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A mass balanced model of trophic structure and energy flows of a semi-closed marine ecosystem

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Abstract

The marine ecosystem of the Jiaozhou Bay has degraded significantly in fisheries productivity and its ecological roles as spawning and nursery ground for many species of commercial importance has been declining in recent years. A mass-balanced trophic model was developed using Ecopath with Ecosim to evaluate the trophic structure of the Jiaozhou Bay for improving ecosystem management. The model were parameterized based on the fisheries survey data in the Jiaozhou Bay in 2011, including 23 species groups and one detritus group according to their ecological roles. The trophic levels of these ecological groups ranged from 1 (primary producers and detritus) to 4.3 (large demersal fishes). The estimated total system throughput was 12 917.10 t/(km^2·a), with 74.59% and 25.41% contribution of the total energy flows from phytoplankton and detritus, respectively. Network analyses showed that the overall transfer efficiency of the ecosystem was 14.4%, and the mean transfer efficiency was 14.5% for grazing food chain and 13.9% for detritus food chain. The system omnivory index (SOI), Finn's cycled index (FCI) and connectance index (CI) were relatively low in this area while the total primary production/total respiration (TPP/TR) was high, indicating an immature and unstable status of the Jiaozhou Bay ecosystem. Mixed trophic impact analysis revealed that the cultured shellfish had substantial negative impacts on most functional groups. This study contributed to ecosystem-level evaluation and management planning of the Jiaozhou Bay ecosystem.

Key words: Ecopath with Ecosim, Jiaozhou Bay, energy flow, trophic structure

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1 Introduction

Coastal ecosystems are productive and critical to the functioning of the earth's life-support system (Costanza et al., 1998). Coastal ecosystems provide ecological services such as nursery grounds for fish, water purification and various economic services such as support for fisheries and tourism, which are critical for human living. However, many coastal ecosystems are highly susceptible to anthropogenic perturbation (Byron et al., 2011a). Human activities such as fishing not only remove target species directly, but also change marine sediment habitat (Jennings and Kaiser, 1998) and affect other organisms in the ecosystem through biological interactions such as predation and food competition (Pauly et al., 1998; Hobday et al., 2011; Bacalso and Wolff, 2014). Fisheries crises have been acknowledged worldwide with the increasing capacity of industrial fisheries. Recent studies have paid attention to ecosystem-based management (EBM) as a promising strategy for current fisheries crises (Witherell et al., 2000; Cury et al., 2005; Greenstreet and Rogers, 2006; Garcia et al., 2012), which explicitly considers the interactions between exploited marine species and their biotic and abiotic environment to define management strategies (Grüss et al., 2015). Ecological models that deal with trophic interactions among multiple fisheries species play pivotal roles in supporting EBM.

Understanding the status of ecosystems and quality the trophic flow between each trophic group is necessary to evaluate the effect of human activities and management strategies. Various ecosystem models have been used for supporting ecosystem-based fisheries management, e.g., Atlantis model (Fulton et al., 2004), OSMOSE (Shin and Cury, 2004), Ecopath with Ecosim model (Christensen and Walters, 2004) and size-spectrum model (Andersen and Beyer, 2015). The Ecopath modeling approach has been widely applied to inform ecosystem-based management (Link et al., 2009; Guo et al., 2013; Colléter et al., 2015). The relative simplicity of Ecopath modelling, moderate data requirements, and flexibility to accommodate future updates in inputs make it a very useful ecosystem modelling tool to generate information on the overall structure and functioning of a variety of marine ecosystems (Bacalso and Wolff, 2014). The Ecopath model is based on the mass-balance of trophic interactions among all the functional groups (Panikkar and Khan, 2008) and quantifies energy flow between trophic levels to measure the ecosystem stability and resilience (Christensen and Walters, 2004).

This study built a mass-balanced model to evaluate the ecological characteristics of a temporal, semi-enclosed marine ecosys-

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tem, using the Jiaozhou Bay, China as an example. This bay used to be productive and of high diversity, with more than 100 fish species recorded in the 1980s (Liu, 1992). It was reported to be an important spawning and nursery ground for more than 40 juvenile fish species captured, including many commercially important species such as *Sebastes schlegeli* and *Pseudopleuronectes yokohamae* (Zeng et al., 2012). However, currently the Jiaozhou Bay is widely influenced by human perturbations such as transportation, coastal engineering and land reclaiming. In addition, the Jiaozhou Bay also hosts intensive shellfish farming, which occupied nearly 20% area of the bay and has reached of an annual production nearly 0.3 million tons (Guo et al., 2012). The fishery resources in the Jiaozhou Bay ecosystem have declined significantly in recent years. The number of fish species has decreased sharply compared to the literature of the past 30 years, with 57 fish species caught from a seasonal bottom trawl survey in 2011 (Han et al., 2015). The ecosystem has been dominated by small demersal fishes, such as *Amblychaeturichthys hexanema* and *Chaeturichthys stigmatias* (Mei et al., 2010). The degradation of fishery resources in the Jiaozhou Bay ecosystem gives rise to an urgent need for scientific managements based on solid ecological considerations.

We used the Ecopath approach to model the structure of the food web in the Jiaozhou Bay. The objectives of this study are to quantify the trophic web structure and to evaluate the status and ecological properties of the ecosystem. The ecological mode of Jiaozhou Bay could be used for better understanding the ecological characteristics of semi-closed marine ecosystem and future management planning.

2 Methods and materials

2.1 *Data collection*

The Jiaozhou Bay is situated in the southern Shandong Peninsula of China, connecting with the Yellow Sea through a narrow mouth and with a mean water depth of 7 m (Wang, 1993). This bay is a typical, semi-enclosed bay covers an area of 350 km^2. It provides feeding, spawning and nursery ground for many commercial marine species, such as *Paralichthys olivaceus*, *Liza haematocheila*, and *Konosirus punctatus* (Liu, 1992). As an important shellfish farming area, the dominant species grown in this bay is Manila clam (*Ruditapes philippinarum*), and small quantities of oyster (*Crassostrea ariakensis*).

Data were collected from four seasonal bottom-trawl surveys in the Jiaozhou Bay (35°59′–36°07′N, 120°13′–120°23′E) during winter (February), spring (May), summer (August), and autumn (November) in 2011. Because most inshore areas in the Jiaozhou Bay with a water depth less than 5 m are allocated to shellfish aquaculture, sampling stations were sited outside this area. The survey employed a stratified random sampling design with strata defined by embayment degree. The sampling area was divided into three parts based on the embayment degree: inner bay, bay mouth and outer bay (Fig. 1). During each survey, a total of 12 sampling stations were randomly selected, and the number of stations per stratum was five, three and four, respectively. The surveys were conducted in the daytime using a 10-mm stretched mesh cod-end, with a tow duration of 30 min at a speed of ~2 knots/h.

2.2 *Mass-balanced modeling approach*

A mass-balanced trophic model was constructed using the Ecopath with Ecosim software, Version 6.4 (Christensen et al., 2005). The model includes a set of linear equations that describe

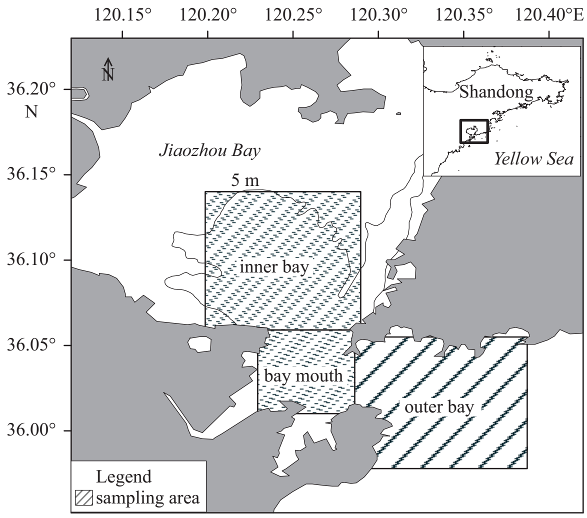

Fig. 1. Sampling areas in the Jiaozhou Bay.

mass balance over a given time, which can be expressed as follows:

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i = \sum_{j=1}^{j} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij} + Y_i + BA_i + E_i,$$

where B_i and B_j represent the biomass of Groups i and j, respectively; $(P/B)_i$ is the production/biomass ratio of Group i, which is equal to the instantaneous rate of total mortality; $(Q/B)_j$ is the consumption/biomass ration for predator Group j; EE_i (ecotrophic efficiency) can be described as the proportion of the production of Group i that is utilized in the ecosystem; DC_{ij} is the fraction of prey i in the diet of predator j; Y_i is the fishery yield of Group i; BA_i and E_i is the biomass accumulation rate and net migration rate, respectively.

For each functional group, the DC_{ij} and at least three out of the four parameters B, P/B, EE and Q/B must be provided to build the model, and other parameters can be estimated in the model.

The food web of the Jiaozhou Bay was divided into 24 functional groups based on their ecological and biological features such as feeding type and habitat preference (Table A1). The functional groups included detritus, phytoplankton, zooplankton, five groups of benthic organisms, three groups of cephalopod, mantis shrimp, shrimp, crab, and ten groups of fishes. The initial biomass of fish and cephalopod was estimated by swept-area method based on the four seasonal bottom trawl surveys in 2011. The mean biomass in these seasons was used to represent the annual average biomass for each species. The biomass of benthic invertebrate, zooplankton and phytoplankton were obtained from published literatures (Sun et al., 2000, 2011; Sui et al., 2010). The EE_i of majority groups were estimated by the model while an EE value of 0.95 was used for the functional groups of small pelagic fish, small benthic fish, small demersal fish and cultured shellfish.

The P/B and Q/B referred to published literature or other Ecopath models in similar ecosystem (Pranovi et al., 2003; Li et al., 2009; Ouyang and Guo, 2010; Nuttall et al., 2011; Liu et al., 2012, 2014; Wu et al., 2012; Lin et al., 2013; Torres et al., 2013). Diet composition of most fish groups were weight average based on individual species diet composition calculated by stomach contents analysis of samples collected by four seasonal bottom trawl survey in 2011. A total of 31 fish species were analyzed in this study, accounting for 84.77% of total fish species biomass. Diet information of other groups was derived from Fishbase and previous literatures (Deng et al., 1988; Xu et al., 1996; Cheng and Zhu, 1997; Yang and Tan, 2000; Yang, 2001; Xue et al., 2004; Zhang, 2007; Suh and Shin, 2013). The diet composition matrices of the model are shown in Table A2.

The yield data of cultured shellfish was obtained from official statistics. For other groups, the yield data were calculated by the following equation:

$$Y = BF,$$

where Y, B and F represent yield, biomass and fishing mortality, respectively. The biomass values B were calculated from survey data, and the fishing mortality obtained from the relevant studies in the Jiaozhou Bay and adjacent area (Liu et al., 2012, 2014; Lin et al., 2013).

When all the necessary parameters were obtained, the model could be balanced by checking: (1) the *EE* value for each group is less than 1; (2) the P/Q values of most groups are physiologically realistic (within 0.1–0.3). The input data with high uncertainty were modified following Christensen et al. (2005), especially for diet composition and parameters obtained from areas other than the Jiaozhou Bay. A "Pedigree" routine was used to quantify the uncertainties of input parameters of Ecopath model (Christensen and Walters, 2004).

The imprecise data inputs, especially for biomass and P/B, could lead to greater variation in prediction errors (Essington, 2007). A simple sensitivity analysis was used to evaluate the robustness of model predictions to small variations in input data. The biomass and P/B of function groups varied in steps of 10% from –50% to 50% and the impact of the changes on other parameters was assessed by a proportion, which is given as the ratio (estimated parameter-original parameter)/original parameter.

2.3 *Network analysis*

After balancing the model, ecological analysis integrated in Ecopath with Ecosim was used to understand trophic structure and function of the Jiaozhou Bay ecosystem. The definitional trophic level of primary producer and detritus was assigned to 1 and the trophic level of consumers was 1+[the weighted average of preys' TLs]. Multiple indicators were used to analyze the trophic structure:

(1) Trophic interactions between groups were represented by ecotrophic efficiency (*EE*).

(2) The Omnivory index (OI) of groups was defined as the variance of the trophic level of its prey groups. The zero value of OI indicated specialized predator while a higher value indicated a consumer feeding upon multiple trophic levels.

(3) The mixed trophic impact (MTI) routine was used to quantify direct and indirect trophic effects among functional groups, which indicates the effects that a small change in the biomass of a function group will have on the biomass of other groups in a system (Ulanowicz and Puccia, 1990).

(4) The overall status of the Jiaozhou Bay ecosystem was evaluated by the model's global indices, including: total consumption, export, respiration, total system throughput (TST), and primary production. Additional indices, such as total primary production/total respiration (TPP/TR), total primary production/total biomass (TPP/TB), connectance index (CI), system omnivory index (SOI) and Finn's cycling index (FCI) were also calculated to examine the maturity of the Jiaozhou Bay ecosystem.

3 Results

3.1 *Trophic structure*

The basic input values and the output parameters estimated by Ecopath for the Jiaozhou Bay ecosystem model were shown in Table A3. The pedigree index value of the final balanced model was 0.47, lying in the upper range of 150 previous Ecopath models (Morissette et al., 2006). And the measure of fit is 2.44 in this model, indicating that the model was robust with high confidence (Christensen and Walters, 2004). Sensitivity analysis revealed the impact of altering input parameters on the output parameters. In this study, the largest impact of one parameter on another usually happened within the same group. For example, 20% decrease of P/B ratio of aquaculture shellfish resulted in 25% increase of shellfish biomass. In contrary, changing parameters for one group had a slight impact on other groups. Take mantis shrimp for instance, a 50% change of biomass for mantis shrimp had a 14% impact on the *EE* of crab, and a 19% impact on the *EE* of shrimp (Fig. 2).

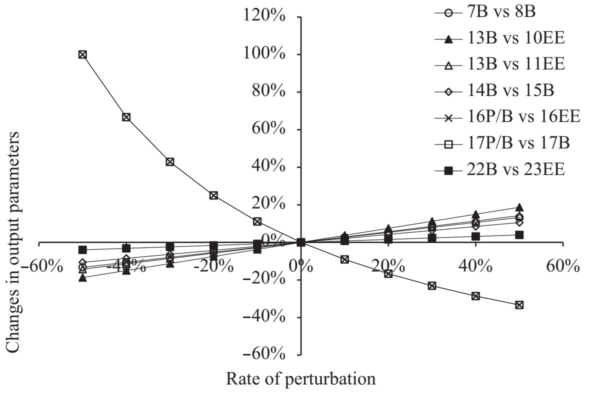

Fig. 2. Partial sensitivity analysis of Ecopath model for the Jiaozhou Bay ecosystem. *X*-axis shows the rate of perturbation and *Y*-axis the rate of change of the model outputs.

The estimated trophic levels of each functional group ranged from 1 (phytoplankton and detritus) to 4.29 (large benthic fish). The second TL comprised all benthic invertebrate and zooplankton. Gizzard shad (*Konosirus punctatus*) showed the lowest TL in fish community. The TLs of other fishes, mantis shrimp and cephalopods were larger than 3 and the piscivorous fish such as large benthic fish and large demersal fish occupies the top trophic level in the Jiaozhou Bay ecosystem.

EE values of most fishes, crustacean, and cephalopoda were higher than 0.5, especially for gunnel (*Pholis fangi*, 0.998) and pinkgray goby (*Amblychaeturichthys hexanema*, 0.907). In contrast, echinoderm showed extraordinarily low *EE* value (0.026), followed by demersal mollusca and polychaetes. The *EE* values of phytoplankton and detritus were 0.038 and 0.109, respectively. The OI of fishes ranged from 0.05 to 0.33, and the highest OI were obtained from mantis shrimp (0.54), indicating the multi-trophic level feeding strategies of mantis shrimp. Shellfish had an OI of 0, as this group only feeds on phytoplankton and detritus.

3.2 *Food chains and transfer efficiencies*

Detrital based food chain and grazing food chain are two main types of food chains in the Jiaozhou Bay ecosystem. Phytoplankton contributed 74.59% of total flow and detrital contributed 25.41%. There were 2 418 t/(km²·a) matter flowing to trophic level 2 in the grazing food chain, compared with 823.7 t/(km²·a) in the detrital food chain (Fig. 3).

The transfer efficiencies from TL2 to TL5 in the grazing food chain of the Jiaozhou Bay ecosystem were 23.8%, 12.5% and 10.2%, respectively, and transfer efficiencies were 19.7%, 9.6% and 14.0% in the detrital food chain, respectively. Mean transfer efficiencies are 14.5% and 13.9% for the grazing food chain and detrital food chain, respectively. The geometric mean of the trophic transfer efficiency for the Jiaozhou Bay ecosystem was 14.4% (Fig. 3).

3.3 *Trophic interactions*

Direct and indirect trophic interactions between different functional groups were analyzed using the "mixed trophic impact" routine in EwE. Detritus, phytoplankton and zooplankton had a largely positive influence on most other function groups (Fig. 4). Small pelagic fishes had strong positive impact on the Pacific mackerel; shrimps had strong positive impact on the large benthic fishes and large demersal fishes. Small demersal fishes had a negative impact on pinkgray goby because they both mainly fed on shrimp. Human activities substantially influenced most functional groups in the ecosystem. Specifically, the cultured shellfish had negative impacts on most functional groups, and fishing activities had negative impacts on large demersal fish

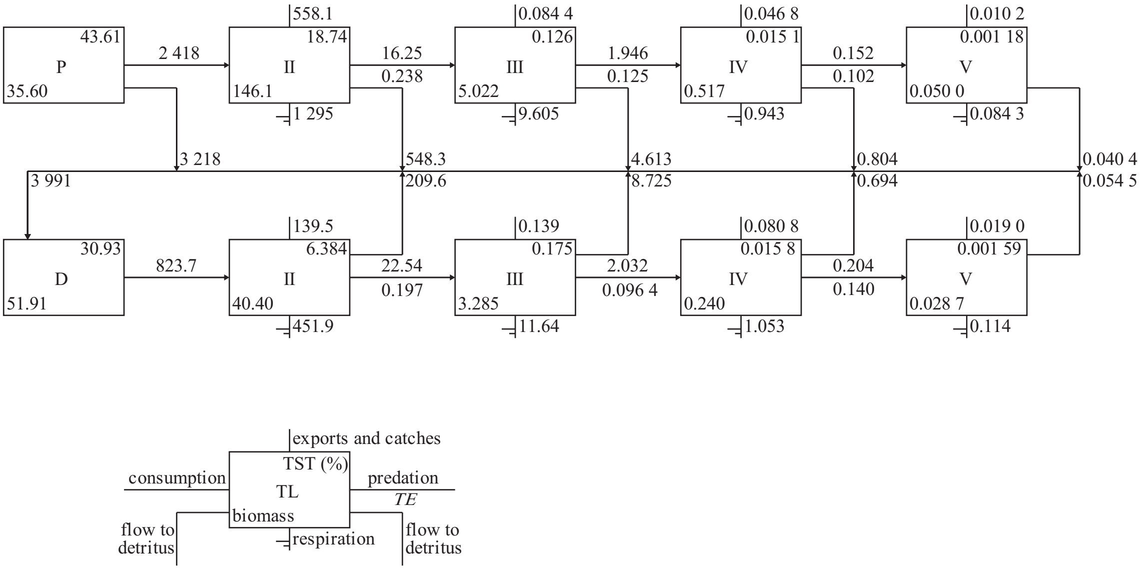

Fig. 3. A Linderman spine of the Jiaozhou Bay ecosystem model: flows between trophic levels. P represents primary producer and D detritus.

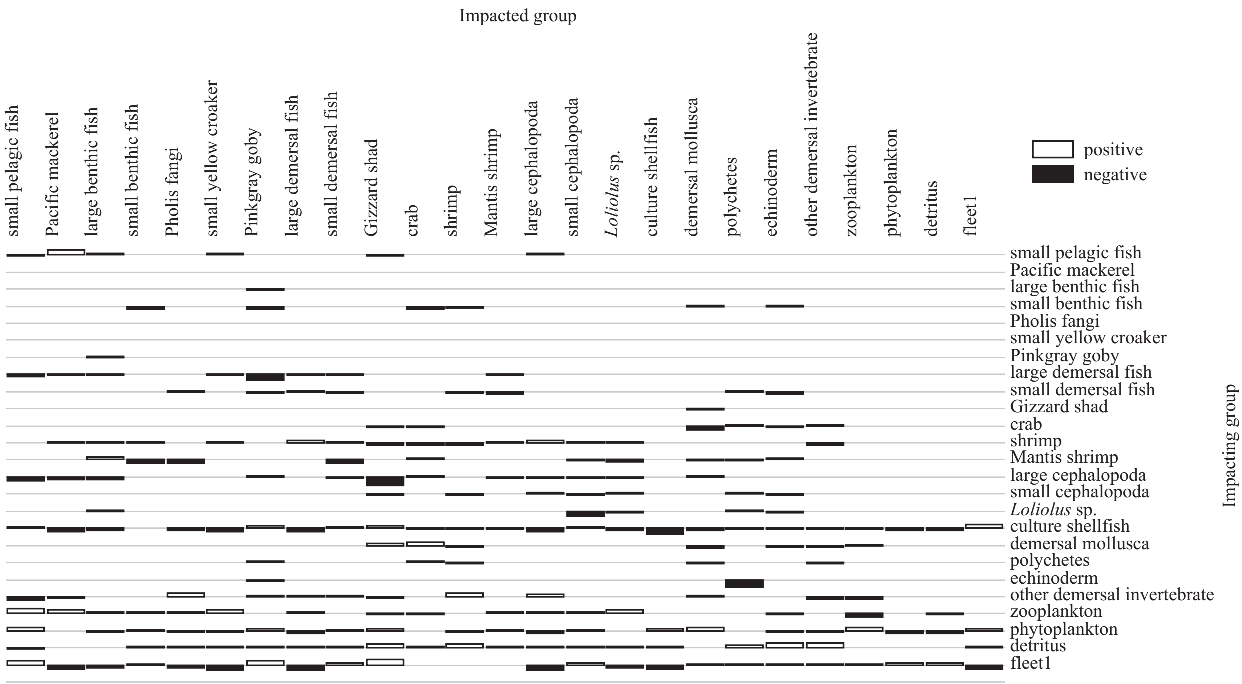

Fig. 4. Mixed trophic impacts between functional groups in the Jiazhou Bay ecosystem.

such as small yellow croaker and large cephalopoda while positive influence on small pelagic fish, such as pinkgray goby and gizzard shad.

3.4 *Ecosystem status*

The total system throughput of the Jiaozhou Bay ecosystem was 12 917.1 t/(km²·a), of which 22.54% derived from consumption (3 299.58 t/(km²·a), 29.85% from exports (3 855.53 t/(km²·a)), 13.71% from respiration (1 770.69 t/(km²·a)), and 30.90% eventually flowed into detritus (3 991.30 t/(km²·a)) (Table 1). The total net primary production and the total biomass were 5 626.22 t/(km²·a) and 187.28 t/(km²·a), respectively. The ratio of total primary production/total respiration and total primary production/total biomass were 3.18 and 30.04, respectively. The CI and SOI for the Jiaozhou Bay ecosystem were 0.31 and 0.16 respectively. FCI and Finn's mean path length calculated by the model were 2.47% and 2.30, respectively.

4 Discussion

The present paper describes the trophic structure of the Jiaozhou Bay ecosystem. The trophic levels of different functional groups in the Jiaozhou Bay ecosystem ranged from 1 (phytoplankton and detritus) to 4.29 (large benthic fishes). Besides the primary producer, the second TL comprised all benthic invertebrate and zooplankton, which were characterized by detritus and phytoplankton diet habits. Large benthic fish and demersal fish had the highest TLs, as these species mainly fed on crustaceans and other fishes. In general, TLs for most groups were similar to those previous studies in the adjacent areas and other temperate ecosystems (Wu et al., 2012; Lin et al., 2013; Zhang et al., 2013), suggesting that these groups have similar trophic roles in these ecosystems. It should be noted that Gizzard shad had the lowest TL in among all fish species as a result of the large proportion of detritus and phytoplankton diet.

In the sensitivity analysis, the largest impact of one input parameter on estimate parameter usually happened within the same group. This could be easily understood that the Ecopath master equation seeks model solutions that balance total production to total losses. Thus, error in these input variables translated directly into error in estimated values of same groups, and affected the estimated values of other groups indirectly (Essington, 2007). Generally speaking, the sensitivity of estimated parameters to changes in the input parameters of different groups depended on the degree of trophic connection between those groups (Chen et al., 2008). In the Jiaozhou Bay ecosystem, the high SOI make changing parameters for one group had a slightly impact on other groups, which indicated that the Jiaozhou Bay Ecopath model was robust to uncertainty in the input parameters.

The *EE* values of many functional groups were high in the Jiaozhou Bay ecosystem, including both large predator species groups such as pacific mackerel, large demersal fishes, large cephalopoda and mantis shrimp, as well as prey groups, such as gunnel, pinkgray goby, and shrimp. The results implied a high predation mortality and fishing pressure on the nekton species in the Jiaozhou Bay ecosystem. For example, 83.7% of shrimp production was used in the ecosystem, of which 80.2% was consumed by fish groups. Shrimp was the most important forage species of many fishes, such as *Synechogobius ommaturus*, *Amblychaeturichthys hexanema*, and *Pholis fangi* (Han et al., 2013; Li et al., 2014). The *EE* value of phytoplankton and detritus were also high, indicating that a major fraction of these primary producers were consumed. This pattern could be largely attributed to the high biomass of cultured shellfish, which occupy 63.24% of total biomass of the Jiaozhou Bay ecosystem and consumed great, amounts of phytoplankton and detritus. In contrast, most benthic invertebrate groups had remarkably low *EE* values, for example, the *EE* of demersal mollusa and echinoderm was 0.04 and 0.03, respectively, indicating that a large proportion of these groups were not consumed by high trophic levels but rather contributed to detritus. This is ascribed to the low level of ecological functioning of the benthic feeding groups. The biomass of benthic feeding groups including small benthic fish and small

Table 1. Summary statistics for the Jiaozhou Bay ecosystem

Parameter	Units	Value
Sum of all consumption	t/(km²·a)	3 299.58
Sum of all exports	t/(km²·a)	3 855.53
Sum of all respiratory flows	t/(km²·a)	1 770.69
Sum of all flows into detritus	t/(km²·a)	3 991.30
Total system throughput	t/(km²·a)	12 917.10
Sum of all production	t/(km²·a)	6 495.19
Mean trophic level of the catch		2.00
Gross efficiency (catch/net p.p.)		0.12
Calculated total net primary production	t/(km²·a)	5 626.22
Total primary production/total respiration		3.18
Net system production	t/(km²·a)	3 855.53
Total primary production/total biomass		30.04
Total biomass/total throughput	a^{-1}	0.01
Total biomass (excluding detritus)	t/km²	187.28
Total catch	t/(km²·a)	698.01
Connectance Index		0.31
System Omnivory Index		0.16
Finn's cycling index	% (of total throughput)	2.47
Finn's mean path length		2.30
Ecopath pedigree index		0.47
Measure of fit, t*		2.44

Note: p.p. means primary production.

demersal fish were substantially low, occupying only 0.13% of total biomass in the Jiaozhou Bay.

As an important shellfish farming ground, the density of shellfish in the Jiaozhou Bay was 118.438 t/km^2, much higher than those of other similar ecosystems with shellfish farming, such as Puget Sound, Rhode Island and Venile lagoon (Pranovi et al., 2003; Byron et al., 2011b; Ferriss et al., 2016). Our study showed that the intensive shellfish farming may have significant impact on the trophic structure of the Jiaozhou Bay. For example, mixed trophic impact analysis indicated a negative impact of culture shellfish on other groups. Mean transfer efficiency of the Jiaozhou Bay ecosystem was 14.4%, which was higher than the 10% assumed by Lindeman (1942), to which the comsumption of shellfish has made large contribution. The highest TE was observed between TL2 and TL3 (23.8%), which was much higher than those of temperate ecosystems, such as 11.2% of Lidao Island ecosystem (Wu et al., 2012), 8.6% of the Bohai Sea (Lin et al., 2009) and 5.0% of the southern Yellow Sea (Lin et al., 2013). The high TE of TL2–TL3, corresponding to the large biomass and high *EE* value of cultured shellfish. Similar phenomena were also observed in other ecosystems which the shellfish farming was active, for instance the Monte Saint Michel Bay (Leloup et al., 2008), Golden and Tasman Bay (Jiang and Gibbs, 2005). In contrast, the TE between TL3 and TL4 dropped to 10.8%, much lower than 21.3% of the Bohai Sea (Lin et al., 2009) and 18.5% of the Yellow Sea (Lin et al., 2013). The low biomass of top predators in the Jiaozhou Bay was probably one reason. We found that the Jiaozhou Bay trophic network was separated into two partly disconnected trophic sub-systems. One is a short shellfish farming chain (TL2) with high biomass, and the other is a residual "natural" unstable system with relatively low biomass.

Our results suggested that the Jiaozhou Bay ecosystem was in an unstable state. Specifically, primary producer and detritus-based food chains are important components in aquatic ecosystems (Christensen and Pauly, 1993). Studies suggested that a mature ecosystem may depend more on the detritus pathway (Odum, 1969), whereas in the Jiaozhou Bay ecosystem, the producer was the most important food source. Secondly, TPP/TR and NSP are also related to the maturity of ecosystem (Odum, 1969; Christensen, 1995). In a mature ecosystem, the value of TPP/TR should be close to 1 and the NSP should be close to 0 (Christensen, 1995). The value of TPP/TR in the Jiaozhou Bay ecosystem was much larger than 1 (3.18) and NSP is larger than 0, which confirmed the under development stage of the Jiaozhou Bay ecosystem. However, it should be noted that TPP/TR may be overestimated when the decomposer organisms were ignored in the model (Christensen and Pauly, 1993). In addition, FCI represents the fraction of an ecosystem's throughput that is recycled compared to total system throughput (Finn, 1976), a measurement correlated with ecosystem stability. The FCI value of 2.47% in the Jiaozhou Bay ecosystem was low compared with those given by Lin et al. (2013) for the southern Yellow Sea and Wu et al. (2012) for the Lidao Island, but was similar with the reports for the Maine Gulf (Zhang and Chen, 2007) and Gulf of Cadiz (Torres et al., 2013). Besides, the SOI and CI of an ecosystem which are related to the complexity of food web (Odum, 1971), were similar to other immature ecosystems such as the southern Yellow Sea (Lin et al., 2013), Gulf of Mexico (Geers et al., 2016) and the Lidao Island ecosystem (Wu et al., 2012). In general, the evidence indicated that the food web of the Jiaozhou Bay ecosystem is rather linear like and the ecosystem was unstable.

In summary, we found that this semi-closed bay had a high primary production, immature state, and the intensive aquaculture activities might have substantial effects on this ecosystem. The high primary production implies that the Jiaozhou Bay ecosystem can still support a considerable fisheries resource, however, the current trophic structure has largely diminish the potential. The very pattern arises the urgency for proper ecosystem management in this bay based on deeper understanding the ecological interactions within ecosystem, as provided by this study. Besides, the ecological influences of intensive aquaculture should be seriously considered in making management plans. Further studies are needed to simulate and evaluate the influence of shellfish aquaculture on the trophic structure of the Jiaozhou Bay to provide important information for the management of shellfish aquaculture.

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Appendix:

Table A1. Functional groups of the Jiaozhou Bay in the Ecopath ecosystem model

No.	Function group	Dominant species composition
1	Small pelagic fish	*Thryssa chefuensis*, *Thryssa mystax*
2	Pacific mackerel	*Pneumatophorus japonicus*
3	Large benthic fish	*Platycephalus indicus*, *Trichiurus lepturus*, *Nibea albiflora*
4	Small benthic fish	*Azuma emmnion*, *Argyrosomus argentatus*, *Pampus argenteus*, *Sillago sihama*, *Sillago japonica*
5	Gunnel	*Pholis fangi*
6	Small yellow croaker	*Pseudosciaena polyactis*
7	Pinkgray goby	*Amblychaeturichthys hexanema*
8	Large demersal fish	*Sebastes schlegelii*, *Hexagrammos otakii*, *Conger myriaster*, *Synechogobius ommaturus*
9	Small demersal fish	*Liparis tanakai*, *Johnius belangeri*, *Sebastes hubbsi*, *Cynoglossus lighti*
10	Gizzard shad	*Konosirus punctatus*
11	Crab	*Charybdis bimaculata*, *Charybdis japonica*, *Enoploambrus valida*, *Dorippe japonica*
12	Shrimp	*Trachysalambria curvirostris*, *Parapenaeopsis tenella*, *Palaemon gravieri*, *Alpheus japonicus*
13	Mantis Shrimp	*Oratosquilla oratoria*
14	Large cephalopoda	*Octopus variabilis*, *Octopus ochellatus*
15	Small cephalopoda	*Sepiola birostrata Sasaki*, *Euprymna morsei*
16	Squid	*Loliolus* sp.
17	Culture shellfish	*Ruditapes philippinarum*, *Sinonovacula constricta*
18	Demersal mollusca	*Rapana venosa*, *Pleurobranchaea maculata*, *Atrina pectinata*, *Philine kinglippini*
19	Polychaetes	
20	Echinoderm	*Asterias rollestoni*, *Asterias amurensis*, *Temnopleurus hardwickii*
21	Other demersal invertebrate	*Urechis unicinctus*, Gammarid, Isopoda
22	Zooplankton	Copepoda, Cladoceran, Mysid, Acetes, fish egg
23	Phytoplankton	Bacillariophyta, Dinophyta, Chrysophyta, Cyanophyta
24	Detritus	

Table A2. Diet composition of function groups in the Jiaozhou Bay ecosystem

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1		0.500	0.100			0.100		0.050						0.080								
2																						
3														0.001								
4			0.030	0.038		0.011		0.103	0.020				0.080	0.050								
5			0.010			0.010		0.003					0.030	0.010								
6								0.000														
7			0.100	0.006		0.020		0.068	0.000													
8								0.000	0.000													
9			0.150	0.001	0.012	0.039	0.007	0.150	0.026	0.009			0.070	0.100								
10								0.000						0.010								
11			0.020	0.070	0.001	0.080	0.013	0.065	0.013		0.005	0.005										
12	0.090	0.230	0.200	0.300	0.143	0.230	0.337	0.300	0.330		0.050		0.200	0.245	0.230	0.150						
13			0.300			0.005	0.000	0.106	0.041					0.050								
14								0.001														
15		0.040				0.020		0.000	0.000				0.050	0.125	0.003	0.150						
16		0.050	0.090			0.015		0.020					0.040	0.050								
17																						
18				0.050	0.063		0.114	0.050	0.103	0.249	0.400		0.100	0.068								
19	0.005	0.030		0.080	0.064	0.020	0.189	0.053	0.097		0.205	0.001	0.030							0.074		
20					0.000			0.010	0.065		0.050			0.061	0.050	0.050						
21	0.005			0.102	0.428	0.050	0.140	0.020	0.130	0.100	0.090	0.640	0.050	0.150	0.203	0.150		0.100	0.050	0.150		
22	0.900	0.150		0.353	0.279	0.400	0.200		0.171	0.007		0.100	0.250		0.514	0.500				0.067	0.150	0.048
23					0.009				0.002	0.035		0.054					0.800	0.700	0.150	0.047	0.050	0.619
24										0.600	0.200	0.200	0.100				0.200	0.200	0.800	0.662	0.800	0.333

Table A3. Input and estimated parameters (in bold) for the Ecopath model of the Jiaozhou Bay

No.	Group name	TL	B/t·km^{-2}	*P*/*B* (per year)	*Q*/*B* (per year)	EE	P/Q	OI
1	Small pelagic fishes	3.123	**0.025**	2.370	11.650	0.950	0.203	0.053
2	Pacific mackerel	3.888	0.000	1.370	11.040	**0.730**	0.124	0.172
3	Large benthic fish	4.286	0.004	0.850	4.560	**0.478**	0.186	0.062
4	Small benthic fish	3.431	**0.126**	1.480	6.600	0.950	0.224	0.192
5	Gunnel	3.224	0.030	2.790	7.540	**0.998**	0.370	0.103
6	Small yellow croaker	3.580	0.003	1.150	5.910	**0.567**	0.195	0.264
7	Pinkgray goby	3.367	0.018	1.590	7.350	**0.907**	0.216	0.145
8	Large demersal fish	4.044	0.040	2.060	7.050	**0.701**	0.292	0.204
9	Small demersal fish	3.491	**0.120**	1.600	6.580	0.950	0.243	0.218
10	Gizzard shad	2.423	0.018	0.600	28.900	**0.325**	0.021	0.328
11	Crabs	2.936	0.068	3.500	12.000	**0.595**	0.292	0.250
12	Shrimps	2.857	0.205	8.000	28.000	**0.837**	0.286	0.254
13	Mantis Shrimp	3.480	0.137	1.340	7.430	**0.678**	0.180	0.542
14	Large cephalopoda	3.893	0.050	2.000	7.000	**0.695**	0.286	0.250
15	Small cephalopoda	3.275	**0.073**	3.000	9.750	**0.950**	0.308	0.110
16	Squid	3.384	0.076	3.000	9.750	**0.753**	0.308	0.216
17	Culture shellfish	2.000	**118.438**	6.200	22.980	0.950	0.270	
18	Demersal mollusca	2.116	6.590	3.000	7.000	**0.038**	0.429	0.121
19	Polychaetes	2.058	2.780	6.730	23.350	**0.109**	0.288	0.064
20	Echinoderm	2.323	5.960	1.200	3.700	**0.026**	0.324	0.254
21	Other demersal invertebrates	2.157	14.390	1.570	8.600	**0.692**	0.183	0.141
22	Zooplankton	2.050	2.527	25.000	122.100	**0.587**	0.205	0.050
23	Phytoplankton	1.000	35.600	158.040	0.000	**0.428**		
24	Detritus	1.000	51.912			0.206		0.167