**	**0.24**	250.03	
Rup	51.46	0.62	10.16	**0.92**	**0.06**	29.42	
Mab	0.73	2.15	7.16	**0.32**	**0.30**		
Mib	2.39	3.08	10.25	**0.06**	**0.30**		
Maz	12.30	13.86	47.81	**0.41**	0.29		
Miz	0.67	90.05	310.50	**0.73**	0.29		
Beb	35.59	25.50	84.60	**0.02**	0.30		
Bap	10.59	22.73	69.78	**0.51**	**0.33**		
Mip	5.24	53.98		**0.67**			
Nap	12.24	62.56		**0.42**			
Pip	13.05	69.09		**0.41**			
Pep	10.13	9.63		**0.12**			
All	36.94			**0.83**			1108.16
Shf	27.31			**0.84**			819.36
Des	4159.63			**0.95**		150.55	
Dew	287.24			**0.57**			

Values in bold are the parameters estimated by the model. B, biomass; P/B, production/biomass; Q/B, consumption/biomass; EE, ecotrophic efficiency; P/Q, production/consumption. P/B, Q/B, and detritus import were calculated for the 30 d experimental period.

from the early to the middle and late period, with the values of 17,176.73, 25,211.79, and 33,803.86 kJ m^{-2} 30 days^{-1}, respectively. Total primary production, total production, and total biomass also showed an increasing trend from the early to the middle and late period. The ratio of total primary production to total respiration (TPP/TR) was 0.61, 0.43, and 0.50 in the early, middle, and late periods, respectively. On account of the high energy import *via* the addition of *A. laevis* and shrimp feed to support the growth of the cultured organisms, net system production had values of -1330.67, -2950.29, and -3752.76 kJ m^{-2} 30 days^{-1} in the early, middle, and late periods, respectively. FCI was calculated as 20.38%, 17.90%, and 12.28% for the early, middle, and late periods, respectively. FML decreased from the early to the middle and late period, with values of 5.08, 4.89, and 4.50, respectively. Values of ascendancy showed an increasing trend from the early to the middle and late period. The A/C in the early, middle, and late periods was 41.51%, 42.41%, and 45.05%, respectively, and a pronounced increase was noted in late period. The O/C in the early, middle, and late periods was 58.49%, 57.59%, and 54.95%, respectively, and a marked decrease was noted in the late period.

TABLE 4 | Ecopath inputs and outputs for a *Portunus trituberculatus* polyculture ecosystem model during the middle period.

Groups	Biomass(kJ m^{-2})	*P/B*(30 d^{-1})	*Q/B*(30 d^{-1})	*EE*	*P/Q*	Biomass accumulation (kJ m^{-2} 30 d^{-1})	Detritus import (kJ m^{-2} 30 d^{-1})
Pot	350.76	1.05	3.18	**0.93**	**0.33**	343.28	
Liv	464.93	0.96	5.05	**0.97**	**0.19**	431.28	
Rup	79.44	0.51	9.27	**0.94**	**0.06**	37.92	
Mab	0.58	2.15	7.16	**0.89**	**0.30**		
Mib	2.15	3.08	10.25	**0.06**	**0.30**		
Maz	14.94	20.54	70.84	**0.30**	0.29		
Miz	1.56	55.74	192.21	**0.79**	0.29		
Beb	41.76	24.10	79.15	**0.01**	0.30		
Bap	16.94	27.32	81.38	**0.51**	**0.34**		
Mip	10.49	44.26		**0.70**			
Nap	20.51	48.68		**0.37**			
Pip	9.13	61.32		**0.50**			
Pep	20.25	9.42		**0.11**			
All	75.76			**0.95**			2272.80
Shf	50.63			**0.90**			1518.60
Des	4284.26			**0.99**		28.63	
Dew	382.99			**0.75**			

Values in bold are the parameters estimated by the model. Group abbreviations as in ***Table 2****. B, biomass; P/B, production/biomass; Q/B, consumption/biomass; EE, ecotrophic efficiency; P/Q, production/consumption.*

TABLE 5 | Ecopath inputs and outputs for a *Portunus trituberculatus* polyculture ecosystem model during the late period.

Groups	Biomass (kJ m^{-2})	*P/B* (30 d^{-1})	*Q/B* (30 d^{-1})	*EE*	*P/Q*	Biomass accumulation (kJ m^{-2} 30 d^{-1})	Detritus import (kJ m^{-2} 30 d^{-1})
Pot	550.99	0.58	2.32	**0.98**	**0.25**	313.59	
Liv	795.55	0.63	4.88	**0.99**	**0.13**	494.24	
Rup	101.51	0.40	8.16	**0.95**	**0.05**	38.61	
Mab	0.36	2.15	7.16	**0.82**	**0.30**		
Mib	1.91	3.08	10.25	**0.04**	**0.30**		
Maz	11.42	13.61	46.93	**0.78**	0.29		
Miz	0.87	53.30	182.75	**0.86**	0.29		
Beb	51.53	19.20	91.00	**0.01**	0.21		
Bap	7.41	18.21	123.79	**0.85**	**0.15**		
Mip	3.72	76.79		**0.81**			
Nap	8.54	80.28		**0.49**			
Pip	18.27	139.68		**0.24**			
Pep	24.30	9.81		**0.04**			
All	99.90			**0.88**			2997.00
Shf	78.41			**0.91**			2352.30
Des	5450.97			**0.86**		750.11	
Dew	239.37			**0.43**			

Values in bold are the parameters estimated by the model. Group abbreviations as in ***Table 2****.*

4 DISCUSSION

4.1 Biomass Dynamics of Phytoplankton With Different Particle Sizes

During the 90-day culture period in the present study, the biomass of micro-, nano-, and pico-phytoplankton expressed varying fluctuating trends. The biomass of both micro- and nano-phytoplankton increased from the early to the middle period, and then decreased from the middle to the late period. In contrast, the biomass of pico-phytoplankton showed the opposite trend: it decreased from the early to the middle period, and then increased from the middle to the late period. The total phytoplankton biomass and primary production increased from early to middle and late periods. In line with Ban et al. (2015), inorganic nutrients (e.g., NH_4^+, NO_3^-, and NO_2^-) increased remarkably from the early to the middle period in this *P. trituberculatus* polyculture ecosystem, considering the input of artificial foods. It was speculated that the increase in inorganic nutrients may have led to the increase in total phytoplankton biomass and primary production from the early to the middle period (Ramírez et al., 2005). The dominant phytoplankton community changed from nano-phytoplankton to pico-phytoplankton from the middle to the late period. This phenomenon may be correlated with the polyculture of *R. philippinarum*. The filter-feeding *R. philippinarum* efficiently transfers particulate matter present in the water column to the sediments by filtration coupled with biodeposition (Kautsky and Evans, 1987). Prins et al. (1998) and Souchu et al. (2001) reported that the consumption of phytoplankton by filter feeders could induce a shift in the phytoplankton composition towards phytoplankton with smaller cells and faster growth rates. *R. philippinarum* exhibits the highest phytoplankton consumption in the late period compared to the early and middle periods; thus, phytoplankton consumption by *R. philippinarum* may induce a change in the phytoplankton composition, mainly comprising pico-phytoplankton, which has a higher turnover rate. However, the low *EE* value (0.24) of pico-phytoplankton in the late period indicates that phytoplankton consumption by *R. philippinarum* could not suppress the growth of pico-phytoplankton, and that *R. philippinarum* was not food limited in this ecosystem.

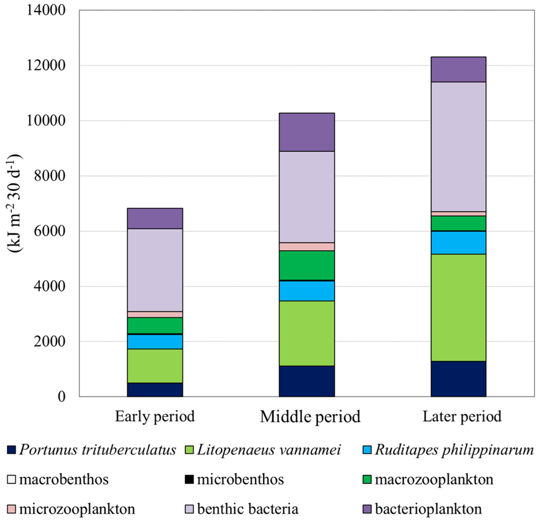

FIGURE 1 | Allocations of total consumption (kJ m^{-2} 30 d^{-1}) of each consumer for a *Portunus trituberculatus* polyculture ecosystem during the early, middle, and late periods, respectively.

4.2 Analysis of Dynamics of Energy Flow Structure From Early to Late Period

The energy input in aquaculture pond ecosystems mainly comprises primary production and imported foods (Feng et al.,

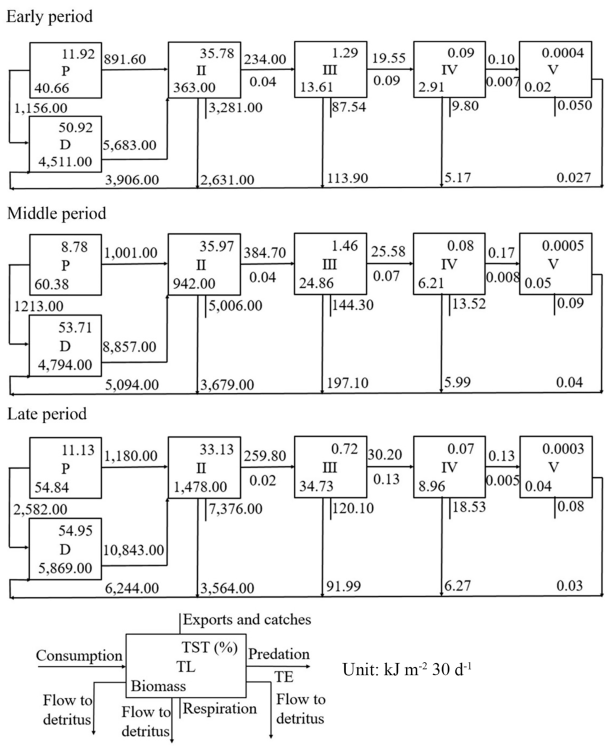

FIGURE 2 | Aggregation of flows and biomass (kJ m^{-2} 30 d^{-1}) of a *Portunus trituberculatus* polyculture ecosystem during the early, middle, and late periods, respectively (D, detritus; P, primary production; TL, trophic level; TE, transfer efficiency; TST, total system throughput).

2015; Dong et al., 2017). Primary production and imported foods (blue clam *A. laevis* and shrimp feed) increased from early to late period in this ecosystem. Primary production accounted for 50.29%, 34.79%, and 39.71% of total energy input in the early, middle, and late periods, respectively. However, approximately 59.28%, 59.97%, and 73.29% of primary production was not utilized by consumers and flowed to detritus groups. Energy originating from detritus accounted for 83.00%, 87.00%, and 85.00% of total system throughput in early, middle, and late period, respectively. As a result, the polyculture ecosystem remained a detritus-dominated ecosystem throughout, which was in accordance with the results of Feng et al. (2017) and Feng et al. (2018a), showing that the detritus food chain is predominant in *P. trituberculatus* polyculture systems.

The group of benthic bacteria was the largest consumer over the entire culture period, thus the associated energy pathway of detritus in sediment to benthic bacteria was the main energy flow pathway. However, the energy flow structure showed some changing trends associated with organisms as total consumption by *P. trituberculatus*, *L. vannamei*, and *R. philippinarum* to total system consumption showed an increasing trend from early to middle and late periods, which accounted for 32.99%, 40.90%, and 48.64% of the total system consumption, respectively. Increased consumptions of these three functional groups led to increased energy flow to detritus during the entire culture period; moreover, pico-phytoplankton showed the highest energy flow to detritus in the late period. The total energy flow to detritus groups thus showed an increasing trend from the early to the middle and late period (4,221.29, 5,366.55, and 6,810.27 kJ m^{-2} 30 $days^{-1}$, respectively), and large amounts of energy were accumulated in the detritus group of detritus in sediment. Increased detritus accumulation was considered a potential risk to the ecosystem, which may cause deterioration of the bottom environment in a pond ecosystem (Lin et al., 2005). Management practices such as increasing bottom oxygen supply should be implemented to reduce this risk.

TABLE 6 | Absolute flows of each group by trophic level decomposition of a *Portunus trituberculatus* polyculture ecosystem during the early period.

Groups	Trophic levels					FD (kJ m^{-2} 30 d^{-1})	ETL
	I	II	III	IV	V		
Pot		324.40	10.24	3.60	0.03	141.37	2.05
Liv		934.80	29.38	10.55	0.04	289.22	2.05
Rup		486.50	6.91	0.00		107.05	2.01
Mab		4.46	0.42	0.30		3.13	2.20
Mib		8.56	15.90	0.00		14.23	2.65
Maz		432.30	155.20	0.62		335.42	2.27
Miz		205.30	2.92			99.57	2.01
Beb		3011.00				1493.45	2.00
Bap		738.90				266.48	2.00
Mip	283.10					92.55	1.00
Nap	765.80					445.28	1.00
Pip	901.60					532.80	1.00
Pep	97.52					85.76	1.00
All	1108.00					184.69	1.00
Shf	819.40					130.29	1.00
Des	2993.00					0.00	1.00
Dew	1078.20					820.80	1.00
Total value	8046.62	6146.23	220.97	15.07	0.08		

*Group abbreviations of each functional group as in **Table 2**. FD, flow to detritus; ETL, effective trophic level.*

TABLE 7 | Absolute flows of each group by trophic level decomposition of a *Portunus trituberculatus* polyculture ecosystem during the middle period.

Groups	Trophic levels					FD (kJ m^{-2} 30 d^{-1})	ETL
	I	II	III	IV	V		
Pot		740.50	23.40	8.18	0.08	248.10	2.05
Liv		1878.00	28.21	10.08	0.04	484.64	2.03
Rup		681.00	17.46			149.88	2.03
Mab		3.57	0.34	0.24		1.79	2.20
Mib		7.71	14.32	0.00		12.86	2.65
Maz		778.90	278.20	1.17		638.61	2.27
Miz		294.80	5.10			138.11	2.02
Beb		3306.00				1703.20	2.00
Bap		1379.00				504.53	2.00
Mip	464.20					139.17	1.00
Nap	998.60					624.64	1.00
Pip	559.90					279.07	1.00
Pep	190.80					169.62	1.00
All	2273.00					123.78	1.00
Shf	1519.00					148.55	1.00
Des	3424.00					0.00	1.00
Dew	1914.22					621.78	1.00
Total value	11343.72	9069.48	367.03	19.67	0.12		

*Group abbreviations of each functional group as in **Table 2**. FD, flow to detritus; ETL, effective trophic level.*

4.3 Analysis of Ecosystem Attribute Dynamics Using Ecological Network Analysis

Biomass change of each functional group during the entire culture period could lead to changes in ecosystem structure, which in turn could lead to changes in ecosystem function. The indices of TST, AMI, A/C, and O/C are assigned to a number of groups that describe ecosystem properties in terms of ecosystem structure (Tomczak et al., 2013). In the polyculture ecosystem of the present study, TST, AMI, and A/C all increased from the early to the late period. The increase in TST indicated that the ecosystem size increased from the early to the late period. The increase in AMI indicated that the inherent organization, i.e. the degree of specialization of flow in the network of this polyculture ecosystem, increased from the early to the late period, which represents a trend of simplification of the food web structure (Latham and Scully, 2002). The A/C, which is the ratio of AMI to H, showed a marked increase from the middle to the late period, because of the decrease in H and increase in AMI, and this indicated that the ecosystem had the highest level of system organization in the late period. The system overhead represents

TABLE 8 | Absolute flows of each group by trophic level decomposition of a *Portunus trituberculatus* polyculture ecosystem during the late period.

Groups	Trophic levels					FD (kJ m^{-2} 30 d^{-1})	ETL
	I	II	III	IV	V		
Pot		925.20	29.95	9.54	0.06	261.65	2.05
Liv		3327.00	46.10	14.83	0.04	783.41	2.02
Rup		768.40	21.32			167.66	2.03
Mab		2.23	0.21	0.15		1.18	2.20
Mib		6.85	12.72	0.00		11.52	2.65
Maz		405.30	130.40	0.40		248.26	2.24
Miz		158.10	1.60			70.22	2.01
Beb		4689.00				1914.31	2.00
Bap		917.60				203.93	2.00
Mip	285.80					53.86	1.00
Nap	685.90					349.84	1.00
Pip	2552.00					1950.37	1.00
Pep	238.40					227.70	1.00
All	2997.00					356.51	1.00
Shf	2352.00					209.85	1.00
Des	4687.00					0.00	1.00
Dew	1373.00					1816.00	1.00
Total value	15171.10	11199.68	242.30	24.93	0.10		

*Group abbreviations of each functional group as in **Table 2**. FD, flow to detritus; ETL, effective trophic level.*

TABLE 9 | System attributes for a *Portunus trituberculatus* polyculture ecosystem during the early, middle, and late period, respectively.

System attribute parameters	Early period	Middle period	Late period	Units
Total consumption	6828.50	10268.38	12313.51	kJ m^{-2}
Total respiration	3378.62	5163.70	7514.78	kJ m^{-2}
Total flow to detritus	6969.61	9779.72	13975.57	kJ m^{-2}
Total system throughput	17176.73	25211.79	33803.86	kJ m^{-2}
Total production	9751.87	16364.67	22005.13	kJ m^{-2}
Total primary production	2047.95	2213.41	3762.02	
TPP/TR	0.61	0.43	0.50	
Total net production	-1330.67	-2950.29	-3752.76	
TPP/TB	4.87	2.14	2.39	
Total biomass (no detritus)	420.25	1033.45	1576.40	kJ m^{-2}
Connectance index	27.20	27.20	27.20	%
System omnivory index	0.06	0.05	0.05	
Finn's cycling index (FCI)	20.38	17.90	12.28	%
Finn's mean path length (FML)	5.08	4.89	4.50	
Total development capacity (C)	81781.80	122382.40	154362.50	Bits m^{-2}
Overhead (O)	47837.00	70479.30	84822.50	Bits m^{-2}
Redundancy (R)	34880.80	49135.20	58158.70	Bits m^{-2}
Ascendancy (A)	33944.80	51903.10	69540.00	Bits m^{-2}
Relative ascendancy (A/C)	41.51	42.41	45.05	%
Relative overhead (O/C)	58.49	57.59	54.95	%
Average mutual information (AMI)	1.98	2.06	2.06	
Flow diversity (H)	4.76	4.85	4.57	
Proportion of total flow originating from detritus	83.00	87.00	85.00	%
Pedigree	0.86	0.86	0.86	

Units were calculated over each 30d experimental period. TPP/TR, Total primary production/total respiration; TPP/TB, Total primary production/total biomass.

the resilience of an ecosystem against external perturbations (Ulanowicz and Norden, 1990; Christensen, 1995). The O/C in the late period was lower than that in the early and middle periods, indicating that the ecosystem was less resilient in late period than in the early and middle periods.

FCI and FML are indices that describe the system attributes of energy flow (Tomczak et al., 2013). The values of FCI and FML decreased from the early to the middle and late periods. The fluctuating trends of FCI was contrary to that of A/C. which was in accordance with Baird et al. (1991), who demonstrated an inverse relationship between FCI value and A/C. The decreased FCI value indicated that the proportion of the TST that is recycled decreased from the early to the late period. Considering that the food composition of each consumer was almost unchanged during culturing, the decreased FCI may explain the decreased FML during the entire culture period. The decreased FML also indicated a simplification of the food web structure.

4.4 Ecosystem Optimization

The polyculture system structure changed gradually to an ecosystem with larger size and higher level of organization from the early to middle and late periods. However, the overly increased TST and AMI may jeopardize the stability of ecosystem structure (Ulanowicz, 2003). It was demonstrated that the introduction of *R. philippinarum* may improve H through increasing total energy flow pathways (Feng et al., 2018a); improved H will decrease the AMI and increase system resilience (Ulanowicz, 2004). Moreover, as *R. philippinarum* was not food-limited in the late period, increasing the biomass of *R. philippinarum* may increase the *EE* value of pico-phytoplankton, thereby increasing the energy utilization of primary production. As a result, increasing the stocking density of *R. philippinarum* to maintain higher biomass may be an effective way to optimize such polyculture ecosystems.

Large amounts of detritus energy were accumulated in the group of detritus in sediment. Increased detritus accumulation may cause deterioration of the bottom environment of the pond ecosystem, which would further affect growth of organisms, especially the cultured organisms (Lin et al., 2005). In the present study, energy flow from pico-phytoplankton contributed the largest part of the total energy flow to the detritus. As the growth of phytoplankton was mainly supported by inorganic nutrients (Ban et al., 2015), introduction of macro-algae at a suitable biomass into this ecosystem may help absorb superfluous inorganic nutrients, thereby reducing phytoplankton production, detritus accumulation, and increase ecosystem stability. Moreover, macro-algae can also be used as aquatic products.

5 CONCLUSIONS

The dynamics of biomass composition, energy flow structure, and system function of *P. trituberculatus* was investigated by using the Ecopath model. This study illustrated that the growth of cultured organisms and aquaculture activities such as imported artificial food showed large impacts on the biomass structure of the polyculture ecosystem. *R. philippinarum* was considered to have a dominant influence on the phytoplankton community, which changed from nano- to pico-phytoplankton-dominated from the middle to the late period. Because of the increased primary production, imported artificial food, and consumption of the cultured organisms, the energy flow structure showed some remarkable changes from the early to the middle and late period, and large amounts of detritus energy were accumulated in the sediment in the late period. System network analysis indicated that ecosystem size and level of system organization increased from the early to the middle and late periods, whereas food web complexity and system resilience decreased from the early to the middle and late periods, which may indicate decreasing ecosystem stability. Increasing the stocking density of *R. philippinarum* may help increase the energy flow diversity of this ecosystem, which would also increase the system's resilience and energy utilization. Moreover, introducing macro-algae to this ecosystem may help reduce superfluous inorganic nutrients, which may decrease phytoplankton production and detritus accumulation. These two measures are thus proposed to optimize such ecosystems.

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.

AUTHOR CONTRIBUTIONS

JF carried out the experiments, constructed the models and drafted the manuscript. X-LT and S-LD contributed to the design of the experiment and revised the manuscript. R-PH, KZ, and D-XZ prepared materials and carried out the experiments. D-XZ and Q-QZ revised the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/articles/10.3389/fmars.2022.873643/full#supplementary-material

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