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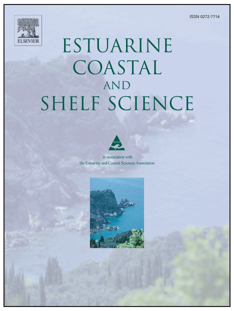

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Trophic flows, kelp culture and fisheries in the marine ecosystem of an artificial reef zone in the Yellow Sea

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Abstract

This study evaluates the ecosystem structure and function of the nearshore reefs in the Lidao coastal ecosystem of northern China, a region of intensive kelp aquaculture, and fisheries enhancements, including the deployment of artificial reefs and release of cultured marine species. An Ecopath model, with 20 functional groups representing 81 species, was developed for a representative area in the region and Ecosim was used to explore two scenarios for alternative fishing practices and surrounding aquaculture activities. The mean trophic levels (TLs) of the functional groups ranged from 1.0 for the primary producers (phytoplankton, benthic algae and seagrass) and detritus to 4.14 for Type III fishes (fishes found in the water column above the artificial reefs, e.g., *Scomberomorus niphonius*). The mean transfer efficiency through the whole system was 11.7%, and the ecosystem had a relative low maturity, stability and disturbance resistance, indicating that it was at a developing stage. Nearly half of the total system biomass (48.9% of 620.20 t km^{-2} year^{-1}), excluding detritus, was comprised of benthic finfish and invertebrates. The total yield from all fisheries (86.82 t/km^{2}/year) was dominated by low trophic level herbivorous and detritivorous species, such as the sea cucumber *Apostichopus japonicus* (TL = 2.1, 46.07%), other echinoderms (sea urchins *Asterias amurensis* and *Strongylocentrotus nudus*, TL = 2.1, 34.6%) and abalone *Haliotis discus hannai* (TL = 2.0, 18.4%), and as a consequence, the mean TL of the catch was low (2.1). The results from the Ecosim simulation of closing all fisheries for 20 years predicted an increase of about 100% in the relative biomass of the main exploited species, *A. japonicus* and *H. discus hannai*. The simulated removal of all kelp farms over 10 years resulted in a two fold increase in the relative biomass of Type III fishes and a 120% increase in their main prey (i.e. Small pelagic fish), while the relative biomass of *A. japonicus* and Heterotrophic bacteria decreased by 31.4% and 12.7%, respectively. These predictions indicate that nearshore kelp cultivation favours benthic, rather than water column production, and is likely to be providing energy subsidies for the stock enhancement of benthic species in this region.

Keywords: Ecosystem mass-balanced models; artificial reefs; fishing impact; intensive aquaculture; release programs; Northern China.

1. Introduction

The yield from marine capture fisheries has plateaued from the mid-1990s (Pauly et al., 2002; FAO, 2014) and concerns have been expressed about the future of the world's fisheries because of over-capitilisation and over-exploitation (Myers and Worm, 2003). Global declines in the mean tropical level of marine fisheries and ecosystems have also been documented because of the removal of top-level predators and larger exploited individuals by fishing (Pauly et al., 1998; Pauly et al., 2002; Myers and Worm, 2003). In most seas of the Chinese exclusive economic zone, including the Yellow and Bohai seas in northern China, fisheries resources have been overfished since the late 20th century (Shen and Heino, 2014).

In addition to the decline in capture fisheries in Chinese waters, the fishery resources in these waters have shown marked changes in community structure and diversity since the late 1980s (Jin and Tang, 1996; Jin, 2004; Xu and Jin, 2005). For example, commercially important, high-value demersal species such as largehead hairtail

(*Trichiurus haumela*) have been replaced by lower-value pelagic stocks (e.g., Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea and Bohai Sea (Jin and Tang, 1996; Tang et al., 2003; Jin, 2004). Moreover, despite recent acoustic surveys of the Japanese anchovy indicate that it is declining, verging on collapse (Zhong and Power, 1997; Jin et al., 2001; Zhao et al., 2003; Jin, 2004; Dong et al., 2010; Liu, 2013; Tang et al., 2015). Simultaneously, the frequency of jellyfish blooms along the inshore of Shandong peninsula adjacent to the Bohai Sea has increased, probably through a release from competition with the Japanese anchovy for food resources (Dong et al., 2010).

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 sea cucumber *Apostichopus japonicus* (Chen, 2005; Choo, 2008; Han et al., 2016). In order to protect and restore marine aquatic resources, the Chinese government and industry have also implemented a large-scale deployment of artificial reefs along the coast of China, first launched by the Guangdong Provincial Government in 2001 (Shen and Heino, 2014). By the end of October 2013, in Shandong Province alone, approximately 10 million m^3 of artificial reefs of various types, covering 15,000 ha, had been deployed at 170 sites along the coast of Shandong Peninsula (Marine and Fisheries Department of Shandong Province, unpublished data). In addition to release programs and the deployment of artificial reefs, intensive kelp culture is practiced in the region, mainly for *Laminaria japonica*, an important species in China that in 2012 contributed about 17% (979,006 tons) (China Fishery Statistical Yearbook, 2013) of the total *L. japonica* world production (5,682,078 tons) (FAO, 2014).

Ecosystem models (Ecopath with Ecosim [EwE]) have been used to evaluate the ecosystem effects of fishing and the response of marine systems to management interventions such as reductions in fishing effort (Lozano-Montes et al., 2011), spatial closures (Lozano-Montes et al., 2013) and artificial reefs (Pitcher et al., 2002; Shipley, 2008). The EwE software has been under development since the 1980s and it is the most applied tool for modelling marine and aquatic ecosystems globally, with over 400 models published to date. It is grounded in general ecological theory and it has proved capable of capturing real ecosystem dynamics in a variety of ecosystems (Walters et al., 2005; Brown et al. 2010)

In this study, an Ecopath model was developed for a typical artificial reef zone in the northern coast of the Yellow Sea to explore how artificial reefs and intensive kelp culture may have influenced the productivity and trophic dynamics of the system. The possible effects of related fishing and aquaculture activities on the biomass of the major groups in the system were evaluated in Ecosim by simulating the two scenarios to investigate:

1. the impact of fishing on the system by reducing the current fishing effort to zero over 3 years and then simulating forward for 17 years.

2. the potential subsidy of detritus from kelp farms on the ecosystem by increasing the biomass of phytoplankton by 100% and reducing the biomass of detritus by 40% over 10 years and projecting forward for 10 years.

Although the study area and bounds of the model were relatively small, they are representative of the shallow coastal systems in this region (see study site description below).

2. Material and Methods

2.1 Study area

The Lidao artificial reef zone (37°13′N, 122°36′E, Fig. 1), in the Shandong Peninsula of China, has reef clusters deployed in the nearshore (mean water depth 9-11 m) and offshore waters (mean water depth 20-30 m). Between 2006 and 2008, more than 7.5 million stone reefs, with a volume of 1 million m^3, 13,015 concrete reefs (650,000 m^3) and 60 derelict vessels (4,300 m^3) were deployed to construct the artificial reef zone, consisting of 12 artificial reef groups (Wu et al., 2012; Fig. 1). The nearshore artificial reef zone was designed to expand the boundary of the subtidal natural rocky reefs using man-made structure, and to enhance fish and invertebrate stocks in an area of 0.97 km^2 (Fig. 1). The model domain covered an area of 1.49 km^2, including both the natural and artificial reefs in the nearshore (Fig. 1).

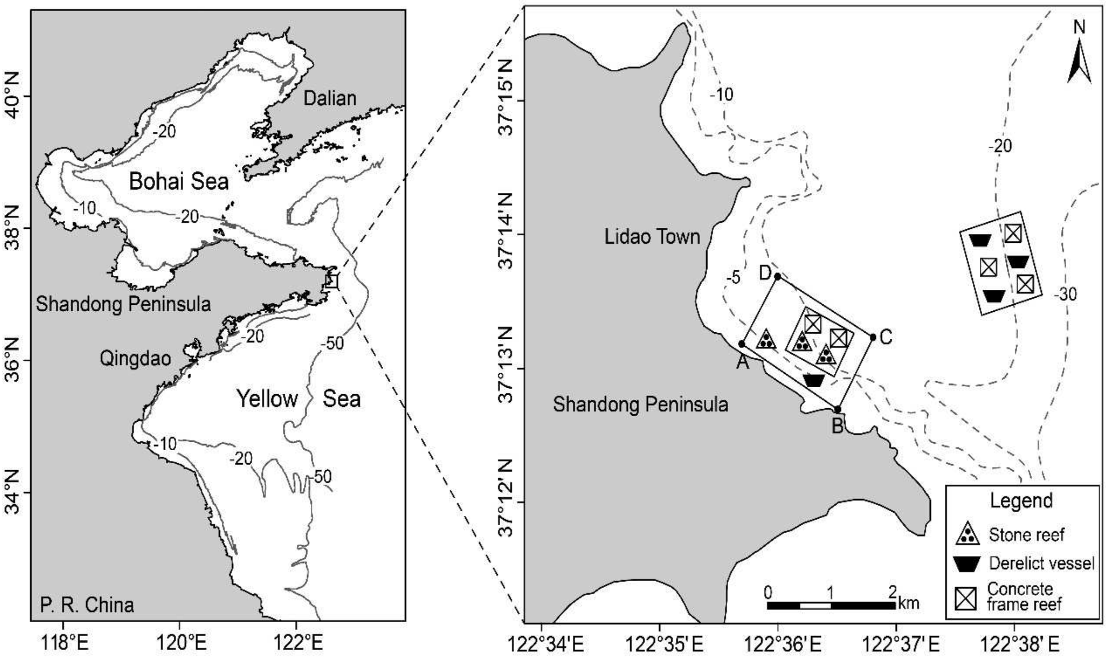

Figure 1. Schematic map showing the model domain, denoted by square ABCD (A and B represent the upper and lower boundary of the managed zone of Lidao Gaolv fishery company; C and D represent the points 1 km from the coast) in the Lidao nearshore artificial reef zone, northern China. The second square on the 20 m depth contour shows the offshore artificial reef zone, outside the model domain.

2.2 Aquaculture and fisheries

The Lidao artificial reef zone ecosystem is similar to the nearshore rocky reef waters of northern coast of China, where the natural resources have a diversity of uses, such as intensive suspended raft aquaculture to culture kelp. Lidao Bay is the main cultivation area for kelp (*Laminaria japonica*) in China, e.g., in 2013, 1,200 t/ km^2 wet weight of kelp were harvested over a cultivation area of 5,000 ha by the Gaolv Fishery Company (Gaolv Fishery Company, unpublished data). Commercial fishing in the nearshore zone is characterized by small-scale commercial fisheries. The artificial reefs were deployed in the area (starting in 2006) and release programs of cultured aquatic animals were initiated (in 2006) for species such as sea cucumber *Apostichopus japonicus*, abalone *Haliotis discus hannai* and Japanese flounder *Paralichthys olivaceus* to increase the productivity and restore fisheries resources in the region (Zhang et al., 2009). About 1.5 million abalone (shell width ≈ 30 to 40 mm) are released each year. Two size categories of sea cucumber are released each year: about 30 to 45,000 larger individuals (80 to 100 mm long) and 0.3 to 0.4 million smaller individuals (30 to 40 mm long) (Gaolv Fishery Company, unpublished data).

2.3 The Ecopath model

An Ecopath food web model was developed to describe the trophic flows in the Lidao nearshore ecosystem, covering both natural rocky reefs and artificial reefs, and Ecosim (EwE) was used to simulate the two different scenario (for details of the approach see Christensen and Walters, 2004). The model was parameterized based on two linear equations for each species or functional group to represent the energy balance between production and energy losses. During model development, biomass flows within groups are mass-balanced, such that consumption by a group accounts for its respiratory losses, biomass growth or decline and biomass production. Flows between groups are also balanced so that the biomass production of each group is sufficient to account for consumption by its predators and fishery catches (Walters et al. 2005). Thus, the production for each group can be expressed as follows:

$$B_i\left(\frac{P_i}{B_i}\right)\mathrm{EE}_i - \sum_{j=1}^{n} B_j\left(\frac{Q_j}{B_j}\right)\mathrm{DC}_{ji} - \mathrm{Y}_i - \mathrm{E}_i - \mathrm{BA}_i = 0 \qquad (1)$$

Where for each group *i*, B_i is biomass, EE_i is ecotrophic efficiency (≤ 1), P_i/B_i is the production/biomass ratio, Q_i/B_i indicates the consumption/biomass ratio of predator *j*, DC_{ji} is the proportion of prey *i* in the diet of predator *j*, Y_i is the fishery capture when the group is exploited, E_i is the net migration rate, and BA_i is the biomass accumulation rate. Few data were available for E_i and BA_i and they were not included in the model, i.e. this is equivalent to assuming that they have insignificant flows in this system. The input parameters for each functional group include B, P/B, Q/B, and DC_{ji}.

2.4 Model structure

We defined 20 functional groups (representing ~81 species and 11 aggregated taxonomic groups (e.g., copepods, isopods)), based on either similar biology and taxonomy (e.g., the Crustacean and Echinoderm groups) or ecological roles they played (e.g., Small pelagic fishes and Small demersal fishes) (see Appendix 1). Five single-species functional groups were included in the model because of their commercial (*A. japonicus, H. discus hannai*) or ecological importance (Korean rockfish *Sebastes schlegelii*, Fat greenling *Hexagrammos otakii*, Spottybelly greenling *Hexagrammos agrammus*) (Appendix 1). Three functional groups of fish were defined based on how they used the artificial reefs (Nakamura, 1985): Type I fishes represent benthic fishes that reside inside the structure of the rocky reef and come into direct contact with it (reef residents e.g., *Conger myriaster, Chirolophis otohime, Sebastiscus marmoratus*); Type II fishes are those species found closely associated with reefs (reef associated species), without coming into direct contact with it (e.g., *Kareius bicoloratus, Raja porosa* and *Cynoglossus joyneri*); and Type III fishes are those not closely associated with the artificial reefs, living primarily in the mid-water or pelagic zones over the reefs (water column species e.g., *Scomberomorus niphonius* and *Scomber japonicus*) (Appendix 1). Heterotrophic bacteria were also included in the model as an important link between primary production by kelp and detritus (Bengtsson et al., 2011; Duggins et al., 1989).

2.5 Input data and information sources

The sources of data for all the parameters for each functional group and species in the model are summarised in Appendix 2. Parameter estimates came from the study region wherever possible, other studies, estimates from equations and by the model itself.

(1) Biomass

Biomass data for 14 of the 20 functional groups were estimated from data collected during biological surveys in the model region in 2009 (Appendix 2). Fish and macroinvertebrates were surveyed using remotely operated video (ROV) census, SCUBA quadrat surveys, fence traps and long fishing traps (Wu et al., Ocean University of China, unpublished data). The density and the length-weight relationships for each fish species were used to estimate the biomass per km^2 (Wu et al., Ocean University of China, unpublished data). The species composition of the Cephalopods and Type III fishes functional groups were determined from the annual sampling with fence traps and long fishing traps within the study area, which provided data on numbers only. The biomasses for these groups were estimated from the surveys of the biotic community in the nearby waters of the Yellow Sea (Cheng, 2004).

The average biomass and production of the Heterotrophic bacteria were obtained from research in the Yellow Sea (Zhao, 2002) by multiplying the carbon units by 6.06 to convert them to wet weight. The biomass of phytoplankton was estimated by converting the average annual chlorophyll concentration (mg/m^3) to biomass from the following relationships: the ratio of organic carbon: chlorophyll a = 43:1 (Wang et al., 1998), the organic carbon: dry weight ratio = 35:100 (Ning et al., 1995), and the dry weight: wet weight ratio = 1:2.86 (Su and Tang, 2002). For detritus, biomass was calculated using the empirical equation of Pauly et al. (1993).

(2) Production/Biomass (P/B), and Consumption/Biomass (Q/B)

The P/B and Q/B ratios (year^{-1}) were calculated for the most representative species of each functional group. The P/B ratio is equivalent to the natural mortality (*M*, year^{-1}) for unfished species and it was estimated using the empirical equation from Pauly (1980). For exploited fish groups, fishing mortality (*F*, year^{-1}) was added to *M*. The P/B values of other benthic groups were taken from an *in situ* study for the same species (Zhou and Xie, 1995). The estimates of Q/B for most fish groups, except the Small pelagic and demersal fishes, were also obtained from the empirical equation of Palomares and Pauly (1998). For *H. discus hannai*, the P/B and Q/B ratios were taken from energy budget experiments for a similar species of abalone *Haliotis midae* Linnaeus in South Africa (Barkai and Griffiths, 1988). The P/B value of water column heterotrophic bacteria followed the study of Zhao (2002) in the same ecosystem Yellow Sea, while the Q/B ratio was estimated by the model. The estimates for P/B and Q/B of the remaining functional groups were taken from other related studies including the subtidal reefs of the Galapagos Islands (for *A. japonicus* and Benthic algae and seagrass), adjacent Eastern China Sea (Cephalopods and Small demersal fishes) and Bohai Sea (for Crustaceans, Echinoderms, Zooplankton, Small pelagic fishes, Molluscs and Phytoplankton) with similar species (see Appendix 2 and references cited therein).

(3) Diet composition

A predator/prey matrix was constructed based on stomach content studies conducted in the region where 423 stomachs were analyzed for Type I fishes, Type II fishes and Korean rockfish *S. schlegelii* (Wu et al., Ocean University of China, unpublished data). Also, unpublished feeding data in the same area was used for the construction of the matrix (Appendix 2).

(4) Landings

Three fishing gear types were defined for the artisanal fishery in the model: fence trap targeting Type II, Type III fishes and Small pelagic fishes; long fishing traps targeting *S. schlegelii* and *H. otakii,* and diving for *A. japonicus, H. discus hannai* and sea urchins. Landing data were obtained from Gaolv Fishery Company for the years from 2009 to 2012.

2.6 Model balancing

The Ecopath model was balanced following Blanchard et al. (2002) by checking that 1) all model input values were examined to determine whether they were within biologically plausible limits, 2) the ecotrophic efficiency (EEs) values were < 1.0, i.e. consumption was not allowed to exceed production for any group. The diet matrices for each of these groups with EE > 1 (initially Crustaceans, Cephalopods, and *H. otakii*) were adjusted manually until all EEs were < 1. The gross food conversion efficiencies (GE), representing the ratio of production to consumption, were also checked to ensure that they were in the range of 10% – 30% after balancing (see Wolff, 1994; Blanchard et al., 2002).

2.7 Model indicators

The uncertainty associated with the input values of the model was quantified based on the Pedigree routine in EwE, which provides a measure of the “quality” of data in the model (range = 0 to 1) based on the origin of the data used, assuming that parameters calculated from local data provide better estimates than those drawn from other regions. Each input is ranked from 0 (low quality, not rooted in local data) to 1 (high-quality, fully rooted in local data). The overall pedigree index (P) is calculated as:

$$P = \sum_{i=1}^{n} \frac{I_{ij}}{n}$$

where I_{ij} is the individual pedigree index value for group *i* and parameter *j* for each of the *n* living groups in the system.

The Ecopath model quantifies food web energy and biomass flows and several indices were employed to describe the structure and functioning of the artificial reef. We conducted a mixed trophic impact (MTI) analysis to assess the direct and indirect trophic interactions among compartments, including impacts of fishery practices throughout the system (Ulanowicz and Puccia, 1990; Christensen et al., 2005). This routine evaluates the effect of small increases in the biomass of one group on the biomass of the other groups, and thus provides a form of sensitivity analysis.

To assess the ecological role played by the groups within the artificial reef, we conducted a keystone species index (KS_i) (see Libralato et al., 2006).

$$KS_i = \log[\varepsilon_i * (1\text{-}p_i)]$$

where ε_i= overall effect of group *i* on other groups calculated by the MTI, and p_i represents the contribution of biomass from species *i* or functional group *i*, with respect to the total biomass of the food web.

We conducted a network analysis following Ulanowicz (1986) to estimate the following ecosystem indices: a) total system throughput, b) mean transfer efficiency (%) between trophic levels, c) Finn’s cycling index (FCI) (Finn, 1980), d) Finn’s mean path length (FML) (Finn, 1980), e) Connectance index and f) Omnivory index. The estimated net primary production, Phytoplankton and Zooplankton biomasses, total catches, mean trophic level of the catch, gross efficiency, the primary production required to sustain the fisheries and total biomass (excluding detritus), system overhead were also calculated (Christensen et al., 2005).

2.8 Simulations of temporal dynamics

Ecosim is time dynamic simulation module of EwE developed for policy exploration (Christensen and Walters, 2004). A key concept of Ecosim modelling is foraging arena theory, which partitions the availability of a prey group’s biomass to each predator group into vulnerable and refuge states (Christensen and Walters, 2004). The maximum mortality rate that a predator can exert on a prey is determined by the vulnerability (v) parameter in Ecosim. High values of v (top-down control) mean that predator consumption can control biomass, whereas a low value of v means prey biomass controls predator biomass (bottom-up control). We used Ecosim to evaluate the effects of fishing and aquaculture activities on this coastal ecosystem over a 20-year period. The two scenarios evaluated using this approach were:

1. Reduce all the current fishing effort to zero gradually in the first 3 years and then simulate forward for the remaining 17 years.

2. Increase the phytoplankton biomass by 100% and reduce the biomass of detritus by 40%, using a linear rate of change over 10 years and then project forward over 10 years. This scenario was used to represent a removal of kelp farms from the waters surrounding the modeled area and an increase in phytoplankton production.

Here, we took the average detrital biomass (83.320 t km^{-2}) of the Southern Yellow Sea (Lin et al., 2013) as the background value of detritus in the absence of values from the study area. A value of 40% was assumed for the detrital biomass contributed by culture kelp export, a value slightly lower than ~50% in California rocky habitats (Harrold and Reed, 1985) and 71% in Washington rocky habitats (Britton-Simmons et al., 2009). Our values may thus be an underestimate of the detrital subsidy from kelp culture in the adjacent waters.

The vulnerability setting was varied from 1 to 10 for each scenario to explore the corresponding responses of the ecosystem. Following these simulations, vulnerabilities of 2 and 3 were applied separately to all functional groups for Scenarios 1 and 2.

3. Results

3.1 Energy and mass flows

The highest contribution to the total biomass in the Lidao artificial reef model was from the benthic primary producers, comprising about 49% of the total biomass in the system (Table 1). Trophic levels 2-2.5 contributed the second highest biomass (about 40%) to the system. Trophic levels higher than 2.5, which included functional groups such as Small demersal fishes, Small pelagic fishes, *Hexagrammos agrammus*, Cephalopods, *Hexagrammos otakii*, *Sebastes schlegelii*, and Type I, II, and III fishes, contributed only < 3% to the total system biomass. Benthic finfish and most invertebrates (*Apostichopus japonicus*, *Haliotis discus hannai*, Crustaceans, Molluscs, Echinoderms, Other benthos), particularly *A. japonicus* (15.8%), Echinoderms (15.4%), *H. discus hannai* (8.5%), comprised about 48.9% of the total system biomass (620.20 t km^{-2} year^{-1}), highlighting the dominance of benthic components in the food web.

The trophic levels (TLs) of the 20 functional groups ranged from 1.0 for the primary producers (phytoplankton, benthic algae and seagrass) and detritus to 4.14 for Type III fishes (*Scomberomorus niphonius*) (Table 1). The mean TL (± 1 SD) for all fish groups was 3.6 ± 0.36, with Small pelagic fishes having the lowest trophic level (TL= 3.2). The mean TL for all the invertebrate groups was almost one trophic level lower than the fish (2.35 ± 0.52), with sea cucumber *A. japonicus* (TL = 2.1) and abalone *H. discus hannai* (TL = 2.0) having the lowest TLs of all invertebrate consumers, while the Cephalopod group had the highest invertebrate TL (3.5). Most of the functional groups (14 of 20) had a trophic level lower than 3.5, indicating that the Lidao artificial reef ecosystem was dominated by lower trophic groups.

Table 1 Summary of the input and output parameters for the 20 functional groups in the Ecopath model of the Lidao artificial reef ecosystem. P=Production; B=Biomass; Q=Consumption; E=Ecotrophic Efficiency. **Bold** = parameters estimated by the model. **—** = no value.

Functional group	Biomass （t/km^2· year）	P/B(year)	Q/B(year)	EE	Catch (t/km^2· year)	Trophic level
Type III fishes	0.252	1.1	8.8	**0.148**	0.040	4.1
Type I fishes	0.091	0.9	4.8	**0.243**	0.010	**3.8**
Type II fishes	0.083	0.9	3.8	**0.247**	0.005	**3.8**
Sebastes schlegelii	1.126	0.9	6.8	**0.386**	0.400	**3.8**
Hexagrammos otakii	0.583	0.7	3.4	**0.816**	0.060	**3.7**
Cephalopods	0.250	2.9	12.0	**0.858**	—	**3.5**
Hexagrammos agrammus	1.673	1.4	6.7	**0.440**	—	**3.3**
Small demersal fishes	**4.030**	1.3	9.3	0.950	—	**3.1**
Small pelagic fishes	2.600	2.4	7.9	**0.808**	0.300	**3.1**
Crustaceans	11.403	5.6	16.9	**0.905**	—	**2.8**
Other benthos	**13.554**	6.4	27.8	0.628	—	**2.2**
Apostichopus japonicus	98.000	0.6	3.4	**0.688**	40.000	**2.1**
Molluscs	24.700	4.4	17.2	**0.793**	—	**2.1**
Echinoderms	95.600	1.3	4.7	**0.282**	30.000	**2.1**
Haliotis discus hannai	52.500	0.5	9.9	**0.773**	16.000	**2.0**
Zooplankton	10.738	25.0	122.1	**0.482**	—	**2.0**
Heterotrophic bacteria	1.258	84.1	**171.6**	**0.321**	—	**2.0**
Benthic algae and seagrass	283.000	9.9	—	**0.379**	—	**1.0**
Phytoplankton	18.763	71.2	—	**0.881**	—	**1.0**
Detritus	130.000		—	**0.420**	—	**1.0**

The mean transfer efficiency for the system originating from primary producer and detritus was 11.7%. The total estimated energy transferred from TLI to TL II was 3,524 t km^{-2} year^{-1}, where 2,237 t km^{-2} year^{-1} t (63%) was from primary producers, and 1,287 t km^{-2} $year^{-1}$ from detritus. The detritivore: herbivore ratio (D: H ratio) was 0.58, indicating the herbivory is more important than detritivory in this ecosystem. Over half (54%) of the total system throughput in TL I was consumed directly by predators, indicating a strong interaction between TL I and II, far greater than the total system throughput for TLs II to IV (≈ 9%) (Fig. 2). In contrast, the respiration consumption increased after TL II, accounting for 60% of the total throughput from TLs II to IV, where the proportion of flows to detritus was 7 to 12% (Fig. 2).

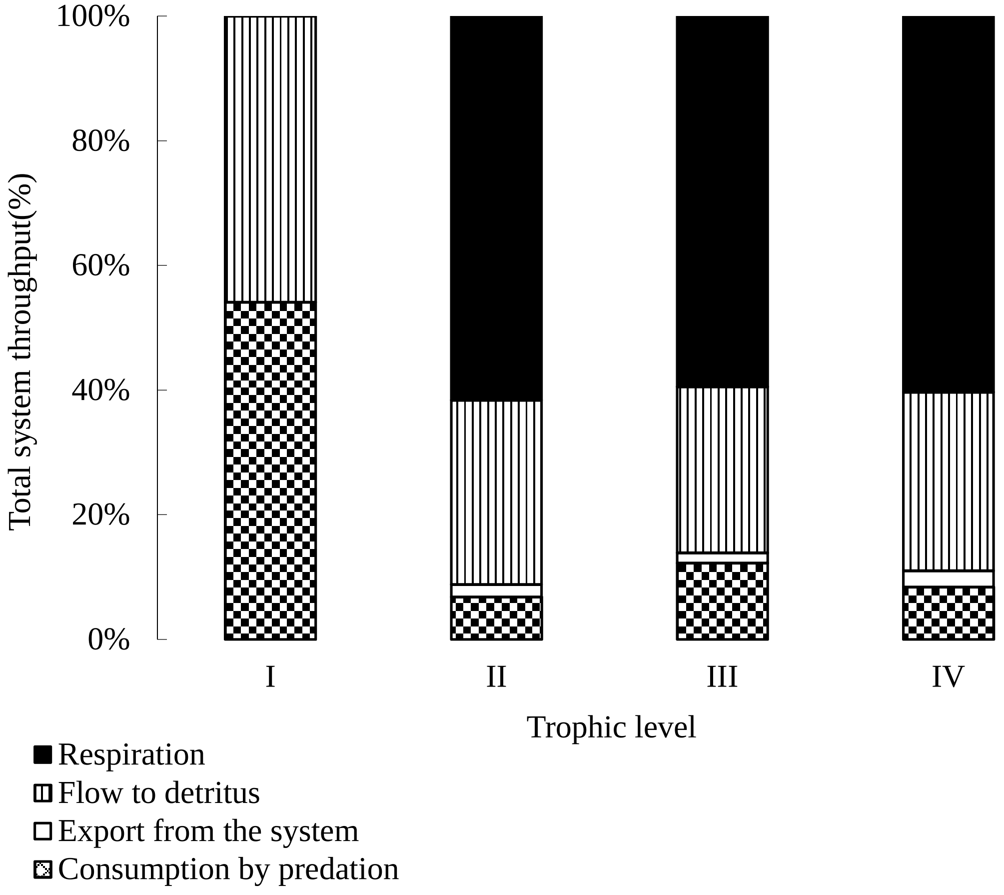

Figure 2. The proportion of main energy flow (%) in the total system throughput for each trophic level in the Lidao artificial reef ecosystem estimated by the balanced Ecopath model.

3.2 Mixed trophic impacts (MTI) and keystone indices

The MTI analysis showed that a 10% increase in the biomass of Benthic algae and seagrass had a positive effect on the biomass and trophic flow of herbivorous predators (grazers), such as abalone *H. discus hannai*, Echinoderms (*Strongylocentrotus nudus, Hemicentrotus Pulcherrimus*), Molluscs (small gastropod *Chrysostoma rustica*), and an associated increase in the catch of abalone and Echinoderms (particularly sea urchins) by divers (Fig. 3A). The major negative impacts observed from a 10% increase in biomass of benthic macrophytes were a reduction in biomass of benthic algae and seagrass, of nearly 30% and 10% for heterotrophic bacteria, due to the increase in the biomass of herbivorous groups (abalone, Echinoderm) and Other benthic group (i.e., Polychaetes) that consume algal detritus (Fig. 3A).

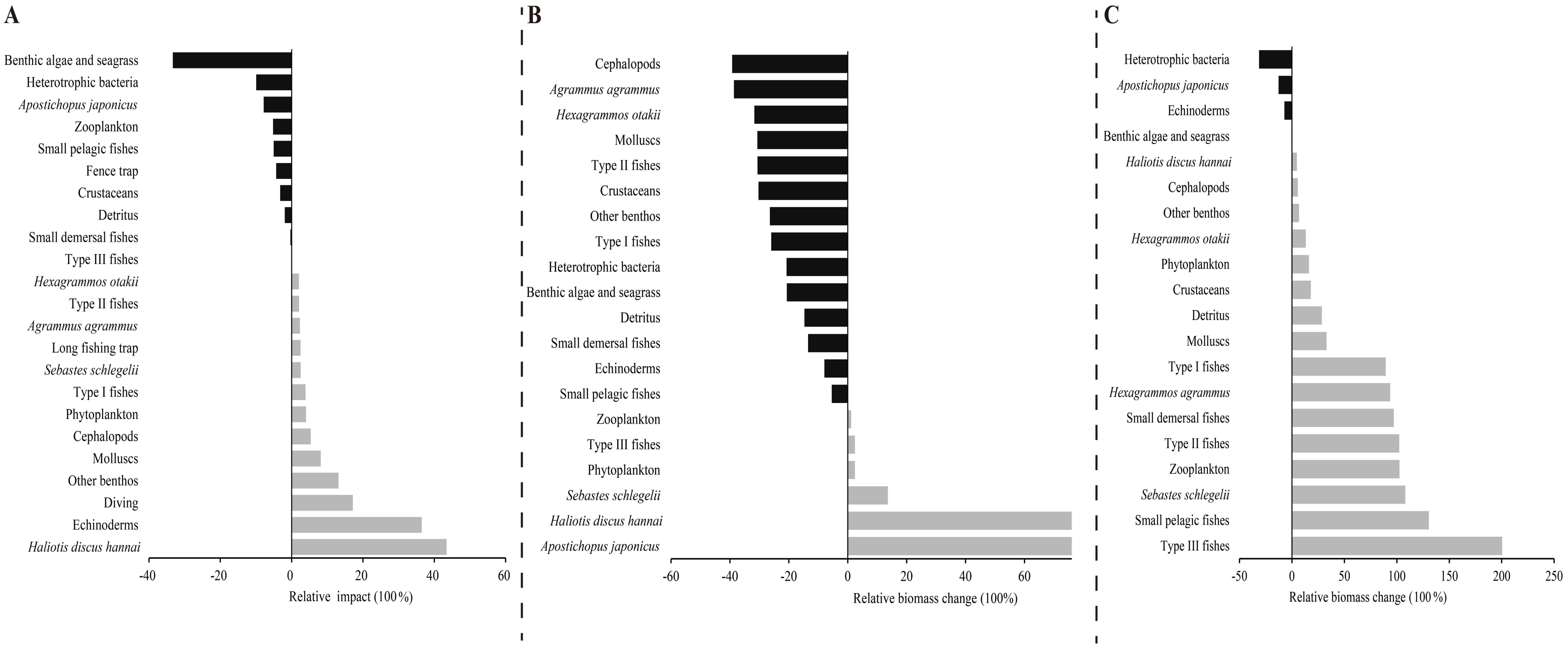

Figure 3. The change in relative biomass of functional groups or species in the Ecopath model of the Lidao artificial reef from A) the mixed trophic impact analyses of a 10% increase in the biomass of benthic algae and seagrass; B) after 20 years of closing all fisheries (keeping the original effort for the first 3 years); and C) at the end of 20-year simulated period for the scenario of increasing the biomass of phytoplankton by 100% and reducing the biomass of detritus by 40% over 10 years and simulating the changes for 10 years. Black = predicted decrease; grey = predicted increase in relative impact.

Table 2. Keystones indices and relative total impact for the functional groups of the Lidao artificial reef Ecopath model (modified from Libralato et al., 2006). Relative total impact is based on the Mixed Trophic Impact analysis and is the impact for each group, relative to the maximum effect measured.

Group number	Group name	Keystone index	Relative total impact
16	Zooplankton	-0.18	1.00
4	*Sebastes schlegelii*	-0.20	0.94
8	Small pelagic fishes	-0.23	0.88
15	Other benthos	-0.23	0.88
11	Crustaceans	-0.26	0.83
19	Phytoplankton	-0.26	0.84
13	Molluscs	-0.43	0.57
10	*Haliotis discus hannai*	-0.45	0.58
14	Echinoderms	-0.45	0.62
6	*Hexagrammos agrammus*	-0.46	0.52
18	Benthic algae and seagrass	-0.48	0.91
3	Type III fishes	-0.51	0.45
7	Small demersal fishes	-0.51	0.46
9	*Apostichopus japonicus*	-0.65	0.40
1	Type I fishes	-0.91	0.18
5	*Hexagrammos otakii*	-0.91	0.18
12	Cephalopods	-1.05	0.13
17	Heterotrophic bacteria	-1.14	0.11
2	Type II fishes	-1.39	0.06

Sebastes schlegelii had the second highest rank order in the relative total impact (0.94) and keystone index (-0.20) of all given groups (Table 2), but the lowest biomass of all the functional groups, indicating that it is a potential keystone species. The highest ranked group for these indices was the Zooplankton (-0.18, 1.00) and high values were also recorded for Other benthos and Small pelagic fishes (-0.23 and 0.88, Table 2). These groups had much higher biomass than *S. schlegelii* and therefore may be defined as structuring groups.

3.3 Network analysis and ecosystem properties

The total system throughput estimated for the Lidao model was 11,103.57 t km^{-2} year^{-1}, with a moderate proportion (41%) coming from the detritus. The system has a lower total biomass (excluding detritus) (620.205 t km^{-2} year^{-1}) than other tropical and subtropical rocky reef ecosystems such as the Galápagos subtidal rocky reef, Eritrean coast of the Red Sea, and Jurien Bay of Western Australia (Table 3). The primary production exceeded respiration (TPP/TR = 1.844) and the ratio of total primary production to total biomass of all functional groups in the model was 6.74. The mean trophic level of the catch in the Lidao artificial reef ecosystem (2.09) was the second lowest value of all the ecosystems, close to the value of the subtidal area in the Calvi Bay, Corsica (2.07) and slightly lower than Tongoy Bay, Chile (2.14) (Table 3). The catch gross efficiency (0.021), representing the ratio of the yield to the primary production, was similar in magnitude to that in Tongoy Bay (0.02) and higher than those for the other systems (Table 3). The values of the Connectance and the Ominivory indices for the Lidao artificial reef ecosystem (0.32 and 0.14) were similar in magnitude to those for a western Scotland coast ecosystem, but far less than those for the Red Sea coast (Table 3). The Lidao system had a low degree of detritus recycling and relative short trophic pathways that are similar in magnitude to those for Tongoy Bay, the Red Sea coast and the Mediterranean rocky littoral communities. Although the primary production required (PPR) to sustain the fisheries in the Lidao system (18.6%) was lower than that for Jurien Bay, Western Australia (36.9%) (Table 3), it is high compared with other coastal and reef systems (5.4 - 19.8%, Pauly and Christensen, 1995).

Table 3． A summary of the ecosystem attributes of the Lidao artificial reef estimated by the balanced Ecopath model compared with other coastal reef ecosystems.

Statistics and Flows	Lidao artificial reef China 37°13' N	Galápagos subtidal rocky reef Ecuador (Okey et al., 2004) 01°40' N	Jurien Bay Western Australia (Lozano-Montes et al., 2011) 30°18' S	Red Sea coast Eritrean (Tsehaye and Nagelkerke, 2008) 15°61'N	Subtidal area in Tongoy Bay Chile (Ortiz and Wolff, 2002) 30°15'S	Shallow water in Tongoy Bay (Wolff, 1994) 30°15'S	Western Scotland coast (Haggan and Pitcher, 2005) 55.30'N	Rocky coastal ecosystem Bahia Tortugas , Mexico (Morales-Zárate et al., 2011) 27.67'N	Sublittoral community of the Bay of Calvi, Corsica (Pinnegar, 2000) 42°35'N	Median	Units
Total system throughput	11103.57	94850	15343	66249	20593.9	20834.9	13672	553	13535	15343	t km^{-2} year^{-1}
Sum of all production	4990.33	17337	4318	25927	9976.4	9689.1	6267	-	3670.0	7978.05	t km^{-2} year^{-1}
Calculated total net primary production	1865.24	13250	2598	18179	8541.6	7125	5600	-	1929.396	6362.5	t km^{-2} year^{-1}
Phytoplankton biomass	18.763	12	17.1	20.5	28	28	80.000	-	4.570	19.6315	t km^{-2} year^{-1}
Total primary production/total respiration	1.82	0.48	1.1	1.002	2.7	1.772	4.509	1.05	0.796	1.1	dimensionless
Total primary production/total biomass	6.66	5.06	2.1	11.95	12.22	30.148	31.608	1.34	1.503	6.66	dimensionless
Total biomass/total throughput	0.06	0.03	0.08	0.023	0.034	0.011	0.013	-	0.095	0.032	dimensionless
Total biomass(excluding detritus)	620.20	2620	1229	1521	699.03	236.3	177.168	119.13	1284.056	699.03	t km^{-2}
Prop. Total flux originating from detritus	0.41	0.62	0.35	-	0.35	0.46	-	-	0.56	0.435	dimensionless
Mean transfer efficiency between TL	11.7	-	9.6	8.6	11.5	14.7	-	-	11.3	11.4	%
Mean trophic level of the catch	2.09	2.27	2.9	3.84	2.14	3.63	3.5	2.07	3.77	2.9	dimensionless
Gross efficiency (catch/net p.p.)	0.02	0.0003	0.0006	0.00011	0.02	0.0089	0.000335	-	-	0.0006	dimensionless
Primary production required to sustain the fishery	18.62	-	36.9	-	-	-	-	-	-	28.365	%
Finn’s cycling index	5.46	-	-	10.76	2.6	10.1	0.54	-	21.69	7.78	%
Mean length of trophic pathway	2.69	-	-	3.644	2.41	4.91	2.06	-	4.26	3.167	dimensionless
Connectance index	0.32	-	0.16	0.463	0.195	-	0.288	0.23	-	0.259	dimensionless
Omnivory index	0.14	-	0.25	0.206	0.139	-	0.175	0.23	0.344	0.206	dimensionless
Overhead (% of capacity)	-	-	-	72	72	67.4	-	80	-	-	%
Study Area	1.49	6.44	823	6000	-	-	31085	-	22		km^{2}
Number of groups	20	43	80	19	24	17	37	23	27		groups

3.4 Simulations of the impact of fishing and kelp cultivation activities

The Ecosim simulation of closing all fisheries (keeping the original state for the first 3 years) over 20 years resulted in an estimated near doubling in the relative biomass of the two commercially exploited species; *A. japonicus* (112% increase) and *H. discus hannai* (99%) (Fig. 3B). The biomasses of the targeted fish *S. schlegelii* and Type III fishes were also estimated to increase slightly (13.6% and 2.4%, respectively). In contrast, the relative biomasses of Type I, Type II fishes and *H. otakii* were predicted to decrease by about 30% at the end of the simulation (Fig. 3B).

The simulation of gradually removing kelp farms over 10 years and then projecting forward for 10 years resulted in estimated increases in the biomasses of Type III fishes by about 2 times and 1.2 times for Small pelagic fishes, the main prey of Type III fishes (Fig. 3C). In contrast, the relative biomasses of the Heterotrophic bacteria and detritivorous *A. japonicus* were predicted to decrease by 31.4% and 12.7%, respectively (Fig. 3C). Overall, the relative biomass of various epibenthic and pelagic groups increased significantly, while those of detritus-feeding taxa or functional groups declined (Fig. 3C).

4. Discussion

The Lidao artificial reef ecosystem, an area representative of the nearshore rocky reef waters of the northern coast of China, was characterized in the Ecopath model by greater benthic than water column productivity and the dominance of lower trophic level consumers in the ecosystem and commercial catch, particularly the detritivorous sea cucumber *Apostichopus japonicus* and herbivorous abalone *Haliotis discus hannai*. The simulation of closing the area to the culture of kelp predicted that the biomass of *A.japonicus* and Heterotrophic bacteria would decline by over 10%, while the biomasses of several fish species, particularly those of the small pelagic fishes and fish living in the mid-water over reefs (Type III fishes), were predicted to increase greatly. In contrast to the predicted decline in *A. japonicus* after stopping kelp culture, its biomass and that of *H. discus hannai* were predicted to increase by about 100% after 20 years of closing the area to fishing.

These estimates of ecosystem attributes and the model results depend on the quality of the data for the parameters in the model and the model structure and the definition of the modeled systems (Freire et al., 2008; Metcalf et al., 2008). The overall pedigree index (0.57) for the Lidao model, an indicator of how much data comes from the modeled region, was intermediate to high compared with the pedigree of 150 Ecopath models worldwide (0.16-0.68, Morissette et al., 2006). The major uncertainties in the input data were for some of the biological parameters for some of the functional groups (e.g. Crustaceans) and gaining knowledge on these components of the ecosystem would enhance the model and its predictions for understanding this ecosystem.

4.1 Energy and mass flow

Almost all the biomass in this system was concentrated in the first two trophic levels, with the sea cucumber, abalone and Echinoderms comprising a major component of the biomass of consumers. This dominance of the lower trophic level consumers might be attributed to the high productivity and standing crop of benthic macroalgae and seagrass in the area, which has been confirmed by the previous surveys (Guo et al., 2010; Zhang et al., 2012). Benthic macrophytes provide not only habitat but also food sources through various trophic pathways for marine organisms in coastal waters (Ortiz and Wolff, 2002; Okey et al., 2004; Pinnegar and Polunin, 2004; Gao et al., 2011; Lozano-Montes et al., 2011; Liu et al., 2013; Loneragan et al., 2013).

The high biomass of sea cucumber and other benthic species and functional groups may also be related to nutritional support of the much higher biomass of detritus in this system (130 t km^{-2}) than in the South Yellow Sea (Lin et al., 2013). According to Krumhansl and Scheibling (2012), the global average rate of detrital production by kelps accounts for 82% of the annual kelp productivity. In the Lidao region, the detrital pool is thus likely to be supplemented from the surrounding cultivated kelp farms with an estimated production of 1,200 tons/km^2 wet weight of kelp per year (Gaolv Fishery Company, unpublished data, 2013).

Three trophic pathways were identified in the nearshore Lidao artificial reef ecosystem, two involving grazing: one based on macrophytes and supporting the production of abalone and sea urchins; one based on the planktonic trophic pathway, connecting Zooplankton and the Small pelagic fishes and Type III fishes at the top of the pelagic food web; and the third based on detritus and dominated by sea cucumber and other benthos. In general, the grazing pathway, supported by benthic algae and seagrass, was more important than the detrital pathway in the system as the ratio of detritivores : herbivore was 0.58. This conclusion contrasts with some temperature systems where the detrital pathway dominates (Berry et al., 1979; Manickchand-Heileman et al., 1998; Pinnegar, 2000; Pinkerton et al., 2008). The difference in the Lidao region may be caused by the human interventions of deploying artificial reefs and releasing high value commercial fishery species on these reefs, particularly *A. japonicus, H. discus hannai* and *Paralichthys olivaceus*. The artificial reefs provide structure and attachment sites for sessile macroalgae, thus enhancing the food sources for those reef-based released species using the artificial reefs adjacent to natural reefs. This 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 (Spanier, 1989; Bell et al., 2006)

The mean transfer efficiency in the Lidao ecosystem is close to the mean value proposed by Ryther (1969) for temperate coastal ecosystems (15%) and close to the average transfer efficiency often assumed for aquatic ecosystems (Pauly and Christensen, 1995).

4.2. Stability and maturity of the Lidao artificial reef ecosystem

The Ecopath model had a low total system throughput and total production, indicating a system with a relatively lower internal energy, compared to other rocky reef or coastal ecosystems globally (Table 3). The ratio of total primary production to total respiration (TPP/TR) in this system (1.84) was greater than the value of mature systems (approaching 1, Odum, 1971), suggesting that the Lidao system is in the developing stage. Currently, the ecosystem overhead estimated for Lidao is intermediate among the temperate reef systems (Table 3), indicating that it has a moderate level of redundancy and is likely to be resilient against disturbances (Ulanowicz, 1986). The current Finn’s Cycling Level (5.46%), another measure of system maturity (*sensu* Rutledge et al., 1976) and system overhead (72.2%) placed the system in the lower intermediate range of these recorded values, indicating that it may fluctuate between stages of development.

System maturity also can be evaluated by the Connectance index and the system Omnivory index, since a food chain is expected to change from linear to web-like as it approaches maturity (Odum, 1971). The low values of these two indices for the Lidao system imply weak trophic interactions between the components of the ecosystem. As a whole, the Lidao artificial reef ecosystem had a relative low maturity, stability and disturbance resistance, indicating a developing, rather than mature system.

4.3 Fishery status and impacts on the ecosystem

Although the total biomass of fishery resources harvested from the system was relatively high (86.82 t/km^2), the average trophic level of the catches was low (2.09), markedly lower than the average estimate of catch trophic level for global coast and reef systems (2.5) (Pauly and Christensen, 1995). These findings are similar to those from other rocky reef ecosystems such as Tongoy Bay, Chile (2.14) (Ortiz and Wolff, 2002), Bahia Tortugas, Mexico (2.07) (Morales-Zárate et al., 2011) and Galapagos rocky reef systems (2.27) (Okey et al., 2004) (Table 3), where lower order invertebrate consumers are important components of the fisheries. Indeed, the low trophic level of the catch in the Lidao ecosystem is mainly because the fisheries are highly selective, targeting herbivorous and detritivorous species, mainly the sea cucumber *A. japonicus* (TL = 2.1, 46.1% of the catch), other echinoderms (TL = 2.1, 34.6%), (sea urchin *Asterias amurensis; Strongylocentrotus nudus*) and abalone *H. discus hannai* (TL = 2.0, 18.4%). The intense fishing pressure in this system is thought to have resulted in recruitment overfishing of depleted top predator stocks in the Yellow Sea (Jin and Tang, 1996; Liu, 2013), leading to a local example of “fishing down marine food webs” (Pauly et al., 1998). The intense fishing pressure is driven by the lucrative financial incentives due to increasing market demands for sea cucumber (Chen, 2005), abalone (Cheung, 2001) and sea urchin (Ding et al., 2007).

Fisheries in the current system have a direct impact on the population of target species, and an indirect impact on non-target species as shown from by results of the mixed trophic impacts analyses and the Ecosim predictions (Fig. 3B). For example, when the fishing pressure was reduced through a total closure over 20 years (keeping the original effort for the first 3 years), the most significant responses were observed among the main target species of sea cucumber *A. japonicus* and abalone *H. discus hannai*, which were predicted to increase in biomass by about 100%. The decline in fishing mortality also resulted in a predicted decrease in the biomass of the group of small demersal fish and *Hexagrammos agrammus*, possibly due to the predicted population increase of their predators or competitors, particularly *Sebastes schlegelii*, which was identified as a keystone species in linking the trophic components of ecosystem. Previous research has also suggested that fisheries have a potential to change the structure and function of small marine ecosystems (e.g., Pauly et al, 2002; Heymans et al., 2004; Frank et al., 2007).

4.4 The impacts of kelp cultivation on the ecosystem

The simulation of the removal of kelp farms from the adjacent waters of the Lidao coastal ecosystem indicated that the nearshore kelp cultivation is likely to have restricted the trophic flow into the water column primary production and strengthened the benthic food web. It is likely that kelp cultivation provides significant energy subsidies for the stock enhancement of benthic organisms. Similar massive kelp culture in Sangou Bay, 10 km south of the current study site, has suppressed the abundance of phytoplankton markedly during the kelp growing season (Shi et al., 2011). In this system, trophic flows were affected by kelp culture, either directly through the increased nutrients introduced for kelp culture (Newell, 2004), or indirectly through changing the local oceanographic currents and nutrient flows caused by the kelp rafts (Shi et al., 2011). Shi et al. (2011) estimated that the suspended kelp aquaculture in Sangou Bay reduced the average surface current speed by 40%, decreasing the water exchange with the open sea. 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).

4.5 Conclusion

The coastal nearshore reef system of northern China with intense kelp culture, release programs and fishing activities was shown to be dominated by benthic production, with fishery catches that are low in the food web, due to the focus on the very high value sea cucumber and abalone species. A series of system attribute parameters indicated the ecosystem had a relatively low maturity, stability and disturbance resistance, and was classified as a developing system. This ecosystem was dominated by benthic production and the simulation results suggest that kelp culture is likely to provide a significant subsidy to the benthic detritus and contribute to the low importance of water column production and grazing in the system.

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Appendix 1. Description of the functional groups for the Ecopath model of Lidao artificial reef ecosystem, Shandong Peninsula, China

Functional Group（Nos of species）	**Species**				
Type I fishes（6）	*Conger myriaster*	*Zoarces elongatus*	*Chirolophis otohime*	*Sebastes hubbsi*	*Sebastiscus marmoratus*
	Sparus macrocephalus				
Type II fishes（6）	*Raja porosa*	*Paralichthys olivaceus*	*Cleisthenes herzensteini*	*Pseudopleuronectes herzensteini*	*Kareius bicoloratus*
	Cynoglossus joyneri				
Type III fishes	*Scomberomorus niphonius*	*Scomber japonicus*			
Sebastes schlegelii	*Sebastes schlegelii*				
Hexagrammos otakii	*Hexagrammos otakii*				
Hexagrammos agrammus	*Hexagrammos agrammus*				
Small demersal fishes（6）	*Tridentiger trigonocephalus*	*Enedrias fangi*	*Ernogrammus hexagrammus*	*Hemitripterus villosus*	*Pseudoblennius zonostigma*
	Synechogobius ommaturus				
Small pelagic fishes（5）	*Strongylura anastomella*	*Engraulis japonicus*	*Sardinella zunasi*	*Thryssa kammalensis*	*Okamejei kenojei*
Apostichopus japonicus	*Apostichopus japonicus*				

Haliotis discus hannai	*Haliotis discus hannai*				
Crustaceans（19）	*Charybdis japonica*	*Oratosquilla oratoria*	*Palaemon gravieri*	*Alpheus distinguendus*	*Alpheus japonicus*
	Tachypenaeus curvirostris	*Crangon affinis*	*Leptochela gracilis*	*Latreutes planirostris*	*Callianassa japonica*
	Pugettia quadidens	*Paguristes*.sp	*Hemigrapsus sanguineus*	*Carcinoplax vestita*	Amphipoda
	Isopoda	*Acanthomysis* sp	Cumacea	*Nebalia bipes*	
Cephalopods（2）	*Octopus variabilis*	*Loliolus japonica*			
Molluscs（9）	*Crassostrea gigas*	*Mytilus edulis*	*Chrysostoma rustica*	*Thais luteostoma*	*Pleurobranchaea novaezealandiae*
	Npatunede cumingi	*Rapana venosa Valenciennes*	*Lepidozona coreanica*	*Pleurobranchaea novaezealandiae*	
Echinoderms（5）	*Asterias amurensis*	*Strongylocentrotus nudus*	*Hemicentrotus Pulcherrimus*	*Asterina pectinifera*	*Ophiuroidea*.sp
Other benthos（4）	*Lumbrineridae*.spp	*polychaete*.spp	*Bryozoa*	*Brachiopoda*	
Zooplankton（8）	Copepods	Chaetognath	Tunicata	Other planktonic larva	Megalopa larva
	Rhopilema esculenta	*Acetes chinensis*	Fish eggs		
Heterotrophic bacteria	Water column bacteria				
Benthic algae （15）and seagrass（2）	*Sargassum thunbergii*	*Cladophora* sp	*Ulva pertusa*	*Gelidium amansii*	*Sargassum Pallidum*

	Chondrus ocellatus	*Plocamium telfairiae*	*Laminaria japonica*	*Gracilaria lemaeiformis*	*Lomentaria* sp
	Sargassum horneri	*Grateloupia turuturu*	*Codium fragile*	*Enteromorpha intestinalis*	*Undaria pinnatifida*
	Zostera marina	*Phyllospadixi watensis Makino*			
Phytoplankton	Dominated by diatoms and dinoflagellates				
Detritus	Organic matter (DOC + suspended POC), organisms dead or dying animals, plants (plankton), protists (diatoms)				

Appendix 2. Sources of data for the input parameters for the Ecopath model of Lidao artificial reef ecosystem, Shandong Peninsula, China.

P/B estimated = estimated from the sum of fishing mortality and natural mortality (by the Pauly [1980] method); Q/B estimated = estimated from Palomares and Pauly (1998) (for details see Methods); Ecotrophic Efficiency values were estimated by the model, except for Small demersal fishes (Jiang et al., [2008] and Other benthos (Lin et al., [2009]). Landings data were provided by GLFCL = Gaolv Fishery Company Ltd.

Trophic group	Biomass	P/B	Q/B	Diet
Type Ⅰ fishes	*in situ* estimation visual line transect surveys	Estimated	Estimated	*in situ* stomach content analysis
Type Ⅱ fishes	*in situ* estimation visual line transect surveys	Estimated	Estimated	*in situ* stomach content analysis
TypeⅢ fishes	modification from initial reference(Cheng,2004)	Estimated	Estimated	Yang (2001a)
Sebastes schlegelii	*in situ* estimation visual line transect surveys	Estimated	Estimated	*in situ* stomach content analysis
Hexagrammos otakii	*in situ* estimation visual line transect surveys	Estimated	Estimated	Ji (2014)
Hexagrammos agrammus	*in situ* estimation visual line transect surveys	Estimated	Estimated	Ji (2014)
Small demersal fishes	model estimation	Jiang et al. (2008)	Jiang et al. (2008)	Yang (2001a)
Small pelagic fishes	modification from initial reference(Cheng,2004)	Tong and Tang (2000)	Tong and Tang (2000)	Yang (2001a)
Apostichopus japonicus	*in situ* measurements by SUCBA quadrat	Okey et al. (2004)	Okey et al. (2004)	Zhang et al. (1995)
Haliotis discus hannai	*in situ* measurements by SUCBA quadrat	Barkai and Griffiths (1988)	Barkai and Griffiths (1988)	Guzman del Proo et al. (2003)

Crustacean	*in situ* estimation visual line transect surveys	Lin et al. (2013)	Lin et al. (2013)	Yang (2001b)
Cephalopods	modification from initial reference(Cheng,2004)	Jiang et al. (2008)	Jiang et al. (2008)	Yang (2001b)
Molluscs	*in situ* measurements by SUCBA quadrat	Tong and Tang (2000)	Tong and Tang (2000)	Tong and Tang (2000)
Echinoderms	*in situ* measurements by SUCBA quadrat	Lin et al. (2009)	Lin et al. (2009)	Tsehaye and Nagelkerke (2008)
Other benthos	model estimation	Zhou and Xie (1995)	Lin et al. (2009)	Christian and Luczkovich (1999)
Zooplankton	*in situ* measurements	Lin et al. (2009)	Lin et al. (2009)	Jiang et al. (2008)
Heterotrophic bacteria	*in situ* estimation (Zhao,2002)	*in situ* measurements (Zhao,2002)	Model estimation	Jiang et al. (2008)
Bethic algae and seagrass	*in situ* measurements by SUCBA quadrat	Okey et al. (2004)		
Phytoplankton	*in situ* chl a concentrations (Ning et al.,1995; Su and Tang,2002; Wang et al.,1998)	Tong and Tang (2000)		
Detritus	*in situ* estimation by empirical relationship(Pauly et al.,1993)			

Appendix 3. Diet matrix for the functional groups in the Ecopath model of the Lidao artificial reef ecosystem, Shandong Peninsula, China.

Group No	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Type I fishes	0.020																
2	Type II fishes	0.010	0.030															
3	Type III fishes																	
4	*Sebastes schlegelii*																	
5	*Hexagrammos otakii*	0.050	0.050		0.030	0.010												
6	*Hexagrammos agrammus*	0.151	0.100		0.120													
7	Small demersal fishes	0.230	0.250		0.226	0.304	0.173	0.010					0.100					
8	Small pelagic fishes		0.050	0.865	0.150	0.092	0.055	0.004	0.017				0.100					
9	*Apostichopus japonicus*	0.001													0.001			
10	*Haliotis discus hannai*	0.001											0.005	0.001	0.005			
11	Crustaceans	0.101	0.120	0.083	0.203	0.203	0.144	0.200	0.158			0.150	0.300		0.030			
12	Cephalopods	0.030	0.050	0.052	0.002				0.023									
13	Molluscs	0.162	0.060		0.007	0.056	0.033	0.065		0.055	0.010	0.175	0.295	0.050	0.010			
14	Echinoderms	0.115	0.020		0.120	0.050						0.020	0.020					
15	Other benthos	0.100	0.170		0.136	0.240	0.205	0.100		0.010	0.010	0.200	0.040					
16	Zooplankton	0.028	0.100		0.007	0.036	0.323	0.564	0.772	0.016	0.021	0.050	0.100	0.050		0.110		
17	Heterotrophic bacteria									0.005		0.020		0.020		0.050		0.005
18	Benthic algae and seagrass				0.000	0.009	0.067	0.057		0.158	0.939			0.180	0.766	0.250		
19	Phytoplankton								0.030	0.005		0.080		0.200		0.040	0.800	0.050
20	Detritus									0.751	0.020	0.305	0.040	0.500	0.188	0.550	0.200	0.945

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