Vol. 11: 111–127, 2019
https://doi.org/10.3354/aei00284

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published March 14

Ecosystem attributes of trophic models before and after construction of artificial oyster reefs using Ecopath

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ABSTRACT: The deployment of artificial reefs (ARs) is currently an essential component of sea ranching practices in China due to extensive financial support from the government and private organizations. Blue Ocean Ltd. created a 30.65 km^2 AR area covered by oysters in the eastern part of Laizhou Bay, Bohai Sea. It is important for the government and investors to understand and assess the current status of the AR ecosystem compared to the system status before AR deployment. We provide that assessment, including trophic interactions, energy flows, keystone species, ecosystem properties and fishing impacts, through a steady-state trophic flow model (Ecopath with Ecosim). The model estimated values of 4721.2 and 4697.276 t km^{-2} yr^{-1} for total system throughput and 534.74 and –519.9 t km^{-2} yr^{-1} for net system production before and after AR deployment, respectively. After AR deployment, sea cucumber and oyster showed the same trophic level (TL = 2.0) while veined whelk *Rapana venosa* had TL = 3.0. The mean TL of catches was 2.484 after AR deployment and the primary production required to support fisheries (PPR) was 1104 t km^{-2}. Detritus production dominated over primary production and represented 73.82% (2530.82 t km^{-2}) of total primary production required. The sea cucumber showed the lowest PPR/catch value (5.6) among functional groups, indicating that fishing catch biomasses were close to primary production values. The total primary production to total respiration and total primary production to total biomass ratios showed higher system maturity after AR deployment. The trophic flow diagram showed 1 grazing and 2 detritus food chains. Pelagic and bottom fish and different benthic organisms, including large crustaceans and zoobenthos, were the dominant community before AR deployment. Zoobenthos was the key functional group, followed by large crustaceans and Gobiidae, which were the most important prey for top predators after AR deployment. We draw the following conclusions for the management of this area: (1) AR deployment contributes to the maturity of the improved ecosystem; (2) the artificial oyster system is similar to a natural reef system; (3) the enhancement and release of benthic animals in the AR area benefit the ecosystem; and (4) low TL catches do not cause the system to collapse.

KEY WORDS: Ecopath model · Artificial oyster reef · *Apostichopus japonicus* · *Rapana venosa* · Ecosystem properties · Sea ranching

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Publisher: Inter-Research · www.int-res.com

1. INTRODUCTION

Artificial reefs (ARs) are often used in sea ranching, and they are considered an effective fisheries management tool to improve impaired habitats (small-scale ecosystems) (Myoung & Park 2001, Sayer & Wilding 2002, Mustafa et al. 2003, Santos et al. 2006). ARs have been built to prevent destructive trawlers from accessing critical shelter, feeding and spawning grounds for commercially important fish species and to improve fisheries by increasing the harvest of sea cucumber, shellfishes and other fishes (Kakimoto et al. 2000, Freitas et al. 2006, Iannibelli & Musmarra 2008, Serrano et al. 2011).

ARs are human-made underwater structures (Baine 2001). They can influence nutrient cycling and transport (Falcão et al. 2007, Vicente et al. 2008) and sediment biogeochemistry (Alongi et al. 2008), with subsequent changes in community structure and richness of associated organisms (Langlois et al. 2006). Lowry et al. (2011) reported higher fish biomasses in reef areas compared to areas without reefs, with reef areas supporting larger numbers of fish. Although quantitative assessments of artificial ecosystems including ARs have been performed in Li Island, Rongcheng City, China (Wu et al. 2016) and Zhangzi Island, Dalian City, China (Z. Xu et al. 2016), few studies have compared ecosystem status before and after AR deployment.

Oysters are filter feeders that feed upon suspended particles in the water column. Their water pumping rates are so high that they are considered an important biofilter that helps maintain system functioning (Grizzle et al. 2006). The biogenic structure formed by vertically upright oyster aggregations creates habitat for dense assemblages of mollusks including oysters, polychaetes, crustaceans and other resident invertebrates (Lenihan et al. 2001, Dillon et al. 2015). Juvenile fish and mobile crustaceans also recruit to and utilize oyster reefs as a refuge and foraging grounds (Luckenbach et al. 2005, Rodney & Paynter 2006). Removal of filter-feeding oysters from estuaries such as in the Chesapeake Bay and Pamlico Sound, USA, resulted in trophic re-structuring that promoted planktonic and microbial organisms over demersal and benthic flora and fauna (Baird et al. 2004).

China's Bohai Sea ecosystem, one of the most intensively exploited areas in the world (Wigan 1998), is heavily degraded due to overfishing, pollution from inland areas and loss of biological habitat. Open-access and unregulated fisheries contribute to this deteriorating tendency and many small-scale fishermen still make a living through illegal fishing and use of destructive fishing gear in this region (Zhang et al. 2012, M. Xu et al. 2016, 2018a). In 2011, Blue Ocean Ltd. created a 30.65 km^2 AR area in the eastern part of Laizhou Bay in the Bohai Sea (see Fig. 1). The company re-organized the scattered small-scale fishermen into coordinated fishing operations and created fishery industries including stock release of the sea cucumber *Apostichopus japonicus* and stock enhancement of *Rapana venosa*. This is called 'Ze-Tan development pattern' in China (Yang 2016).

The marine biota and benthic environments of the area are extremely degraded due to continuous overfishing and bottom trawling fishing, which occurred in the eastern part of Laizhou Bay through 2010, before AR deployment. After AR deployment in 2011, oysters began to gradually colonize AR surfaces, and the abundance of economic species such as *Octopus* spp., *Sebastes schlegelii*, *Hexagrammos otakii*, *Charybdis japonica* and *R. venosa* began to increase. *A. japonicus* juveniles have been released into AR areas each year since 2013 and form an important fishery in this region. Feces produced by shellfish cultivations, which have been implemented in Laizhou Bay since the 1980s, provide large amounts of detritus to support sea cucumber growth.

In this paper, we constructed trophic models using the Ecopath approach to compare ecosystem status before (2010) and after (2016) AR deployment, and answer the following questions: (1) Did AR deployment contribute to the maturity of the improved ecosystem? (2) Is the artificial oyster system similar to a natural reef ecosystem? (3) Did the enhancement and release of benthic organisms in the AR area benefit the system? (4) Can low trophic-level catches cause the system to collapse? Trophic interactions, energy flows, keystone species, ecosystem properties and fishing impacts are presented to identify and compare energy and matter flows in non-AR versus AR areas in the study system.

2. MATERIALS AND METHODS

2.1. Study site

ARs were deployed in 2011 in the eastern part of Laizhou Bay, Bohai Sea, PR China (37° 15′–37° 22′ N, 119° 38′–119° 46′ E) (Fig. 1). Once deployed, the reefs were gradually colonized by pacific oyster *Crassostrea gigas*. Laizhou Bay is a semi-closed basin receiving the inflow of the Yellow River and is characterized by large areas devoted to shellfish cultivation.

The AR area is 30.67 km^2 and includes an *Apostichopus japonicus* catchment area of 5.34 km^2. The mean depth is ~6 m in the whole AR area.

2.2. Mass-balance modeling approach

The Ecopath approach and modeling software (Ecopath with Ecosim [EwE] version 6.5; www.ecopath.org; Christensen & Walters 2004) was used in this study to assess system structure and perform ecosystem trophic analysis.

The Ecopath model is based on the following equation:

$$B_i(P/B)_i = \sum_{j=1}^{n} B_j(Q/B)_j DC_{ji} + Y_i + B_i(P/B)_i \times (1 - EE_i)$$

where B_i and B_j are the biomasses of species (or species group) i and its predator j, $(P/B)_i$ is the production-to-biomass ratio of species i, $(Q/B)_j$ is the consumption per unit biomass of predator j and DC_{ji} is the proportion of species i in the diet of predator j. Y_i is the commercial catch for species i and EE_i is the ecotrophic efficiency of species i (the ratio between the biomass flowing out of a group and the biomass flowing in). We built one model representing the system before AR deployment and another model after AR deployment.

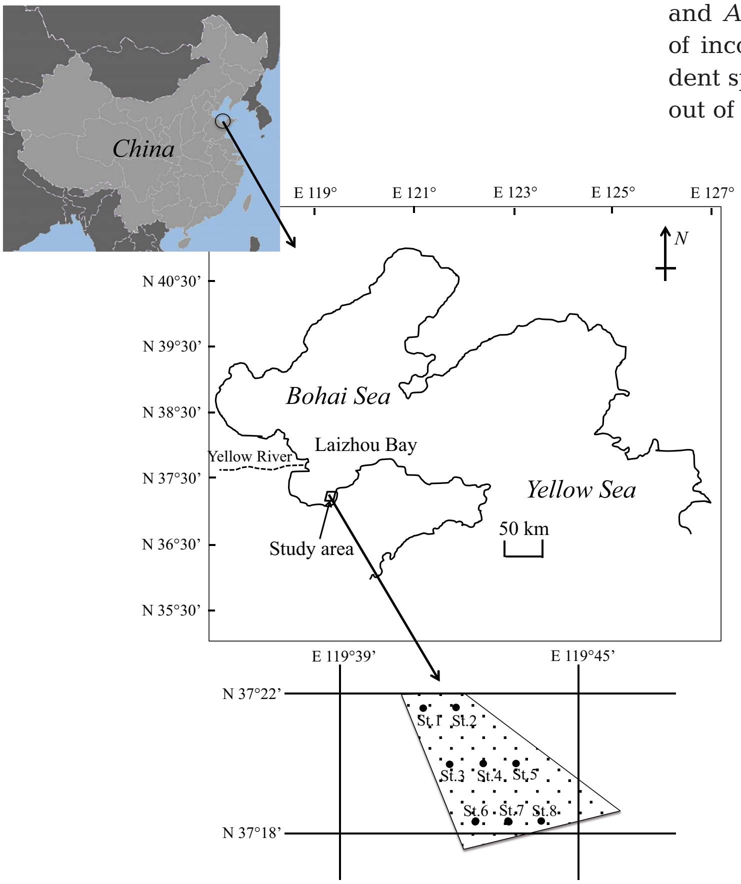

Fig. 1. Model domain in Laizhou Bay, Bohai Sea, PR China. The artificial reef area (~30.65 km^2) is denoted by a white trapezoid outlined in black in the nearshore zone of the bay. The Yellow River delta is located in the northwestern region of Laizhou Bay. The survey station is from Stn1 to Stn 8

2.3. Sampling and Ecopath input values

We collected functional group biomass data at 8 sampling stations across the AR area (ca. 30.65 km^2) (Fig. 1). Samples were collected in 2010 (before AR deployment) and in 2016 (after AR deployment). The main commercial fishing activities in this region include crab pot and diving fishing. Species fished via the crab pot method include benthic organisms such as members of Octopodidae and Gobiidae, *Sebastes schlegelii* and *Charybdis japonica*. Species fished via the diving method include *Rapana venosa* and *A. japonicus*, which represent the main source of income for local fishing communities. Most resident species are important because they feed in and out of the AR area and can therefore be regarded as immigration items when assessing diet composition. We used crab pots and trawl nets to collect functional group biomass data expressed as t km^{-2}. We used crab pots to quantify the biomass of *C. japonica* and trawl nets to estimate the biomass of several functional groups including large crustaceans, benthos, demersal fishes and Octopodidae. We connected five 8 m long crab pots at each survey station so that the total length of our crab pots was 40 m. A trawling survey was carried out at a speed of 2 knots using a trawl net with inner mesh size of 3.5 cm and mouth width of 2.5 m.

Phytoplankton biomass in terms of chlorophyll *a* (chl *a*) was measured using a Turner fluorometer according to standard procedures (Sandu et al. 2003). Zooplankton samples were collected across the water column by means of opening–closing bongo nets with a diameter of 37 cm and a mesh size of 0.03 mm. Zooplankton biomass was estimated by displaced volume according to Wiebe (1988). Oysters, *R. venosa* and *A. japonicus* were collected by SCUBA divers scraping them off 0.5 × 0.5 m^2 quadrats. Sampled organisms were counted and weighed to the nearest 0.1 g (Xu & Komatsu 2016, Xu et al. 2018b). Other functional groups were sampled through crab fishing and trawling. Fish and crustaceans were identified to the lowest possible taxonomic level, counted and weighed to the nearest 0.1 g wet weight.

The system was partitioned into functional groups based on preferred physical habitat, similar diet and other ecological similarities, such as inhabited water layer, taxonomic proximity and ecological role. Marine organisms were divided into 13 and 17 functional groups before and after AR deployment, respectively (Table 1). Functional groups spanned the main trophic components of the system and included target organisms of all the fishing activities operating in the area. Oysters were assigned a separate group due to their ecological function and large biomass. Octopodidae were separated from other cephalopods for their large biomass and economic value. Detritus was assigned a single group and used to accumulate biomass flows deriving from unassimilated food and dead organic matter.

Values of B, P/B, Q/B, EE and landings were determined for all functional groups using literature and empirical regressions (Supplement 1 at www.int-res.com/articles/suppl/q011p111_supp.pdf [for all supplements] and see Table 2). Input parameter values of each group were set equal to the averages of the parameter values for that group, weighted by the relative biomass of each group. Diet composition of each functional group was determined using diet data obtained from the literature (Supplement 2 and see Table 3). Diets were adjusted to obtain a balanced model. Flows were expressed in t wet weight km^{-2} yr^{-1} and biomasses in t wet weight km^{-2}. During the balancing process, Ecopath estimated missing parameter values based on mass balance to obtain *EE* values less than 1.0 for all groups. The years before and after AR deployment (hereafter referred to as S_B and S_{AR+Re}) were set to 2010 and 2016, respectively.

2.4. Ecosystem attributes

The attributes used in the Ecopath model are defined as follows:

- Ecosystem maturity is defined in this study as the culmination of an ecosystem's development into a stable state with maximum biomass and/or information content and is quantified using several of Odum's attributes for ecosystem maturity (Odum 1969, Christensen 1995)

Table 1. Functional groups included in the trophic model before (B) and after (A) artificial reef deployment in Laizhou Bay, Bohai Sea, PR China in 2010 and 2016. DOC: dissolved organic carbon; POC: particulate organic carbon

Group name	Group description
1. Octopodidae (B,A)	*Octopus variabilis*, *Octopus ocellatus*
2. Mesopelagic fishes (B,A)	*Thryssa kammalensis*, *Scomberomorus niphonius*, *Konosirus punctatus*, *Sardinella zunasi*, *Sillago sihama*, *Setipinna tenuifilis*, *Argyrosomus argentatus*, *Johnius belangerii*, *Pampus argenteus, Eupleurogrammus muticus*, *Takifugu pseudommus*
3. Demersal fish (B,A)	*Liza haematocheila*, *Platycephalus indicus*, *Saurida elongate*, *Kareius bicoloratus*, *Cynoglossus joyneri*, *Callionymus kitaharae*, *Paralichthys olivaceus*, *Enerias fangi*, *Cottiusculus gonez*, *Sparus macrocephalus*, *Hippocampus fasciatus*
4. *Sebastes schlegeli* (B,A)	Single species
5. *Hexagrammos otakii* (A)	Single species
6. Gobiidae (B,A)	*Acanthogobius ommaturus*, *Chaeturichthys stigmatias*, *Ctenotrypauchen chinensis*, *Tridentiger trigonocephalus*
7. *Charybdis japonica* (B,A)	Single species
8. *Oratosquilla oratoria* (B,A)	Single species
9. Large crustacean (B,A)	*Palaemon gravieri*, *Fenneropenaeus chinensis*, *Lysmata vittata*, *Trachypenaeus curvirostris*, *Palaemon* (*Exopalamon*) *carincauda* Holthuis*, Alpheus japonicas*, *Portuns trituberculatus*, *Philyra carinata*, *Dorippe japonica*, *Eucrate crenata*, *Matuta planipes*, porcelain crab, *Dorippe polita*
10. Other cephalopods (B,A)	*Loligo chinensis*
11. *Rapana venosa* (A)	Single species
12. *Apostichopus japonicas* (A)	Single species
13. Zoobenthos (B,A)	Gastropods, bivalves, polychaetes, echinoderms, crustaceans
14. Oyster (A)	*Ostrea plicatula*, *Crassostrea gigas*
15. Zooplankton (B,A)	Larva, Copepoda, jellyfish, Cladocera, Chaetognatha, Tunicata, Phylum
16. Phytoplankton (B,A)	*Coscinodiscus* spp., *Chaetoceros* spp., *Navicula* spp.
17. Detritus (B,A)	DOC, suspension POC, detritus from shellfish cultivations

- In Ecopath, trophic levels (TL; dimensionless) are fractional (e.g. 1.3, 2.7, etc.), as suggested by Odum & Heald (1975). A routine assigns a TL value of 1 to primary producers and detritus and a TL value of 1 plus the weighted average of the prey's TLs to consumers
- The Finn cycling index is the fraction of an ecosystem's throughput that is recycled and it is strongly correlated with system maturity, resilience and stability
- The system omnivory index (SOI) is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The SOI is a measure of how the feeding interactions are distributed across trophic levels
- PPr/R is the ratio between total primary production (PPr) and total respiration (R) in a system. In mature systems, the ratio should approach 1, i.e. the energy that is fixed is approximately balanced by the cost of maintenance
- The ratio between a system's PPr and its total biomass, indicated as PPr/B, is expected to be a function of the system's maturity. In immature systems, production exceeds respiration for most groups, and as a consequence, one can expect the biomass to accumulate over time
- The total system throughput (TST) is the sum of all flows in a system and is expressed in t km^{-2} yr^{-1}. TST represents the 'size of the entire system in terms of flow' (Ulanowicz 1986)
- The total biomass (TB) that is supported by the available energy flow in a system (TB/TST) is expected to increase to a maximum for the most mature stages of a system (Odum 1971)
- Based on the options selected for each parameter in each group, a pedigree index can be calculated as the product of all the parameter-specific pedigree indices
- Based on trophic aggregation tables, transfer efficiencies between successive discrete trophic levels can be calculated as the ratio between the sum of the exports from a given TL, plus the flow that is transferred from one TL to the next, and the throughput on the TL. This information is presented in a table with transfer efficiencies (%) by TL
- The connectance index (CI) of a food web is the ratio of the number of actual links to the number of possible links. Odum (1971) expected food chain structure to change from linear to web-like as systems mature. Hence, the CI can be expected to be correlated with maturity
- The mixed trophic impact (MTI) for living groups is calculated by constructing an $n \times n$ matrix, where the i,jth element representing the interaction between the impacting group i and the impacted group j is $\mathrm{MTI}_{i,j} = \mathrm{DC}_{i,j} - \mathrm{FC}_{j,i}$, where $\mathrm{DC}_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i, and $\mathrm{FC}_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i as a predator. The matrix is inversed using a standard matrix inversion routine
- Keystones are defined as relatively low-biomass species with a structuring role in their food webs. The analysis of the MTIs presented here was applied to a suite of mass-balance models, and the results allow us to rank functional groups by their keystoneness
- Net food conversion efficiency (NE) is calculated as the ratio between production and the portion of food that is assimilated, i.e. NE = P/(P + R)
- Gross food conversion efficiency (GE) is the ratio between production and consumption (P/Q)
- The ratio P/(P + R) cannot exceed 1, because respiration cannot exceed assimilation. For top predators, whose production is relatively low, the P/(P + R) ratio can be expected to be close to 1
- The P/R ratio expresses the fate of the assimilated food. Computationally, this ratio can take any positive value, though thermodynamic constraints limit the realized range of this ratio to values lower than 1
- The R/B ratio can be seen as an expression of the activity of a group. The higher the activity level is for a given group, the higher the ratio. The R/B ratio is strongly impacted by the assumed fraction of the food that is not assimilated

2.5. Model calibration and validation

We followed best practices in Ecopath modeling (Heymans et al. 2016) using the following steps: before the first run, we changed the excretion/egestion rate for zooplankton, sea cucumber and oyster from 20% (Ecopath default value) to 40% because it is more realistic from a physiological point of view; we balanced the model to achieve EE values lower than 1.0; and we checked that the following criteria were met: (1) GE values varied between 0.1 and 0.3; (2) the estimated NE values of all functional groups were greater than the GE values; (3) P/(P + R) ratios were lower than 1.0; (4) P/R ratios were lower than 1.0; and (5) R/B ratios varied between 1 and 10 for fish compartments and between 50 to 100 for groups with higher turnover rates (higher P/B and Q/B values).

We also used the pre-balanced (PREBAL) diagnosis (Link 2010) to identify issues in the model structure and in data quality before balancing the network model. Specifically, we checked the following: (1) biomass across taxa and trophic levels; (2) biomass ratio; (3) vital rates across taxa and trophic levels; (4) vital rate ratios; and (5) total production and removals (Link 2010) (Supplement 3). For example, we analyzed the main relationships among B, P, Q and TL. Biomass should span 5–7 orders of magnitude and P/B and Q/B should decrease when TL increases. We also checked vital rates ratios. For example, rates of predators must be lower than prey's rates and R/P rates must be lower than 1 (Link 2010).

To evaluate the quality of input data, we estimated the pedigree index for each input parameter value (B, P/B, Q/B and the diet matrix elements), attributing values between 0 (low quality) and 1 (high quality) according to the source of information. The average values for all parameters and groups provided a general concise index of the model input data quality.

3. RESULTS

3.1. Evaluation of compartment parameter estimates

Table 2 summarizes the input values used in the initial and final model runs and the output parameter values estimated by the model (TL and EE). The diet matrix was modified during the balancing procedure (Table 3). The pedigree index was 0.743–0.826, suggesting that the data used in the model were of very high quality.

Most functional groups, including *Sebastes schlegelii*, *Charybdis japonica*, large crustaceans, zoobenthos and zooplankton, had the same TLs in S_B and $S_\mathrm{AR+Re}$. Sea cucumber and oyster had a TL of 2.0, while *Rapana venosa* had a TL of 3.0 in $S_\mathrm{AR+Re}$ (Table 2).

After AR deployment, detritus showed a high EE (EE = 0.993), implying that biomass accumulation was almost equal to consumption. The comparatively high EE of phytoplankton (EE = 0.950–0.955) indicates that a major portion of phytoplankton production was consumed by grazing and the rest settled as detritus (Table 2).

3.2. Summary of ecosystem attributes

The model estimated TST values of 4721.2 and 4697.276 t km^{-2} yr^{-1} in S_B and $S_\mathrm{AR+Re}$, respectively. Of those values, 37.8 and 47.1 % was due to consumption (1784.55 and 2212.1 t km^{-2} yr^{-1}), 15.64 and 22.91 % to respiratory processes (738.58 and 1076.1 t km^{-2} yr^{-1}), 26.03 and 28.45 % was associated with flows back to detritus (1229.1 and 1336.593 t km^{-2} yr^{-1}), and 20.52 and 1.54 % was due to export processes (969.0 and 72.486 t km^{-2} yr^{-1}) (Table 4). The model estimated values of 1659.1 and 944.439 t km^{-2} yr^{-1} for the sum of all production, 1273.32 and 556.2 t km^{-2} yr^{-1} for total net primary production and 534.74 and −519.9 t km^{-2} yr^{-1} for net system production in S_B and $S_\mathrm{AR+Re}$, respectively (Table 4). The sum of flow to detritus was 795.3 in S_B and 927.6 t km^{-2} in $S_\mathrm{AR+Re}$ (Table 5).

In both S_B and $S_\mathrm{AR+Re}$, TL III had the highest transfer efficiency, while TL II showed the highest sum of flow to detritus, followed by TL I (Table 5). The total primary production to total respiration (TPP/TR), total primary production to total biomass (TPP/TB) and total biomass to total throughput (TB/TST) ratios showed that system maturity was higher in $S_\mathrm{AR+Re}$ than in S_B (Table 4). Finn's cycling index and Finn's mean path length showed that more groups were cycled into energy flows in $S_\mathrm{AR+Re}$.

Modeled flows and biomasses were represented by means of flow diagrams, which included 1 grazing and 2 detritus food chains after AR deployment (Fig. 2). The grazing food chain was based on a planktonic trophic pathway connecting large crustaceans, *C. japonica*, Gobiidae and Octopodidae, the latter being at the top of the food web. Two additional food chains were based on detritus and were dominated by sea cucumber and *R. venosa*, the latter connected to detritus by oyster. Oyster and sea cucumber played a prominent role in the overall flow to detritus (414.84 and 258.79 t km^{-2}, respectively) (Table 2). The net efficiencies of sea cucumber (NE = 0.298), *R. venosa* (NE = 0.355) and oyster (NE = 0.188) were the highest in $S_\mathrm{AR+Re}$ (Table 2).

3.3. MTI and keystone species analyses

Results of the MTI and keystone species analyses are shown in Fig. 3 and Table 6. All functional groups except for detritus had a negative impact on themselves, indicating resource competition within groups (Christensen et al. 2005). Detritus had neither positive nor negative impacts on itself, possibly because it is not a living organism. Cephalopods other than Octopodidae and *Oratosquilla oratoria* showed weak impacts on other groups, either because of their very small populations or lack of diet data.

Model results exhibited several similar positive and negative impacts on each compartment in S_B and $S_\mathrm{AR+Re}$, with the impact magnitudes showing substantial variability (Fig. 3). Octopodidae had a posi-

Table 2. Initial parameter input values included in the trophic model before and after artificial reef (AR) deployment in Laizhou Bay, Bohai Sea, PR China, for each functional group. Numbers in *italics* indicate adjusted input values. B: biomass (t km^{-2}); P/B: production to biomass ratio (yr^{-1}); Q/B: consumption to biomass ratio (yr^{-1}); EE: ecotrophic efficiency; landing (t km^{-2} year^{-1}); value: commercial value ($ US yr^{-1}); Ftd: flow to detritus (t km^{-2} yr^{-1}); NE: net efficiency (ratio between production and assimilated food); PPR (PP): primary production (from primary producers) required to sustain the fisheries (t km^{-2} yr^{-1}); PPR (Det): primary production (from detritus) required to sustain the fisheries (t km^{-2} yr^{-1}); PPR/catch: primary production required to sustain the catches (dimensionless index)

Group	Trophic level	B	P/B	Q/B	EE	Landing	Value	Ftd	NE	PPR (PP)	PPR (Det)	PPR/ catch
Before AR deployment (in 2010)												
1. Octopodidae	4.94	0.00392	2.0 (*2.1*)	7.0	0.96			0.006	0.375			
2. Cephalopods	3.24	0.15605	2.0	7.0	0.36			0.418	0.357			
3. Mesopelagic fishes	3.31	0.03114 (*0.09*)	0.5635 (*3.5*)	22.1	0.90			0.429	0.198			
4. Demersal fishes	2.82	0.142785	0.5934	13.74	0.37			0.446	0.054			
5. Gobiidae	3.79	0.109468 (*0.13*)	1.4758 (*2.2*)	7.51	0.97			0.205	0.366			
6. *Sebastes schlegelii*	4.11	0.00028 (*0.004*)	1.0056 (*1.2*)	5.3	0.99			0.004	0.283			
7. *Charybdis japonica*	3.18	0.01152	1.5	11.6	0.28			0.039	0.162			
8. *Oratosquilla oratoria*	3.06	0.03843	0.8 (*2.1*)	4.0 (*7.0*)	0.99			0.055	0.375			
9. Large crustaceans	3.03	0.06114 (*0.12*)	4.0 (*6.0*)	20	0.82			0.609	0.375			
10. Zoobenthos	2.00	31.05	1.67	8.35	0.06			100.380	0.250			
11. Zooplankton	2.25	5.0547	65.7	328.5 (*300.0*)	0.92			632.651	0.365			
12. Phytoplankton	1.00	9.432	71.2 (*135*)		0.95			60.016				
13. Detritus	1.00	24.8793			0.21							
After AR deployment (in 2016)												
1. Octopodidae	4.17	0.08488 (*0.3*)	2.0 (*2.1*)	7.0	0.602	0.196	853	0.671	0.375	8.81	168.7	281.7
2. Mesopelagic fishes	3.32	0.01275 (*0.2*)	0.5635 (*3.5*)	22.1	0.798			1.026	0.198	13.73	47.11	
3. Demersal fishes	2.82	0.02877 (*0.23*)	0.5934 (*1.0*)	13.74	0.970			0.639	0.091	8.899	52.42	
4. *S. schlegelii*	4.09	0.1505755	1.0056	5.3	0.113	0.007	28	0.294	0.237	5.595	46.68	345.2
5. *Hexagrammos otakii*	3.87	0.05	0.9245	7.3	0.935	0.033	47	0.076	0.158	1.032	12.55	293.7
6. Gobiidae	3.55	0.068871 (*0.47*)	1.4758 (*3.6*)	7.51 (*14*)	0.700	0.033	47	1.823	0.321	5.983	52.61	34.63
7. *C. japonica*	3.15	0.75388	1.5 (*2.0*)	11.6	0.930	0.196	753	1.854	0.216	4.417	157.7	107.5
8. *O. oratoria*	3.06	0.00042 (*0.03843*)	0.8 (*8*)	4.0 (*30*)	0.921	0.005	43	0.255	0.333	1.039	13.04	45.84
9. Large crustaceans	3.03	0.011162 (*0.34*)	4.0 (*6.0*)	20	0.947			1.469	0.375	2.993	90.13	
10. Cephalopods	3.24	0.15605 (*0.21*)	2.0 (*3.0*)	7.0 (*10.0*)	0.976			0.435	0.375	7.198	1.585	
11. *Rapana venosa*	3.00	38.833	0.26 (*0.8*)	2.82	0.956	29.689	64719	23.281	0.355	306.8	562.5	27.98
12. Sea cucumber	2.00	150	0.6	3.36	0.365	32.815	1148509	258.786	0.298		504	5.6
13. Zoobenthos	2.00	31.05	1.67	8.35	0.331			86.532	0.25		259.3	
14. Oyster	2.00	974 (*97.4*)		10.5	0.950			414.844	0.188	306.8	562.5	
15. Zooplankton	2.25	1.402	65.7	328.5 (*200*)	0.675			86.019	0.411	224.3		
16. Phytoplankton	1.00	5.562	71.2 (*100*)		0.955			24.752				
17. Detritus	1.00	24.8793			0.993							

Table 3. Diet composition (proportion) of functional groups before and after artificial reef (AR) deployment in Laizhou Bay, Bohai Sea, PR China, in 2010 and 2016. **Bold** values were modified to fit the mass-balance model. Horizontal groups correspond to the vertical group names

	Predator														
Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Before AR deployment															
1. Octopodidae	0.2875														
2. Other cephalopods			0.01165	0.023	0.04395	0.05									
3. Mesopelagic fishes			0.154 **(0.054)**	0.0894		0.05									
4. Demersal fishes	0.05		0.002	0.0121		0.1									
5. Gobiidae	0.45		0.00522	0.0220	0.419485 (**0.2**)	0.1	0.1								
6. *Sebastes schlegelii*			0.00240												
7. *Charybdis japonica*	0.175														
8. *Oratosquilla oratoria*	0.0375		0.00826 **(0.0)**	0.04											
9. Large crustacean			0.05226	0.0609	0.360765	0.7									
10. Zoobenthos		0.05	0.073137	0.2681	0.1758		0.9	0.75	0.878						
11. Zooplankton		0.95	0.663354	0.0037				0.25	0.122		0.200				
12. Phytoplankton			0.027924	0.0615							0.800				
13. Detritus				0.4193						1.000					
14. Import			0.10826		(**0.219485**)										
15. Sum	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0				
After AR deployment															
1. Octopodidae	0.2875 **(0.0875)**														
2. Mesopelagic fishes		0.153395 **(0.053395)**	0.0894	0.05											
3. Demersal fishes	0.05		0.0121	0.1	0.1										
4. *S. schlegelii*		0.0024													
5. *Hexagrammos otakii*		0.0024													
6. Gobiidae	0.45 **(0.05)**	0.00522	0.022	0.1		0.419485 **(0.0)**	0.1								
7. *Charybdis japonica*	0.175 **(0.575)**														
8. *Oratosquilla oratoria*	0.0375	0.00826	0.04		0.1										
9. Large crustaceans		0.05226	0.0609	0.7	0.6	0.360765 **(0.111)**									
10. Other cephalopods		0.01165	0.023	0.05	0.1	0.04395 **(0.063)**									
11. *Rapana venosa*															
12. Sea cucumber															
13. Zoobenthos		0.073137	0.2681			0.1758	0.9	0.75	0.878	0.05					
14. Oyster											1.0				
15. Zooplankton		0.663354	0.0037		0.1			0.25	0.122	0.95				0.5 **(0)**	0.2
16. Phytoplankton		0.027924	0.0615											0.5 **(0.3)**	0.8
17. Detritus			0.4193									1.0	1.0	**(0.55)**	
18. Import	**(0.2)**	**(0.1)**				**(0.65)**								**(0.15)**	
19. Sum	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 4. Ecosystem attributes estimated by the balanced Ecopath model for artificial oyster reef habitats in the study area in Laizhou Bay, Bohai Sea, PR China, in 2010 and 2016 compared to other coastal reef ecosystems. SR: stock release; AR: artificial reef; AE: artificial ecosystem; NF: natural reef; PP: primary production; –: no data

	Eastern parts of Laizhou Bay			Laizhou Bay	Yellow River Delta	Zhangzi Island	Li Island	Hangzhou Bay	Galapagos rocky
	This study			Lin et al. (2013)	Lin et al. (2015)	Z. Xu et al. (2016)	Wu (2012)	Xu et al. (2011)	Okey et al. (2004)
	Before	AR	SR + AR	SR	SR	AR	AR	AE	NF
Statistics and flows									
Study area (km^{-2})	30.67	30.67	30.67	6966	–	–	–	1.6	28.38
Sum of all consumption (t km^{-2} yr^{-1})	1784.55	1675.478	2212.1	1314.32	716.12	10257.67	–	5191.52	51600
Sum of all exports (t km^{-2} yr^{-1})	969.0	309.683	72.48	434.41	612.46	6326.554	–	4139.15	–5412
Sum of all respiratory flows (t km^{-2} yr^{-1})	738.58	836.725	1076.1	826.97	416.7	4901.347	–	2646.65	27638
Sum of all flows into detritus (t km^{-2} yr^{-1})	1229.1	1102.605	1336.593	1042.24	937.02	7205.479	–	7345.42	21024
Total system throughput (t km^{-2} yr^{-1})	4721.2	3924.49	4697.276	3618	2682	28691.05	11104	19323	94850
Sum of all production (t km^{-2} yr^{-1})	1659.1	855.318	944.439	1549	1185	11227.76	4990.3	8294	17337
Calculated total net PP (t km^{-2} yr^{-1})	1273.32	556.2	556.2	1261.38	1029.1	–	1865.2	6785.8	13250
Total biomass (excluding detritus) (t km^{-2})	46.233	176.88	326.99	51.39	30.9	673.279	620.2	97.99	2620
Mean transfer efficiency (%)	3.47	15.09	13.82	6.2	9.7	11.1	11.7	9.60	–
Proportion of total flow originating from detritus (%)	0.44	0.69	0.73	–	–	–		–	0.62
Community energetics									
Net system production (t km^{-2} yr^{-1})	534.74	–280.525	–519.9	434.41	612.4	6326.414	–	4139.15	–14388
Total PP/total respiration (yr^{-1})	1.724	0.665	0.52	1.53	2.47	2.291	1.82	2.56	0.48
Total PP/total biomass (yr^{-1})	27.541	3.145	1.700	24.54	33.3	16.676	6.66	69.25	5.06
Total biomass/total throughput (yr^{-1})	0.010	0.045	0.07	–	–	–	0.06	–	0.03
Connectance index	0.308	0.236	0.208	0.29	0.3	0.203	0.32	0.31	0.16
System omnivory index	0.23	0.188	0.164	0.17	0.15	0.136	0.14	0.35	0.25
Organic matter cycling									
Finn's mean path length	2.765	3.423	4.09	–	–	2.555	2.69	2.174	–
Throughput cycled (excluding detritus) (t km^{-2} yr^{-1})	303.6	52.73	56.54	–	–	–	–	–	–
Finn's cycling index (% of total throughput)	9.035	16.84	22.52	0.07	6.16	2.18	5.46	25	–
Predatory cycling index (% of throughput without detritus)	13.42	3.067	2.793	–	–	–	–	–	–
Exploitation indices									
Mean trophic level of the catch	–	3.012	2.484	2.74	2.97	–	2.09	–	2.27
Gross efficiency (catch/net PP)	–	0.054	0.113	0.08	0.0002	–	0.02	–	0.0003
Total catch (t km^{-2} yr^{-1})	–	30.155	62.97	–	–	–	–	–	–
PP required to sustain the fishery (t km^{-2} yr^{-1})	–	899.6	1104	–	–	–	18.62	–	–
Model quality									
Ecopath pedigree index	0.826	0.769	0.743	–	–	–	–	–	–

Table 5. Transfer efficiency at trophic levels I to V before and after artificial reef deployment showing the contribution of detritus and primary production to the trophic network in Laizhou Bay, Bohai Sea, PR China, in 2010 and 2016

Sources	I		II		III		IV		V		Sum of I–V	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
Originating from detritus												
Producer (%)			0.225	7.644	11.54	25.75	4.602	14.07	2.376	11.73		
Detritus (%)			1.28	8.478	18.37	25.51	7.625	11.9	2.439	11.4		
Total flow (%)			0.411	8.235	15.23	25.59	6.652	12.52	2.425	11.52		
Total biomass												
Biomass (t km^{-2})	34.310	30.440	36.180	280.000	0.485	40.65	0.132	0.758	0.0055	0.037	71.112	351.885
Total flows												
Import (t km^{-2})	433.800	433.800									433.80	433.800
Consumption by predators (t km^{-2})	1473.0	1859.0	6.059	132.900	0.964	4.894	0.0742	0.669	0.001	0.0256	1480.1	1977
Export (t km^{-2})	969.0	9.516		32.810		29.910		0.228		0.0127	969	72.49
Flow to detritus (t km^{-2})	60.02	24.75	733.3	846.5	1.686	29.28	0.274	2.092	0.015	0.0882	795.3	902.8
Respiration (t km^{-2})			734.1	999.8	3.678	71.94	0.766	4.18	0.044	0.206	738.6	1076
Throughput (t km^{-2})	2936.0	2327.000	1473.0	2012	6.328	136.000	1.115	7.169	0.06	0.333	4416.5	4482

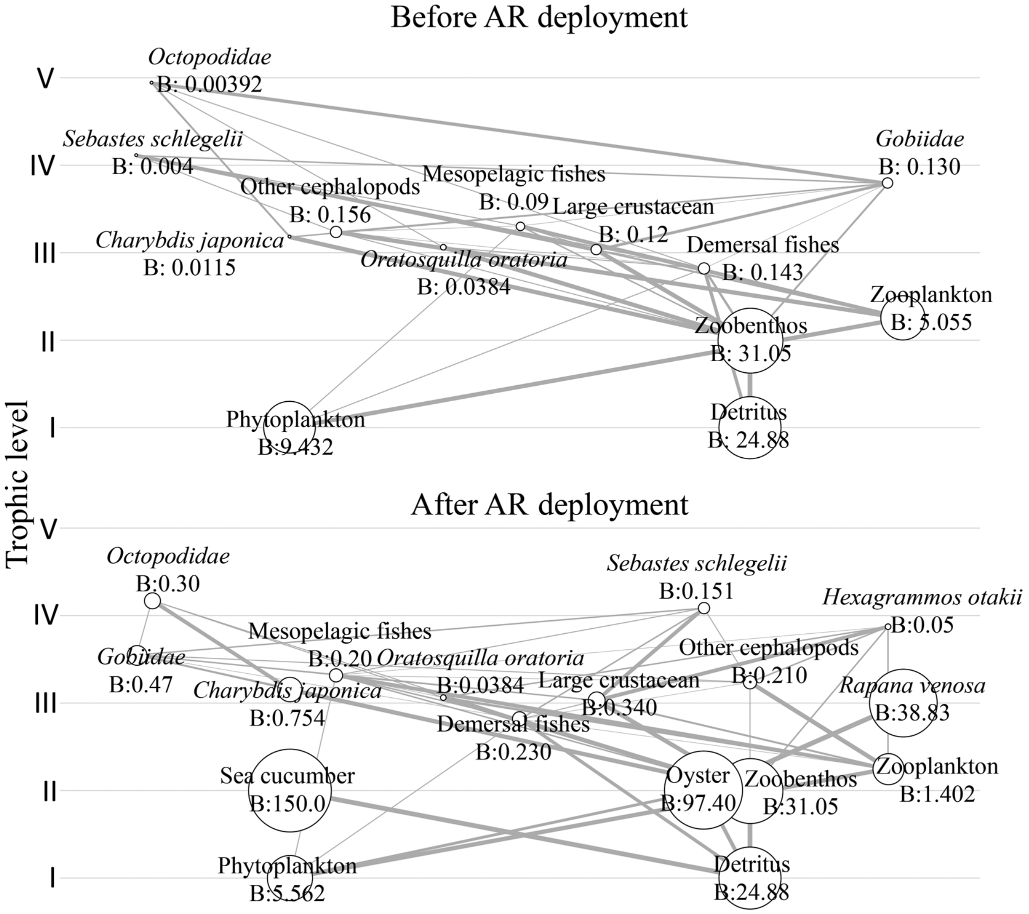

Fig. 2. Flow diagrams representing food web structure (Ecopath with Ecosim modeling) in terms of functional groups and fractional trophic levels before and after artificial reef (AR) deployment. Circles are distributed on the *y*-axis according to trophic level (I–V); circle size is proportional to each group's biomass. Biomass (B) is reported in t km^{-2}. Line thickness illustrates the magnitude of the flow rates

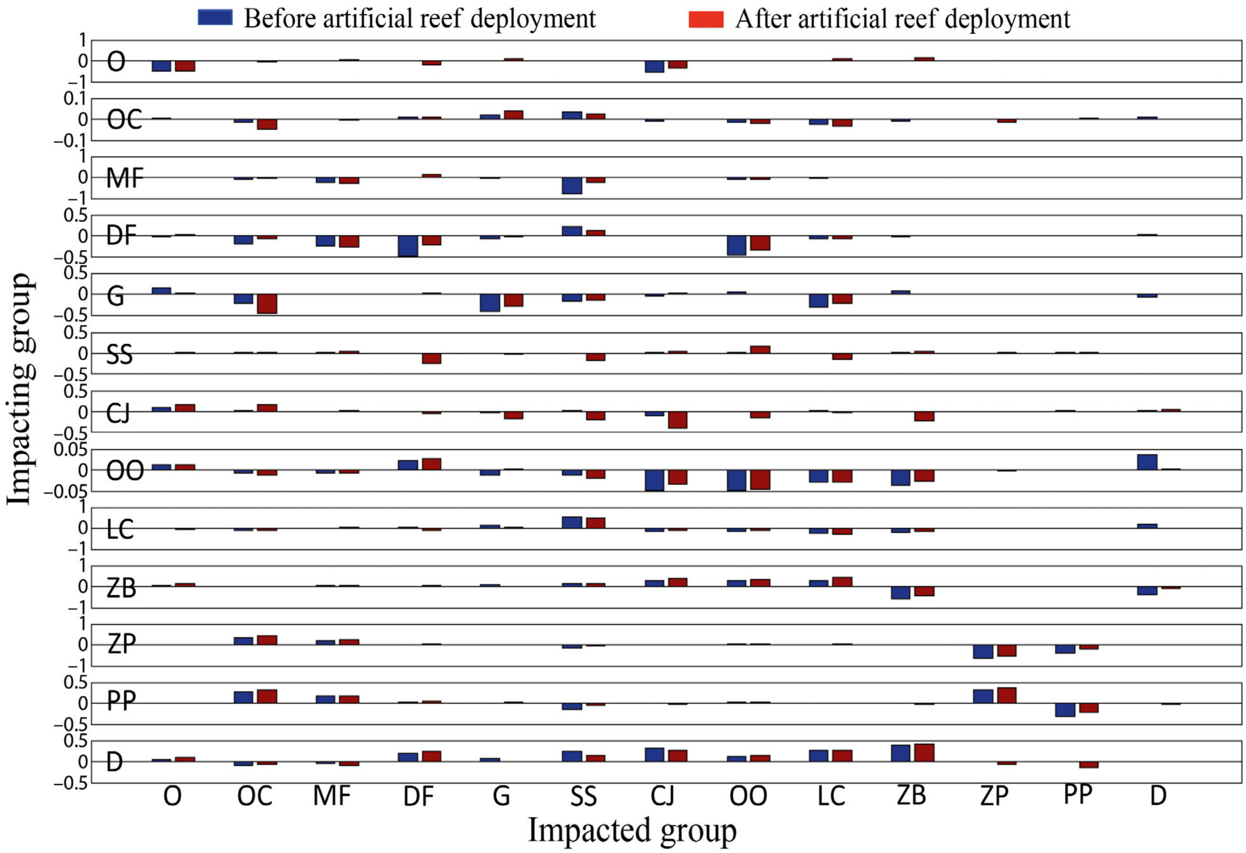

Fig. 3. Comparison of mixed trophic impact analysis results before and after artificial reef deployment. Impacting and impacted groups are placed along the vertical and horizontal axis, respectively. Positive impacts are shown above the baseline; negative impacts are below the baseline. The impacts are relative but comparable between groups. O: Octopodidae; OC: other cephalopods; MF: mesopelagic fishes; DF: demersal fishes; G: Gobiidae; SS: *Sebastes schlegelii*; CJ: *Charybdis japonica*; OO: *Oratosquilla oratoria*; LC: large crustaceans; ZB: zoobenthos; ZP: zooplankton; PP: phytoplankton; D: detritus

tive impact on the biomass of Gobiidae, large crustaceans and zoobenthos, and a negative impact on the biomass of *S. schlegelii*. An increase in the production of *C. japonica* resulted in higher Octopodidae biomass but lower Gobiidae and zoobenthos biomasses. *S. schlegelii* had a positive impact on *C. japonica* and zoobenthos biomass and a negative impact on Gobiidae and large crustaceans.

The biomass of Octopodidae was positively affected by increases in the production of *C. japonica*, zoobenthos and detritus, while the biomass of *S. schlegelii* was negatively affected by decreases in the production of Octopodidae and *O. oratoria.* The biomass of *C. japonica* was positively (or negatively) associated with increases (or decreases) in the production of *S. schlegelii* and zoobenthos (or demersal fishes, *C. japonica* and phytoplankton). The biomass of Gobiidae increased (or decreased) due to an increase (or decrease) in the production of Octopodidae, other cephalopods, zooplankton and phytoplankton (or *S. schlegelii* and *C. japonica*).

According to the keystone species analysis, pelagic and bottom fish groups and different benthic organisms, including large crustaceans and zoobenthos, were the dominant community in S_{B} (Table 6). Zoobenthos was the key group in $S_{\mathrm{AR+Re}}$, followed by Gobiidae and large crustaceans, which are the most important prey compartments for top predators in the system. Plankton and oyster ranked 5th to 7th, exhibiting large populations and negative impacts on each other. *O. oratoria* and cephalopods other than Octopodidae ranked 15th to 16th due to their small population biomass (Table 6).

3.4. Fishing status

The primary production required to support fisheries (PPR, considering primary production and detritus) was 3428.42 t km^{-2} (Table 2). *R. venosa* represented 34.18% (306.8 t km^{-2}) of the PPR fraction coming from primary production and 22.23% (562.5 t

Table 6. Keystone index #3 against relative total impact of each functional group before and after artificial reef deployments in Laizhou Bay, Bohai Sea, PR China, in 2010 and 2016

Group name	Before		Group name	After	
	Relative total impact	Keystone index #3		Relative total impact	Keystone index #3
1. Mesopelagic fishes	1	0.803	1. Zoobenthos	1	0.506
2. Demersal fishes	0.857	0.532	2. Gobiidae	0.876	0.749
3. Large crustaceans	0.794	0.645	3. *C. japonica*	0.853	0.68
4. Zooplankton	0.717	0.233	4. Large crustaceans	0.805	0.764
5. Zoobenthos	0.707	–0.251	5. Oyster	0.668	0.0292
6. Octopodidae	0.66	0.799	6. Phytoplankton	0.666	0.426
7. Phytoplankton	0.565	–0.0467	7. Zooplankton	0.657	0.499
8. Gobiidae	0.541	0.412	8. Octopodidae	0.626	0.7
9. *Charybdis japonica*	0.116	–0.0349	9. Demersal fishes	0.582	0.71
10. *Sebastes schlegelii*	0.0765	–0.175	10. Mesopelagic fishes	0.569	0.772
11. *Oratosquilla oratoria*	0.0732	–0.281	11. *Rapana venosa*	0.533	0.108
12. Other cephalopods	0.0644	–0.689	12. *S. schlegelii*	0.441	0.694
			13. Sea cucumber	0.37	–0.529
			14. *Hexagrammos otakii*	0.192	0.364
			15. Other cephalopods	0.12	0.0611
			16. *O. oratoria*	0.118	0.178

km^{-2}) of the PPR fraction coming from detritus production (Table 2). The sea cucumber exhibited 19.91% (504 t km^{-2}) of the PPR coming from detritus (Table 2). Detritus production (2530.825 t km^{-2}) represented the largest portion (73.82%) of overall PPR (Table 2). The sea cucumber showed the lowest PPR/catch value (5.6) among functional groups, indicating fishing catch biomass values close to primary production values (Table 2).

4. DISCUSSION

4.1. AR deployment contributed to the maturity of the improved ecosystem

Ecosystem maturity improved through AR deployment, as verified by the ratios TPP/TR, TPP/TB and TB/TST. Ecosystem development is seen by Odum (1969) as a process that involves structural changes in the system that are orderly and directional. Ecosystem development is to culminate in a stable system with maximum biomass and/or information content, a state referred to as ecosystem maturity (Christensen 1995). Guan et al. (2016) showed that a restoration project aimed at enhancing biological habitat and improving biotic environment using ARs (Pitcher et al. 2002), hard slope roughing (Moschella et al. 2005) and stock releasing (Borsje et al. 2011) resulted in increased ecosystem maturity in the harbor of the Tianjin Lin Gang Economic Zone, PR China. Similarly, in Hangzhou Bay, China, Xu et al. (2011) found that an artificial coastal ecosystem enhanced system maturity.

ARs have become an important technique to restore degraded habitats and marine resources worldwide (Rilov & Benayahu 2000, Woo et al. 2014), including China. AR ecosystems enhance secondary biomass production through increased survival and growth of new individuals as a result of improved sheltering and food resources provided by the reef (Langlois et al. 2006). Uneven surfaces with cracks, crevices and holes typical of ARs also increase benthic diversity and biomass (Moura et al. 2006, Bruce et al. 2012). As evidence of those improvements, transfer efficiencies were 3.47 and 13.82% in S_B and S_{AR+Re}, respectively (Table 4), the latter being close to the mean value (15%) proposed by Ryther (1969) for temperate coastal ecosystems.

The CI of S_B was higher than that of S_{AR+Re}, showing that ARs can shorten and modify the food web and increase net production. Claudet & Pelletier (2004) and Lowry et al. (2011) reported higher biomasses in reef areas than in areas without reefs, with reef areas supporting large numbers of fish. Pitcher et al. (2002) utilized Ecopath to simulate the marine ecosystem of Hong Kong and investigate the relationship between reef fish biomass and the relative size of ARs inside marine protected areas (AR/MPA). They concluded that total reef fish biomass would increase by 30% (from ~190 to ~247 t) in a 2% AR/MPA system after 10 yr.

In this study, after AR deployment, sedentary organisms such as sea cucumbers and oysters, which feed mainly on detritus, were subjected to stock release and enhancement, respectively. Mobile fauna commonly inhabiting AR structures include burrowing species (infauna) and free-living species that shelter in crevices (sedentary species) (Lira et al. 2010). *Apostichopus japonicus*, whose natural range in Asia covers the coasts of Russia, Japan, China and Korea from 35 to 44° N (Yuan et al. 2009), has become an important component of the mariculture sector in northern China (Zhang et al. 2011). Soaring market prices in China were responsible for stimulating the release of *A. japonicus* in AR areas. Oysters are a major prey for *Rapana venosa* in the system (Golikov & Skarlato 1967), while the economic species *A. japonicus* and *R. venosa* have no predators except for fishing in this area. It was also found that the populations of Octopodidae, *Sebastes schlegelii*, *Hexagrammos otakii* and *Charybdis japonica* began to expand and their juveniles were caught in AR areas, suggesting that AR areas acted as an important fish breeding, sheltering and feeding ground in Laizhou Bay. *H. otakii* and *S. schlegelii*, which are both common along the coast of northern China (Zhang et al. 2008) and have similar feeding modes and habitat preferences, competed for the prey group represented by large crustaceans, while members of the Gobiidae family were a common prey for *S. schlegelii* and Octopodidae. Based on stable isotope analyses, Xu et al. (2017) concluded that *S. schlegelii* was carnivorous in an AR ecosystem in Laizhou Bay, while *H. otakii* had a more complex diet including seaweed debris. In our study, a food chain based on zoobenthos and connected by *C. japonica* to the top predator Octopodidae was found in the system's food web.

4.2. The artificial oyster system is similar to a natural reef ecosystem

The Laizhou AR ecosystem, a representative artificial oyster reef area in the nearshore rocky reef waters of the northern coast of China, was characterized by greater benthic than pelagic productivity. ARs can retain detritus effectively and provide suitable habitat to epifauna and the surrounding natural fauna community (Xu et al. 2017). Several sessile organisms, especially oysters, usually colonize newly deployed reefs very rapidly owing to the complex structure provided to them by reefs. Thus, lower TL consumers such as the detritivorous *A. japonicus* and herbivorous *Crassostrea gigas* dominated the system, and these organisms were the main sources of biomass flowing to detritus (Table 2), thereby contributing to the high productivity and standing crop of benthic organisms in the area. In rocky reef systems, the planktonic–benthic pathway is regarded as an important pathway for importing large quantities of carbon and trapping it by filter- and suspension-feeding invertebrates (Bray et al. 1981).

The high biomass of oyster (B = 97.4 t km^{-2}), sea cucumber (B = 150 t km^{-2}) and other benthic organisms in the system is likely related to the nutritional support provided by the much higher biomass of detritus. The detritus pool was likely supplemented with biomass accumulations from the surrounding shellfish farms that are widespread in the Laizhou region. In an artificial coastal ecosystem in Hangzhou Bay, detritus contributed 57 % of the total energy flux, indicating that the artificial ecosystem depended more on the detritus pool than on primary producers to generate TST (Xu et al. 2011). At the same time, oysters also exerted high predation pressure upon phytoplankton, as indicated by the decrease in phytoplankton biomass after AR deployment (Table 2).

Natural subtidal rocky reefs in Galápagos, Chile (Okey et al. 2004) and artificial oyster reefs in Laizhou, China share general similarities, as suggested by some of the indexes, including TPP/TR, TPP/TB, TB/TST and the proportion of total flow originating from detritus (Table 4). Both systems have negative net system production. However, food web complexity is higher in the subtidal rocky reefs, as indicated by the system omnivory index (SOI = 0.25). In addition, the values of TST, sum of all production, total net primary production and total biomass excluding detritus are several times higher for the AR ecosystems in Zhangzi Island (Z. Xu et al. 2016) and Li Island (Wu et al. 2012) than the values obtained for the AR area in Laizhou Bay, although far lower than the values estimated for rocky reefs in Galápagos. Low TST and total production in Laizhou indicate that this system has relatively lower internal energy compared to other AR ecosystems in China and subtidal rocky reefs. The Laizhou AR area was created only 5 yr before this study, a rather short time, suggesting that the ecosystem is still in an early development stage in terms of production, throughput and biomass.

4.3. Enhancement and release of benthic organisms in AR areas benefit the ecosystem

Stock release, which is generally thought to be more effective in AR areas than in non-AR areas, can induce dramatic ecosystem changes (Watson 1993, Grosholz et al. 2000). In China, significant efforts have been made to increase fisheries production through large-scale release programs of cultured juveniles, e.g. the penaeid prawn *Penaeus chinensis* (Wang et al. 2006) and *A. japonicus* (Chen 2004, Choo 2008, Han et al. 2016).

A. japonicus has been released in the Laizhou AR area while the economic species *R. venosa* has been enhanced owing to the availability of sheltering places and large amounts of prey animals such as oysters. We compared this system with other systems that were subjected to stock release, such as the release of *Fenneropenaeus chinensis* into Laizhou Bay (Lin et al. 2013) and *Portunus trituberculatus* into the Yellow River estuary and adjacent waters (Lin et al. 2015). The TPP/TR and TPP/TB values of S_B were similar to those of the systems where release of *F. chinensis* and *P. trituberculatus* occurred, showing that these systems have similar maturity. TST and total biomass excluding detritus, which represent the system's internal energy, in S_{AR+Re} than in the systems subjected to the release of *F. chinensis* and *P. trituberculatus*. Furthermore, more trophic compartments were involved in energy flows in S_{AR+Re}, according to Finn's cycling index, compared to the other 2 systems. Mean transfer efficiency in S_{AR+Re} was 13.82% compared to 6.2 and 9.7% in the *F. chinensis* and *P. trituberculatus* systems, respectively.

4.4. Low TL catches do not cause the system to collapse

The system of increasing the yield of commercial invertebrate species by enhancing habitat and through release programs clearly approaches a level of mariculture, sometimes referred to as sea or marine ranching (Bell et al. 2006). In the Laizhou AR ecosystem, *A. japonicus* and *R. venosa* represent the most important fishery industries in terms of biomass (ca. 150 versus 116.5 t km^{-2}) and fishery yield (ca. 32.81 versus 89.07 t km^{-2}), respectively (Table 2). Fishing landings of Octopodidae, *S. schlegelii*, *H. otakii*, Gobiidae, *C. japonica* and *Oratosquilla oratoria* totaled 0.468 t km^{-2} yr^{-1} in S_{AR+Re}, reaching 0.75% of total system production and 0.15% of total market value (1772.3 US$ yr^{-1}) (Table 2). The production of *R. venosa* was ca. 47.15% of total production and 5.32% of total market value (Table 2). The production of *A. japonicus* was ca. 52.1% of total production and 94.53% of total market value (Table 2).

In the Ecopath model, fishing activities can be assessed by looking at the mean trophic level of the catch (TLc) and the gross efficiency of the fishery (catch/PP) (Pauly & Christensen 1995, Pauly et al. 1998). The TLc is an index of sustainability and reflects the strategy adopted by a fishery in terms of the targeted food web components. TLc was 2.484 in S_{AR+Re} and 3.012 in S_{AR} compared to a value of 2.09 in the AR area of Li Island, China (Wu et al. 2012) and 2.27 in the natural rocky reefs of Galápagos, Chile (Okey et al. 2004). TLc values in Laizhou are close to the average global estimate for coastal and reef systems (TLc = 2.5) (Pauly & Christensen 1995). The gross efficiency of the fishery can have high values in systems where fisheries harvest fish low in the food web, and in this study the estimated value was substantially higher than the mean global value of 0.0002 reported by Christensen et al. (2005).

Although *A. japonicus* and *R. venosa* are under intense fishing pressure due to considerable economic interests, low TL catches do not cause the system to collapse in the study area. The MTI analysis showed positive impacts of *R. venosa* on most groups except for oyster and sea cucumber. Sea cucumber had negative impacts on detritus, *R. venosa* and diving fishing. This was also supported by the keystone species analysis. After AR deployment, the major economic species *C. japonica*, *R. venosa* and sea cucumber ranked 3rd, 11th and 13th, respectively. These species exhibited few trophic cascade impacts on other functional groups and are thus mainly regarded as exploited species due to their large populations.

According to MTI analysis, diving fishing and crab pot fishing have negative impacts on target species and a small positive impact on groups at lower levels because of reduced predation pressure and competition when the stocks of predators and other major groups decline. Diving fishing showed negative effects on sea cucumber and *R. venosa* while it had a small positive effect on oyster. Crab pot fishing showed negative effects on *H. otakii*, *S. schlegelii* and Octopodidae, but positive effects on large crustaceans and demersal fishes. Compared to ARs, which were shown to only increase recreational fishing opportunities for reef fishes in several areas worldwide (Sutton & Bushnell 2007, Mclean et al. 2015, Keller et al. 2016), artificial oyster reefs support the sustained commercial use of *A. japonicus* and *R. venosa*.

Ecosystem-based fisheries management (Prellezo & Curtin 2015) is an environmental management paradigm that addresses complex socio-ecological problems. The goal of ecosystem-based fisheries management is to maintain an ecosystem in a healthy, productive and resilient condition. AR deployment as a technological means focuses on comprehensive, multi-dimensional, long-term ecosystem improvements in order to increase the health and maturity of ecosystems. Fisheries managers can use AR deployment to manage degrading nearshore marine ecosystems, help local fisheries communities to increase their income through mariculture, and exploit fisheries resources in a sustainable way. In this context, this study provides useful new insights on the effects of AR deployment on marine ecosystems.

5. CONCLUSIONS

This study provides a summary of the knowledge on ecosystem status before and after AR deployment, including trophic interactions, energy flows, keystone species, ecosystem properties and fishing impacts, through a steady-state trophic flow model (EwE 6.5). It is important to implement quantitative assessments of energy and matter flows in coastal AR ecosystems for a better understanding of the underlying ecological processes and to improve our ability to predict changes in ecosystem functions in response to environmental and anthropogenic impacts (Gaedke 1995). The following conclusions can be drawn from this study: (1) AR deployment contributes to the maturity of an improved ecosystem; (2) the artificial oyster system is close to a natural reef ecosystem; (3) the enhancement and release of benthic organisms in AR areas benefit the ecosystem; and (4) low TL catches do not cause the system to collapse. Keystone species and MTI analyses helped explain short-term ecosystem changes (Mavuti et al. 1996) in this study. Future studies should focus on predictions of medium- and long-term ecosystem dynamics.

Acknowledgements. The authors thank Mr. T. Shi and the members of Blue Ocean Ltd. for their help with field sampling, and members of the CAS Key Laboratory of Marine Ecology and Environmental Sciences, the Institute of Oceanology and the Chinese Academy of Sciences for their constructive discussions and encouragement. This research was supported by the Taishan Industry Leader Talent Project, the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDA11020703), the Qingdao Postdoctoral Applied Basic Research (Grant No. Y7KY02106N), the NSFC-Shandong Joint Fund for Marine Science Research Centers (Grant No.U1406403), the Key Research and Development Plan (major key technology) Project in Shandong (Grant No. 2016ZDJS06A02), the National Marine Public Welfare Research Project (Grant No. 201305043), the Postdoctoral International Exchange Program Introduction Project (Grant No. Y8KY02102L), the Laboratory for Marine Fisheries Science and Food Production Processes and the Qingdao National Laboratory for marine science and technology (2016LMFS-B08). This study was also financially supported by a Creative Team Project of the Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology (No. LMEES-CTSP-2018-1). We thank International Science Editing (www.internationalscienceediting.com) for editing the manuscript.

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Editorial responsibility: Gianluca Sará,
Palermo, Italy

Submitted: April 25, 2018; Accepted: September 5, 2018
Proofs received from author(s): March 7, 2019