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Comparing marine ecosystems of Laizhou and Haizhou Bays, China, using ecological indicators estimated from food web models

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ABSTRACT

Two Ecopath mass-balance models are built to describe the structural and functional ecosystems of Laizhou Bay (LZB) for 2014–2015 and Haizhou Bay (HZB) for 2011–2012. This is the first comparative study to analyze the similarities and differences between these two bays using ecological indicators estimated from a food web model. A comparison between the two models highlights similar characteristics in trophic functioning: zooplankton and shrimps as the structuring groups are important organisms enabling the pelagic-benthic coupling in the two ecosystems; and top-down effects are the main mechanism of control within the two ecosystems. Analysis of differences between the two ecosystems indicates that: (1) the ecological size (total system throughput, TST), total exports/TST and ecosystem efficiencies are bigger in LZB; (2) the bottom-up controls from the benthos, shrimps and zooplankton are enhanced in LZB; and (3) the ecosystem state is less mature but more stable in LZB. These differences can be attributed, at least in part, to the effects of sea ranching of low trophic-level species, such as shellfish and the holothurian *Stichopus japonicus*, in LZB. Analysis of similarities and differences may benefit the ecosystem-based approach to fisheries management in different ecosystems.

1. Introduction

Bays play important economic and ecological roles in regional social-ecological systems, and habitats within them connect the land to the ocean. In Laizhou Bay (LZB) and Haizhou Bay (HZB), China, intensive fishing has contributed to biodiversity loss (Jin and Deng, 2000; Tang et al., 2011; Zhang et al., 2014), changes in community structure (Jin and Deng, 2000; Tang et al., 2011), regime shifts in fish trophic ecology (Zhang et al., 2013), and fishing down the food web (Zhang et al., 2015a). To sustainably manage these highly diverse and productive marine ecosystems, models can be developed to parameterize the structural and functional components of food webs to facilitate ecosystem-based approaches to fisheries (EAF).

Anthropogenic impacts have exceeded the ability of natural systems to regulate and adapt to change (Rockström et al., 2009), leading to

changes in the structure and functioning of ecosystems. In recent decades the EAF framework has encouraged development of ecological models, which assist in identifying the structure and function within ecosystems. One popular, freely available modeling framework is Ecopath with Ecosim (EwE). Ecopath was first created by Polovina (1984), before being improved and extended into EwE by Christensen and Pauly (1992) and Walters et al. (1997, 1999). EwE is now the tool most applied for modeling marine and aquatic ecosystems globally (Heymans et al., 2016), and can be used to analyze and document food web structure and ecosystem functioning in a mass-balanced way (Polovina, 1984; Christensen and Pauly, 1992). It describes and parameterizes ecosystem components and their interactions, and has been widely applied to quantify ecosystem status with ecological indicators (Reed et al., 2017), and to track the effects of anthropogenic and environmental stressors on ecosystems (Shin et al., 2010; Heymans et al., 2014;

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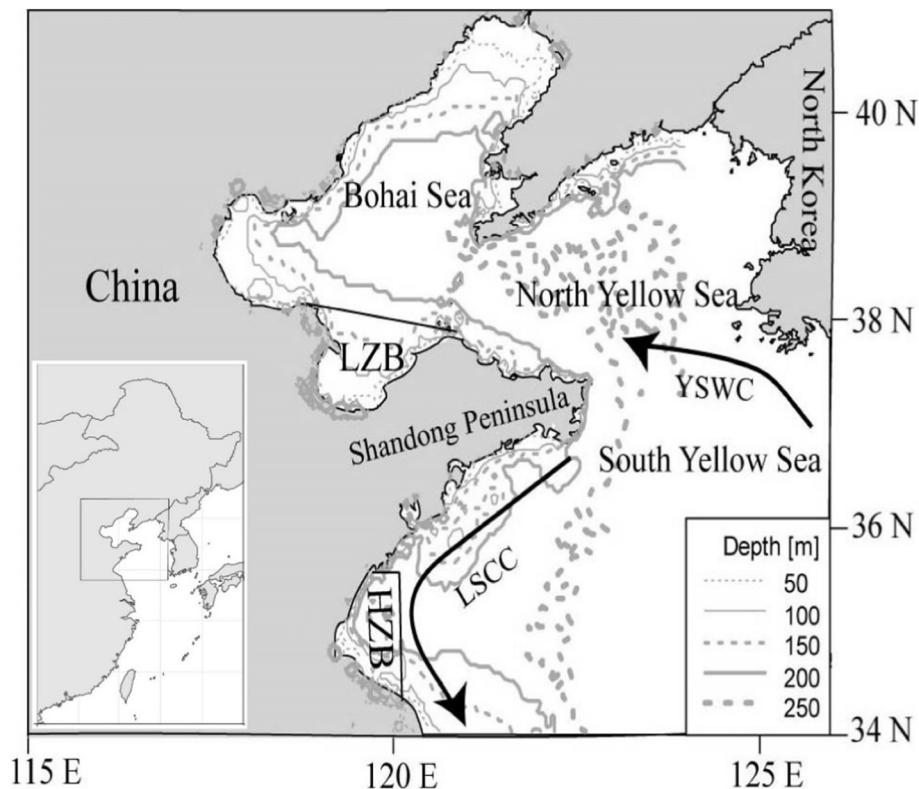


Fig. 1. Modeled areas of LZB (Laizhou Bay) and HZB (Haizhou Bay and its adjacent waters). YSWC is the Yellow Sea Warm Current, LSCC is the Lunan and Subei Coastal Current.

Reed et al., 2017); it has also played a key role in implementing an ecosystem-based approach to fisheries management (Rochet and Trenkel, 2003; Rochet et al., 2010). Here, we explore ecological indicators about flows, ecological roles and maturity of ecosystems estimated from EwE to compare the structure and functioning of LZB and HZB.

Our two survey sites, LZB and HZB, are similar, but are located on opposite sides of Shandong Peninsula (Fig. 1), and have different fishing histories. LZB is a site of considerable low trophic-level species sea ranching (Xu and Kan, 2016). In LZB the artificial elevation of species biomass can modify local food-web structure, and the direction and strength of energy flow, whereas that in HZB is likely to be more natural. However, enhancement of depleted fisheries resources in HZB has not led to their recovery, especially of low trophic-level macrobenthic species (Sun et al., 2011; Fu et al., 2017). Therefore, these two survey sites probably differ in the structure and functioning of their food webs.

If key indicators of ecosystem structure and functioning can be identified, comparisons between different ecosystems can be made (Lassalle et al., 2013). Key indicators must reflect ecosystem characteristics, and be concrete, easily understandable, inexpensive, accurate, sensitive, and respond quickly and in a specific way to a type of pressure (Rice and Rochet, 2005). Their identification will improve understanding of ecosystem structure and functioning, and consequently, improve EAF.

Previous studies in LZB and HZB have focused on reporting the biodiversity of these sites (Jin and Deng, 2000; Tang et al., 2011; Zhang et al., 2014), population structure (Jin and Deng, 2000; Tang et al., 2011), and trophic ecology (Zhang et al., 2013, 2015a). Studies describing food web structure and ecosystem functioning using trophic models are scarce. Modeling studies in these bays have focused on species capacity (LZB: Lin et al., 2013a; HZB: Wang et al., 2016) and energy flow in parts of a bay (HZB: Zhang et al., 2015b). No comparison of the structure and functioning using food-web models for these two

bays exists. Our study objectives are to: 1) develop a food web model for LZB that incorporates sea-ranching species, and a contemporaneous HZB model for a larger area (including the entire bay and adjacent waters); 2) characterize the structure and functioning of food webs within the two bays; and 3) compare food web structure and functioning using ecological indicators from food web models for these two bays.

2. Materials and methods

2.1. Study area

2.1.1. Laizhou Bay

At almost 6966 km², LZB (37°39'–41' N, 119°16'–120°13' E) is the largest bay in Shandong Province. It is relatively enclosed, at its deepest 18 m, but usually shallower than 10 m (Compiling Committee of Records of China Bays, 1991) (Fig. 1). The physical and hydrological features of this bay are influenced by waters of the Yellow Sea Cold Water Mass and outflows of the Yellow, Xiaoqing and Jiaozhou Rivers. These different water masses greatly influence phytoplankton dynamics and food webs (Jin et al., 2013), as a consequence of which LZB is a recognized spawning and fishing ground (Deng and Jin, 2000), and has become an important area for sea ranching (Zhang et al., 2013).

2.1.2. Haizhou Bay

HZB (34°45'–35°05' N, 119°21'–29' E) is a typical open bay of about 876 km² located off the southern Yellow Sea (Fig. 1); the seabed throughout it is typically shallower than 10 m (Compiling Committee of Records of China Bays, 1993). This bay is influenced by the Lunan and Subei Coastal Current, and the Yellow Sea Warm Current (Guo et al., 2004). Waters are highly productive, rich in fisheries resources, and the region is a famous fishing ground in China (Su et al., 2013). However, intensive fishing, pollution, and habitat damage increasingly degrade its fishery resources (Zhang et al., 2006; Su et al., 2013). The model

area of HZB includes the entire bay and adjacent waters (Fig. 1).

2.2. Ecopath approach

The two food web models were built using EwE, version 6.5 (freely available at <http://www.ecopath.org/>). Ecopath model parameterization is based on a system of linear equations, which express the mass balance of energy entering and leaving a system:

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

where B_i and B_j are the biomass of functional groups i and j , respectively, P_i/B_i the production/biomass ratio of group i , EE the ecotrophic efficiency (the proportion of the production that is utilized in the ecosystem), Y_i the fishery catch rate of group i , $(Q/B)_j$ the consumption/biomass ratio for the predator j , DC_{ij} the proportion of prey i in the diet of predator j , BA_i the biomass accumulation of group i and E_i the net migration rate of group i .

To reduce complexity, species with similar ecological characteristics (e.g., diet, habitat) are categorized into functional groups. The same number (33) of functional groups was recognized in LZB and HZB (Appendix Table A1). Commercially farmed species (*Stichopus japonicus*, *Rapana venosa* and *Charybdis japonica*) are treated as separate functional groups in LZB.

Input parameters B , P/B , Q/B , diets and catches, were required to parameterize Ecopath models. We based our estimate of the B of seabirds in both models on the southern Yellow Sea model (Lin et al., 2013b). The B for fishes and invertebrates in both models was estimated by the swept-area method (Gulland, 1969) according to trawl surveys (LZB in Autumn: September 2014, Winter: December 2014, Spring: March 2015, Summer: June 2015; HZB in Autumn: October 2011, Winter: December 2011, Spring: April 2012, Summer: June 2012). The trawl net was 30 m long, 15 m wide and 6 m high at the entrance, and the mesh size was 20 mm. The duration of each haul varied from 1 to 3 h at an average ship speed of 3 nautical mile/h. The B of zooplankton in the two models was estimated by the survey samples (the mesh size was 505 μm and the mouth was 0.25 m^2) couple with trawl surveys. We based our estimate for the B of phytoplankton in both models on the southern Yellow Sea model (Li et al., 2009; Lin et al., 2013b). The P/B in both models was based on total mortality from the literature (Cheng et al., 2009; Li et al., 2010; Huang, 2011; Lin et al., 2006, 2013a,b; Liu et al., 2014; Sun, 2014). The Q/B was obtained from Fishbase (Froese and Pauly, 2019) or literatures (Cheng et al., 2009; Ouyang and Guo, 2010; Lin et al., 2013a,b). Diets (Appendix Table A2) were estimated from literatures (Yang, 2001; Zhang et al., 2012; Lin et al., 2013b). Catch was estimated primarily from fisheries statistics yearbook (Bureau of Fishery of Ministry of Agriculture, 2013).

Models were considered balanced when (a) EE values were < 1.0 , (b) the gross food conversion efficiency (P/Q) was < 0.5 (usually between 0.1 and 0.3), and (c) when P/R values were < 1.0 (Darwall et al., 2010; Heymans et al., 2016). To achieve balanced models, we corrected the diet matrix, P/B and Q/B , especially when information was sourced for areas outside that which we modeled. If models remained unbalanced, we also slightly modified biomass values, as estimates from trawl surveys may be underestimates (Sánchez and Olaso, 2004).

2.3. Ecological indicators and network properties

We used network analysis to calculate ecological indicators. We consider the total system throughput (TST)—the sum of consumption (Q), exports (Ex), respiratory flows (R), and flows into detritus (FD)—as a measure of the ‘ecological size’ of a system (Finn, 1976), and its metabolism (Ortiz et al., 2015). More descriptive indicators, such as the total primary production to total respiration ratio (PP/R), PP /total biomass (PP/B), and B/TST , describe system maturity (Odum, 1969;

Christensen, 1995). Finn's cycling index ($FCI = TST_c/TST$) quantifies the relative importance of cycling to TST, and reflects stress and structural differences (Finn, 1976); TST_c represents recycled total flow. Finn's mean path length (FMPL) indicates food chain length. The connectance index (CI) and the system omnivory index (SOI) reflect the complexity of inner linkages within an ecosystem (Christensen and Walters, 2004). Ascendency (A) is an index of the degree of development and maturity of an ecosystem (Ulanowicz, 1986); it is negatively correlated with ecosystem maturity (Christensen, 1995). Overhead (O) is an indicator of the degree of freedom, and represents the capacity of an ecosystem to withstand perturbations (Ulanowicz, 1986; Christensen, 1995; Angelini and Petrere, 2000). The total mean transfer efficiency (mTE), a geometric mean of transfer efficiencies for each of the integer trophic levels II to IV, is the ratio of the sum of exports from a given trophic level (TL) and flow transferred from one TL to the next, over the TL throughput (Christensen et al., 2005). The mean trophic level of a community (MTL)—the weighted average TL for functional groups with $TL > 2$ —reflects the effect of fishing on a food web (Pauly et al., 1998). Additionally, a marine trophic index (MTI_0), the MTL of group catches with TL exceeding 3.25 (Bourdaud et al., 2016), reflects trophic structure in the upper part of a food web (Pauly and Watson, 2005). The high trophic indicator (HTI) is the percentage of top predators (trophic level ≥ 4) in an ecosystem, and the apex predator indicator (API) is the percentage of top or apex predators (trophic level ≥ 4) to the total number of predators (trophic level > 3.25) (Bourdaud et al., 2016).

2.4. Mixed trophic impact (MTI) assessment and keystoneess

Mixed trophic impact (MTI) as an economic input–output analysis was adapted to ecological networks by Ulanowicz and Puccia (1990), and implemented in Ecopath by Christensen and Walters (2004). MTI analysis is calculated by constructing an $n \times n$ matrix; it provides a preliminary quantification of direct (predation) and indirect (competition) feeding interactions between functional groups in an ecosystem (Ulanowicz and Puccia, 1990; Christensen and Walters, 2004). MIT values are positive if a small increase in the biomass of an impacting group (including fishing fleets) leads to an increase in the biomass of an impacted group, or negative if they cause a decrease (Ulanowicz and Puccia, 1990; Christensen et al., 2008). While negative elements of MTI indicate negative effects, such as the effects of a predator on prey, positive elements indicate the effects of prey on a predator, enabling estimation of top-down (TD) and bottom-up (BU) effects, respectively (Libralato et al., 2006). The TD of the ‘keystoneess’ i can be estimated by the negative contributions to the overall effect ϵ_i (Libralato et al., 2006). The BU equals to 1-TD, with TD calculated:

$$TD = \frac{\sum_{j \neq i}^n m_{ij}^2 (m_{ij} < 0)}{\sum_{j \neq i}^n m_{ij}^2} \quad (2)$$

where m_{ij} , the element of MTI matrix, represents the relative impact of the impacting group i on the impacted group j .

Key functional groups include keystone and structuring species (Power et al., 1996). Keystone species are defined as those predators of relatively low biomass that have a disproportionately high effect on a food web (Valls et al., 2015). Structuring species are those that have a large effect on a food web due to their relatively high biomass (Piraino et al., 2002). We use indices of ‘keystoneess’ indices of Libralato et al. (2006) (KS_L) and Valls et al. (2015) (KS_V) to identify keystone and structuring functional groups:

$$KS_L = \log(\epsilon_i \times (1 - p_i)) = \log \left(\sqrt{\sum_{i \neq j}^n m_{ij}^2} \times \left(1 - \frac{B_i}{\sum_k B_k} \right) \right) \quad (3)$$

Table 1

Input and output (bold) parameters for LZB and HZB: TL, trophic level; C, catch (t, km⁻² y⁻¹); B, biomass (t, km⁻² y⁻¹), P/B, production/biomass ratio (y⁻¹); Q/B, consumption/biomass ratio (y⁻¹); EE, ecotrophic efficiency; P/Q, production/consumption ratio (y⁻¹); F, fishing mortality rate; M_p, predation mortality rate (y⁻¹). * = balanced data. [Numbers in square brackets] refer to data sources: [1] Lin et al. (2013a), [2] Cheng et al. (2009), [3] Bureau of Fishery of Ministry of Agriculture (2013), [4] Sun (2014), [5] Ouyang and Guo (2010), [6] Fishbase, [7] Lin et al. (2013b), [8] Huang (2011), [9] Lin et al. (2006), [10] Liu et al. (2014), [11] Li et al. (2010).

	Group name	TL	C[3]	B	P/B	Q/B	EE	P/Q	F	M _p
LZB No										
1	Seabird	3.151	0	0.002	0.400*	67.022[7]	0	0.006	0.000	0.000
2	Ray	4.382	0.0001	0.001	0.590*	4.900*	0.339	0.120	0.200	0.000
3	Spotted sardine	2.464	0.204	0.533	2.500*	12.100[1]	0.182	0.207	0.383	0.072
4	Madura anchovy	3.345	0.107	0.113	3.260[1]	11.650[5]	0.619	0.280	0.947	1.072
5	Anchovy	3.202	0.084	0.154	3.000[2]	10.200[5]	0.866	0.294	0.545	2.053
6	Spotted spanish mackerel	4.173	0.021	0.040	1.670[1]	5.730[5]	0.383	0.291	0.519	0.120
7	Silver pomfret	3.346	0.037	0.026	2.320[1]	9.100[1]	0.640	0.255	1.443	0.042
8	Other pelagic fishes	3.376	0.035	0.074	1.740*	8.900[1]	0.949	0.196	0.472	1.179
9	Small yellow croaker	3.957	0.090	0.114	1.658[1]	5.910[5]	0.891	0.281	0.786	0.691
10	Others of Sciaenidae	4.110	0.006	0.017	1.068[1]	5.700[1]	0.762	0.187	0.376	0.437
11	Seabass	4.419	0.001	0.002	1.058[1]	4.000[1]	0.891	0.265	0.700	0.243
12	Bartail flathead	4.291	0.002	0.003	1.180*	4.120[5]	0.839	0.286	0.647	0.343
13	Largehead hairtail	4.334	0.001	0.002	1.490*	5.270[5]	0.882	0.283	0.471	0.844
14	Greenling	3.764	0.040	0.036	2.060[4]	7.800[6]	0.626	0.264	1.124	0.166
15	Other demersal fishes	3.566	0.007	0.089	1.210*	4.950[1]	0.591	0.244	0.078	0.638
16	Gobiidae	3.325	0.038	0.068	1.980*	7.613[6]	0.985	0.260	0.561	1.390
17	<i>Sebastes schlegelii</i>	4.434	0.029	0.027	1.730*	6.400[6]	0.616	0.270	1.066	0.000
18	Snailfishes	3.965	0.001	0.002	1.320*	4.600[5]	0.885	0.287	0.429	0.740
19	Slender lizardfish	4.506	0.0003	0.001	0.520[1]	4.510[5]	0.957	0.115	0.250	0.247
20	Other benthic fishes	4.394	0.001	0.003	1.260[1]	4.930[1]	0.788	0.256	0.176	0.817
21	Cephalopods	3.550	0.005	0.029	3.300[1]	15.000[2]	0.957	0.220	0.151	3.006
22	Mantis shrimp	3.353	0.036	0.039	8.000[1]	30.000[1]	0.591	0.267	0.927	3.799
23	Shrimps	2.891	0.034	0.228	8.000*	27.000[2]	0.981	0.296	0.149	7.698
24	<i>Charybdis japonica</i>	2.967	0.401	0.324	3.500*	15.000[5]	0.488	0.233	1.237	0.473
25	Other crabs	2.967	0.043	0.197	3.600*	15.000[5]	0.995	0.240	0.218	3.365
26	<i>Rapana venosa</i>	2.265	10.511	8.377	6.000*	27.000[1]	0.227	0.222	1.255	0.107
27	Other shellfish	2.265	0.780	1.234	6.000*	27.000[1]	0.440	0.222	0.632	2.009
28	<i>Stichopus japonicus</i>	2.275	4.102	4.040	1.200[1]	4.580*	0.857	0.262	1.015	0.013
29	Jellyfish	3.042	0.170	0.069	5.100[1]	25.050[1]	0.849	0.204	2.464	1.868
30	Benthos	2.203	–	4.605	9.000[1]	33.000*	0.878	0.273	0.000	7.902
31	Zooplankton	2.042	–	4.954	25.000[1]	125.000[1]	0.807	0.200	0.000	20.176
32	Phytoplankton	1.000	–	17.716	106.200[1]	–	0.242	–	0.000	25.667
33	Detritus	1.000	–	43.000[2]	–	–	0.280	–	–	–
HZB No										
1	Seabirds	3.520	–	0.001	0.400*	67.022[7]	0.001	0.006	0.000	0.001
2	Sharks and rays	4.280	0.001	0.002	0.590[2]	5.200[2]	0.440	0.114	0.260	0.000
3	Spotted sardine	2.476	0.001	0.012	2.500[8]	10.000[5]	0.948	0.250	0.430	1.941
4	Anchovy	3.209	0.013	0.058	3.000[7]	10.200[5]	0.912	0.294	0.231	2.506
5	Mackerel	3.330	0.005	0.013	2.010[9]	11.040[5]	0.977	0.182	0.433	1.531
6	Silver pomfret	3.286	0.022	0.032	1.130[9]	8.250[5]	0.777	0.137	0.672	0.206
7	Other pelagic fishes	3.375	0.054	0.090	2.277*	14.473[6]	0.774	0.157	0.598	1.164
8	Small yellow croaker	3.868	0.008	0.032	1.658[9]	5.910[5]	0.978	0.281	0.257	1.365
9	Others of Sciaenidae	3.949	0.006	0.018	1.067*	5.700[6]	0.954	0.187	0.314	0.705
10	Bartail flathead	3.869	0.016	0.031	1.180[7]	4.120[6]	0.620	0.287	0.532	0.200
11	Largehead hairtail	3.988	0.029	0.039	1.490[9]	5.270[5]	0.906	0.283	0.744	0.607
12	Greenling	3.872	0.006	0.015	2.060[4]	7.800[6]	0.796	0.264	0.372	1.267
13	Pholis	3.085	0.056	0.187	1.620[10]	7.540[5]	0.500	0.215	0.298	0.511
14	Mullet	2.329	0.083	0.185	1.162[11]	11.600[6]	0.559	0.100	0.451	0.198
15	Other demersal fishes	3.197	0.010	0.099	1.203*	8.088[6]	0.972	0.149	0.105	1.064
16	Gobiidae	3.317	0.016	0.036	1.980*	7.614[6]	0.926	0.260	0.451	1.382
17	Scorpionfishes	4.095	0.002	0.036	1.430*	5.851[6]	0.472	0.244	0.042	0.633
18	Snailfishes	3.970	0.020	0.033	1.320*	4.600[6]	0.675	0.287	0.629	0.263
19	Bluefin gurnard	3.846	0.015	0.038	1.170*	3.910[5]	0.935	0.299	0.395	0.699
20	Pleuronectiformes	4.219	0.007	0.014	2.050[10]	7.590[6]	0.912	0.270	0.469	1.400
21	Congers	4.194	0.020	0.022	1.550[2]	5.400[7]	0.703	0.287	0.915	0.175
22	Other benthic fishes	4.424	0.016	0.027	1.260*	4.950[6]	0.879	0.255	0.570	0.537
23	Cephalopods	3.535	0.015	0.031	3.300[7]	15.000[7]	0.939	0.220	0.485	2.613
24	Mantis shrimp	3.432	0.008	0.025	8.000[1]	30.000[1]	0.814	0.267	0.314	6.199
25	Shrimps	2.862	0.062	0.220	8.000[7]	28.000[7]	0.919	0.286	0.283	7.069
26	Crabs	3.007	0.042	0.172	3.500[7]	12.000[7]	0.815	0.292	0.247	2.607
27	Shellfish	2.294	0.053	0.110	6.000[1]	27.000[1]	0.757	0.222	0.478	4.064
28	Echinoderms	2.293	–	0.080	1.200[1]	4.580[1]	0.416	0.262	0.000	0.500
29	Jellyfish	2.613	0.002	0.026	5.000[7]	20.000[7]	0.793	0.250	0.096	3.870
30	Benthos	2.380	–	4.965	5.000[2]	20.000[2]	0.994	0.250	0.000	4.972
31	Zooplankton	2.053	–	4.555	25.000[7]	180.000[7]	0.393	0.139	0.000	9.817
32	Phytoplankton	1.000	–	9.884	106.520[7]	–	0.357	–	0.000	38.029
33	Detritus	1.000	–	43.000[2]	–	–	0.273	–	–	–

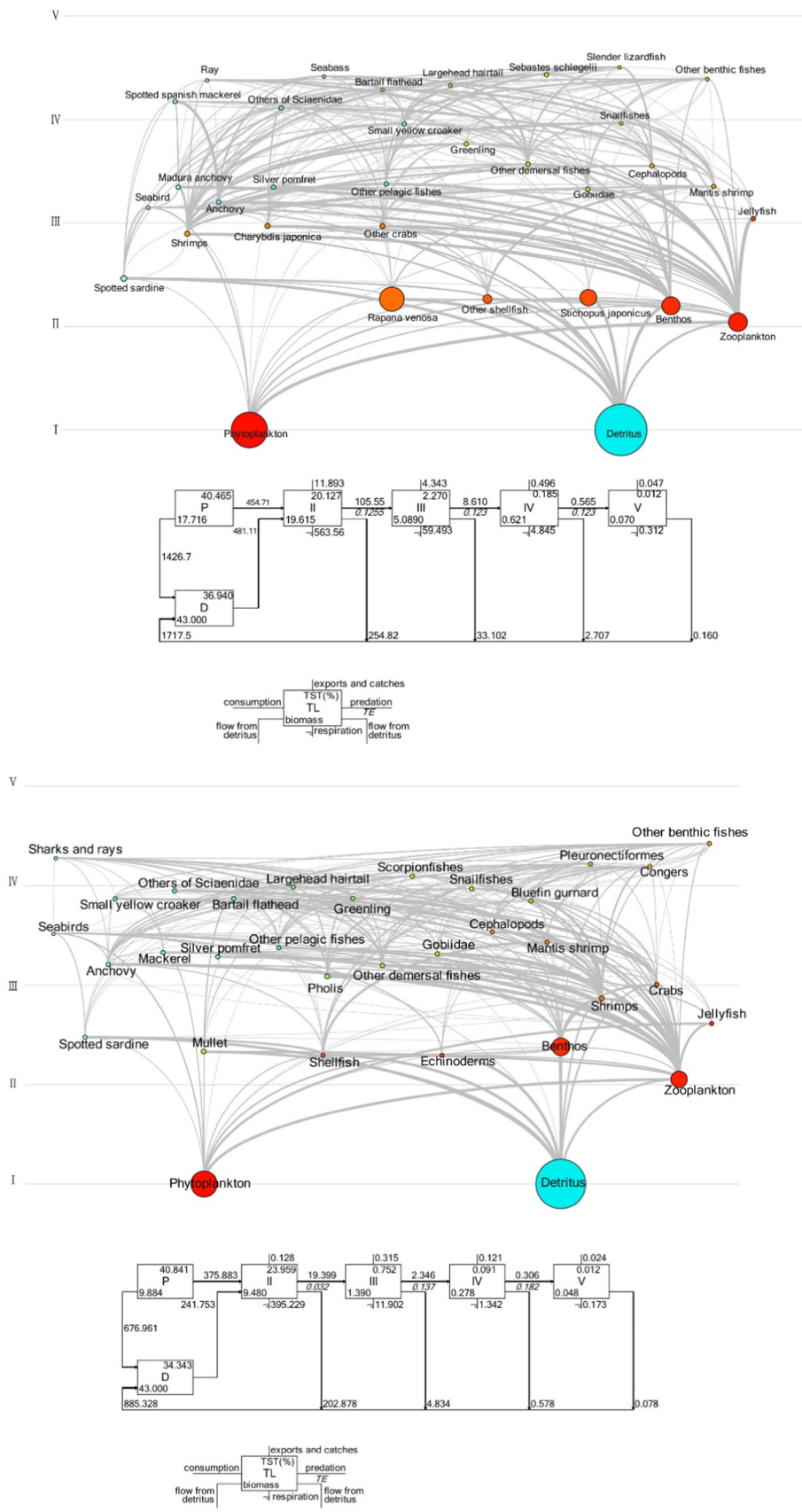


Fig. 2. Trophic structure, biomass, flow and transfer efficiencies for LZB and HZB. Circle size is proportional to biomass; P = primary producer (Phytoplankton), D = detritus.

$$KS_V = \log \left(\sqrt{\sum_{i \neq j}^n m_{ij}^2} \times \text{drank}(B_i) \right) \quad (4)$$

where p_i is the contribution of a functional group i to the total biomass of the food web, and B_i is the biomass of functional group i . The abbreviation 'drank' in Eq. (4) represents the rank of a variable, in descending order (see Valls et al. (2015) for a complete description).

3. Results

3.1. Basic model and ecosystem properties

Pedigree indices (Appendix Table A3) for LZB (0.62) and HZB (0.63) indicate that input data for the two models are of reasonable quality (Morissette, 2007). Basic input (biomass, landing, P/B, Q/B) and estimated output (trophic level, ecotrophic efficiency, predation, and fishing mortality rate) parameters of the two models are summarized in Table 1, and in the appendices (the composition of functional groups in Table A1, and diet composition in Table A2). Quantification of trophic flow among detritus- and grazing-based food webs describes the process of pelagic-benthic coupling (Fig. 2). In each balanced model we organized functional groups into five TLs (Fig. 2): in LZB, TL ranged 1 (primary producers and detritus) to 4.506 (slender lizardfish) (Table 1); in HZB, TL ranged 1 (primary producers and detritus) to 4.424 (other benthic fishes) (Table 1, Appendix Table A1). In each model, biomass decreased with increasing TL (Appendix Fig. A1); low TL species accounted for a large portion of biomass, especially in LZB.

EE varied greatly among functional groups in each model (Table 1). Functional groups containing commercial species had high EE values as they were heavily exploited and had high fishing mortality (Table 1), such as seabass (in LZB), small yellow croaker (in LZB) and largehead hairtail (in HZB). Similarly, high EE values were observed in prey species with high mortality by predation (Table 1), such as benthos and shrimps (in LZB and HZB), and zooplankton (in LZB). The lower EE values for primary producers in each model indicated that a larger percentage of production from these groups flowed through to detritus.

Aggregated summary statistics and indicators of network flows and ecosystem structure for each model are listed in Table 2. For LZB, total system throughput (TST) was $4678.316 \text{ t km}^{-2} \text{ y}^{-1}$, comprising percentage contributions of detritus (36.7%), exports (26.8%), consumption (23.1%), and respiration (13.4%). For HZB, TST was $2628.831 \text{ t km}^{-2} \text{ y}^{-1}$, of which 33.7% flowed to detritus, 26.3% was consumed, 24.5% was exported, and 15.5% was respired.

The flows in each model were directly from detritus, or indirectly from primary production by detritus- and grazing-based food chains, respectively (Fig. 2). The majority of flows in each ecosystem occurred between TLs I, II, and III, collectively representing 99.802% (LZB) and 99.896% (HZB) of TST (Appendix Table A4). The proportion of the total flow originating from detritus was 0.48 in LZB, and 0.44 in HZB (Table 2). Consumption of detritus by TL II taxa, mainly zooplankton and benthic invertebrates, was high in each model (Fig. 2). In LZB, the mean TE (mTE) from the detritus food web (12.431%) was similar to that of the primary producer food web (12.366%), but in HZB the mTE from the detritus food web (8.855%) was lower than that from the primary producer food web (9.245%) (Table 2). The TE of different TL in each model are presented in Appendix Table A4. For LZB and HZB, values for MTL were 2.281 and 2.352, respectively, and for MTI_0 , 3.640 and 3.734, respectively (Table 2).

3.2. The MTI analysis and keystone

MTI analysis indicates fisheries have the greatest, directly negative impact on most functional groups, and for functional groups to also have a negative impact on themselves due to intraspecific competition for prey resources (Fig. 3). The functional groups containing *R. venosa*,

Table 2

Ecological indicator statistics and flows, ecosystem status, ecosystem efficiencies, and trophic level for LZB and HZB models.

Indicators	Acronym	Units	LZB	HZB
Statistics and flows				
Total consumption	Q	$\text{t km}^{-2} \text{ y}^{-1}$	1079.346	690.649
Total exports	Ex	$\text{t km}^{-2} \text{ y}^{-1}$	1253.207	644.177
Flows to detritus	FD	$\text{t km}^{-2} \text{ y}^{-1}$	1717.531	885.338
Total respiration	R	$\text{t km}^{-2} \text{ y}^{-1}$	628.232	408.667
Total production	P	$\text{t km}^{-2} \text{ y}^{-1}$	2116.684	1196.696
Total system throughput	TST	$\text{t km}^{-2} \text{ y}^{-1}$	4678.316	2628.831
Total consumption/TST	Q/TST	–	0.231	0.263
Total exports/TST	Ex/TST	–	0.268	0.245
Flows to detritus/TST	FD/TST	–	0.367	0.337
Total respiration/TST	R/TST	–	0.134	0.155
Total production/TST	P/TST	–	0.452	0.455
Total biomass/TST	B/TST	–	0.009	0.008
Ecosystem maturity status				
Primary production/total respiration	PP/R	–	2.995	2.576
Primary production/total biomass	PP/B	–	43.634	49.930
Finn's cycling index	FCI	%	4.655	6.392
Finn's mean path length	F MPL	%	2.487	2.497
System omnivory index	SOI	–	0.219	0.238
Connectance index	CI	–	0.281	0.297
Ascendency/capacity	A/C	%	32.207	34.781
Overhead/capacity	O/C	%	67.793	65.219
Shannon diversity index	H	–	1.773	1.462
Ecosystem efficiency				
Mean transfer efficiency	mTE	%	12.378	9.245
mTE from primary production	mTEpp	%	12.366	8.855
mTE from detritus	mTEd	%	12.431	8.799
Proportion of total flow originating from detritus	PFFD	–	0.48	0.44
Trophic indices				
Mean trophic level of the community	MTL	–	2.281	2.352
Marine trophic index	MTI_0	–	3.640	3.734
High trophic index	HTI	%	0.112	0.158
Apex predator indicator	API	%	14.041	18.922

zooplankton, and benthos exerted the greatest impact in LZB (Fig. 3). The effects of *R. venosa* were directly negative on prey functional groups, such as benthos, and indirectly negative on interspecific competition functional groups, such as invertebrates and pelagic fishes. However, the impacts of prey functional groups, such as zooplankton and benthos, were directly or indirectly positive in LZB (Fig. 3). In HZB, functional groups including sharks and rays, zooplankton, and shrimps exerted the greatest impact on the food web (Fig. 3). As top predators, sharks and rays exerted a negative top-down effect on the food web; as prey, zooplankton and shrimps exerted a positive bottom-up effect.

The first four functional groups are presented in Table 3 in decreasing order of KS_L and KS_V (Fig. 4). Keystone and structuring groups are identified for each model, according to two keystone indices and corresponding definitions. In LZB, the others of Sciaenidae, other benthic fishes, ray and *Sebastes schlegelii* may represent keystone functional groups (Table 3). In HZB, sharks and rays, mantis shrimp, benthic fishes (other), and Pleuronectiformes are keystone functional groups. Owing to their relatively high biomass and high keystone indices (Tables 1 and 3), *R. venosa*, zooplankton, benthos and shrimps in LZB, in addition to zooplankton and shrimps in HZB, are considered to be structuring groups.

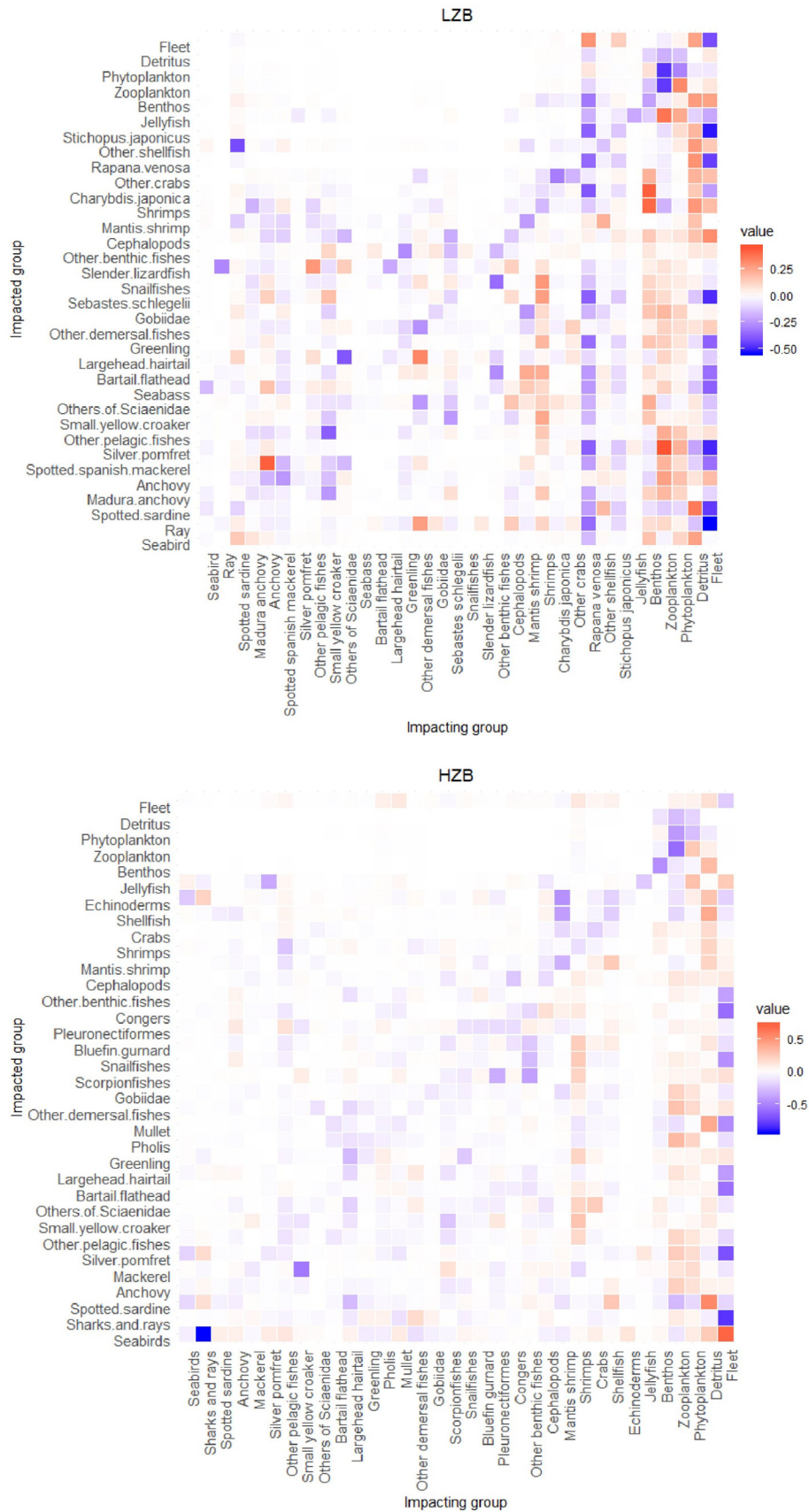


Fig. 3. Mixed trophic impact assessment of the LZB and HZB.

Table 3

Top four functional groups in decreasing order of keystone indices. K, keystone; S, structuring group; TL, trophic level; B%, relative biomass; TD, top-down effect; BU, bottom-up effect; f.g., functional group.

Model	Functional group	Keystoneness rank order							
		KS _L				KS _V			
		1	2	3	4	1	2	3	4
LZB	Functional group	Rapana venosa	Zooplankton	Benthos	Shrimps	Others of Sciaenidae	Other benthic fishes	Ray	Sebastes schlegelii
	KS	-0.025	-0.058	-0.124	-0.180	1.064	1.056	0.952	0.944
	K or S	S	S	S	S	K	K	K	K
	TL	2.265	2.042	2.203	2.891	4.110	4.394	4.382	4.434
	B%	19.428	11.490	10.709	0.529	0.039	0.008	0.001	0.063
	TD	0.934(93.4%)	0.322(32.2%)	0.092(9.2%)	0.037(3.7%)	0.896(89.6%)	0.999(99.9%)	0.998(99.8%)	0.889(88.9%)
	Overall TD: 0.646(64.6%)								
	BU	0.066(6.6%)	0.678(67.8%)	0.908(90.8%)	0.963(96.3%)	0.104(10.4%)	0.003(0.1%)	0.002(0.2%)	0.111(11.1%)
	Overall BU: 0.354(35.4%)								
	HZB	f.g.	Sharks and rays	Zooplankton	Shrimps	Mantis shrimp	Sharks and rays	Mantis shrimp	Other benthic fishes
KS		-0.009	-0.156	-0.174	-0.188	1.483	1.192	1.096	1.044
K or S		K	S	S	K	K	K	K	K
TL		4.280	2.053	2.862	3.432	4.280	3.432	4.424	4.219
B%		0.010	21.600	1.043	0.120	0.010	0.120	0.129	0.068
TD		0.896(89.6%)	0.457(45.7%)	0.108(10.8%)	0.974(97.4%)	0.896(89.6%)	0.974(97.4%)	0.940(94.0%)	0.889(88.9%)
Overall TD: 0.767(76.7%)									
BU		0.104(10.4%)	0.543(54.3%)	0.892(89.2%)	0.026(2.6%)	0.104(10.4%)	0.026(2.6%)	0.060(6.0%)	0.111(11.1%)
Overall BU: 0.233(23.3%)									

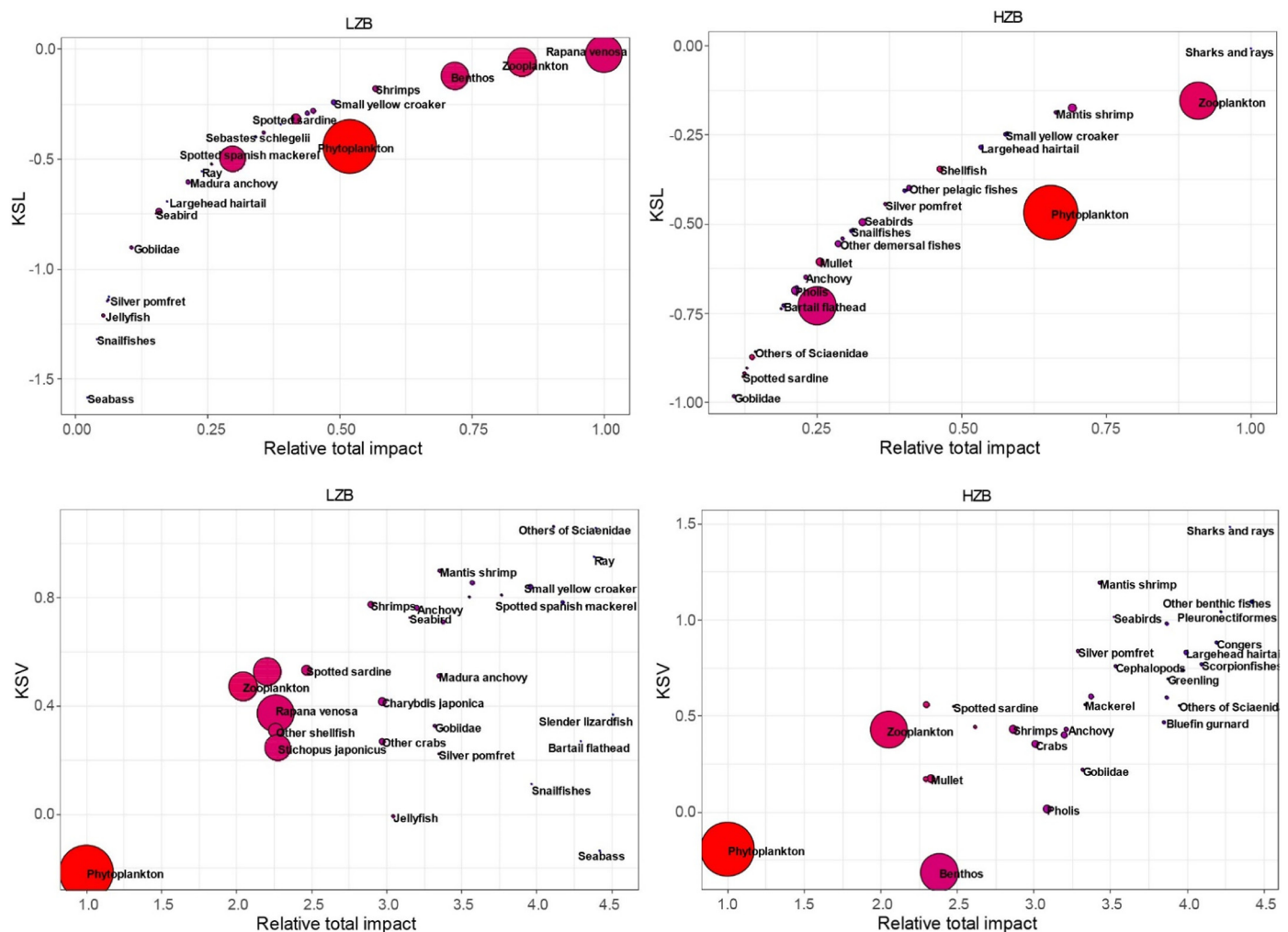


Fig. 4. KS_L and KS_V for functional groups in LZB and HZB. Circle size is proportional to biomass.

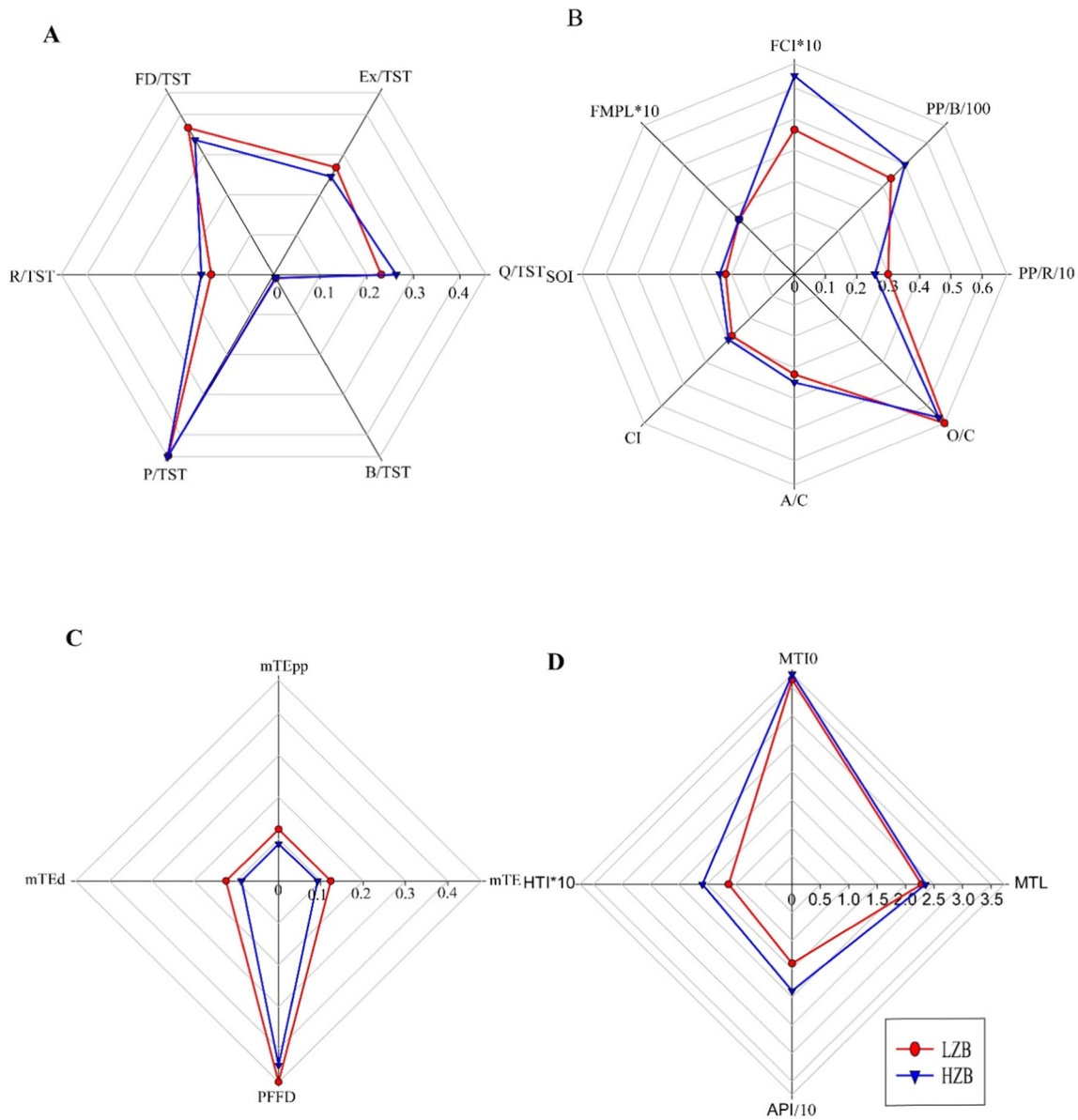


Fig. 5. Radial plot of flows and statistics (A), ecosystem maturity (B), ecosystem efficiencies (C), and trophic level (D) of LZB (red) and HZB (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Comparison of Laizhou and Haizhou Bay ecosystems

Habitat similarities, and connectivity through proximity, render LZB and HZB similar in species composition (Appendix Table A1) and main trophic components (Fig. 2). Structuring functional groups (Table 3) important in pelagic-benthic coupling include zooplankton and shrimps (Fig. 2). Producers are consumed by pelagic taxa (e.g., zooplankton, shrimps, and small pelagic fishes) in both bays; these, in turn are preyed upon by demersal taxa (e.g., small yellow croaker, greenling, and other demersal fishes) and benthic taxa (snailfishes, slender lizardfish, and other benthic fishes). Detritus is important in both food webs because demersal species (e.g., shellfish, echinoderms and crabs) feed upon it.

Ecological differences were existed owing to differential effects of anthropogenic activities on their unique habitats. With respect to statistics and flows, the ecological size (TST), Ex/TST, and FD/TST were all higher or greater in LZB than in HZB (Table 2, Fig. 5). While Q/TST and R/TST were lower in LZB (Table 2, Fig. 5), values for P/TST and B/TST for the two sites were almost identical (Table 2, Fig. 5). As the ecosystem status, value for PP/R, in LZB was higher than in HZB, values

for PP/B, FCI, FMPL, A/C, SOI, and CI in the former were lower (Table 2, Fig. 5). For ecosystem efficiency, mEE, mTE, mTEpp and mTEd in LZB were higher than in HZB; PFFD was greater in LZB. For trophic level, at both the community level (MTL) and in the upper part of the food web (MTI₀, HTI and API), the trophic indices for LZB were lower than those for HZB (Table 2, Fig. 5).

4. Discussion

We characterize and compare the structure and functioning of food webs in two bays in China, LZB and HZB, using input data sourced mainly from scientific surveys and peer-reviewed literature. Relatively high model pedigree indices indicate the input parameters to be of relatively good quality. Using these data and models we identify similarities and differences in the structure, functioning, ecological role, trophic interactions, and maturity of the two ecosystems. We demonstrate how our approach can aid ecosystem-based approaches to fisheries management.

4.1. Structure, flows and functioning of the two ecosystems

The ecological size (TST) of LZB was approximately 80% greater than that of HZB, due mainly to differences in model productivity and structure. LZB lies within the semi-enclosed Bohai Sea, and, relative to HZB, has limited seawater exchange. It is also more greatly influenced by inputs of nutrient-rich continental waters (Yu et al., 2013), which contribute to increased primary productivity. Sea ranching in this bay could change the food web structure and enhance productivity (Li et al., 2014; Taylor et al., 2017) by increasing the biomass of low TL species. In 2015 about 91 tons of hatchery-seeded *S. japonicus*, shellfish and crustaceans were released into LZB (Sun, 2015), increasing both the relative and absolute biomass of taxa in lower trophic levels II and III (Table A4, Fig. 3) and total energy flow (TST) in this system. The Ex/TST in LZB was higher as ranched species almost all of which was extracted as catches. For example, catches of *S. japonicus*, *R. venosa* and *C. japonica* in 2016 were 175 tons, 475 tons and 6 tons, respectively (Blue Ocean Technology Co., Ltd). This rendered the Q/TST in LZB lower, as the energy flow from prey consumed by predators was less, while the Ex/TST was greater. Similarities in P/TST and B/TST between the two bays may be related to similarities in ecological type, geomorphology, temperature, and species composition.

Detritus- and primary-producer energy flows to TL II were similar in both models, illustrating the importance of retaining primary productivity and detritus recycling in a system (Hattab et al., 2013). The relationship between detritus and organisms may be a key functioning process in both models (Corrales et al., 2015). Two trophic pathways coupled with P/TST and B/TST stress the similarities in trophic functioning of the two models.

The transfer efficiencies (TEs) of TIs II–V in both models (Fig. 2, Table A4) increased with TL, due to removal of the biomass of upper TL groups by fishing (Coll et al., 2009), and adequate prey in lower TL groups. Values of mTE including mTEpp and mTEd in LZB were approximately 45%, 40%, and 30% higher than those in HZB, respectively, but mTE in HZB (9.245%) was lower than the worldwide average value of 10% (Pauly and Christensen, 1995). The higher mTE in LZB was related to high predation of TL III taxa on TL II (high consumption) taxa by ranched species. We attribute the lower mTE in HZB to high productivity, leading to high biomass of TL II (nearly 7 times that of TL III), with very little flow (3.1%) from TL II to TL III by predation. The PFFD in LZB was higher than in HZB (Table 2), as ranching artificially increased the biomass of filter feeders, elevating flows from detritus.

The MTL in LZB was lower than in HZB (a reduction of 0.07), due to the greater proportion of low TL ranched species. Indices describing the upper part of the food web (MTI₀) and top or apex predators (HTI and API) in LZB were also lower than those for HZB (reductions of 0.09, 0.05% and 4.88%, respectively), possibly because larger and/or apex predator preferred more open (HZB) than semi-enclosed (LZB) areas. MTL (Pauly et al., 1998), MTI₀ (Pauly and Watson, 2005), and HTI and API (Bourdaud et al., 2016), indicate the effects of fishing on food webs, revealing that LZB has experienced greater fishing pressure than HZB.

4.2. Ecological roles and trophic interactions of the two ecosystems

Zooplankton and shrimps contributed most to pelagic–benthic coupling on the continental shelf (Tsagarakis et al., 2010; Lassalle et al., 2013). Zooplankton are commonly the foundations of food webs (Lassalle et al., 2013), and may be related to possible bottom-up interactions (Hunter and Price, 1992), supported by high BU values in our two models (Table 3). MTI analysis (Fig. 3) demonstrates that zooplankton had negative impacts on spotted sardine (a one-half trophic level above zooplankton) through food competition, and on trophic level I groups (primary producers and detritus) by direct consumption (predation). This suggests the presence of top-down control of these organisms in the two food webs (Table 3). However, as the main prey of

many groups, shrimps had high positive effects on upper trophic level groups (Fig. 3), with control in the two food webs exerted mainly through bottom-up effects (Table 3).

Most functional groups with high KS_L in each food web (Fig. 4) were considered to be important structuring functional groups (Table 3) except for sharks and rays, and mantis shrimps, which were keystone species in HZB (Table 3). However, as top predators (TL > 3.25), all keystone functional groups in both bays had high KS_V (Table 3). Important structuring functional groups, such as zooplankton, shrimps, and benthos were low TL groups, linking phytoplankton and detritus to numerous demersal fishes and commercially targeted invertebrate groups in a bottom-up process (Libralato et al., 2006; Tsagarakis et al., 2010; Hattab et al., 2013). Top-down processes (Table 3) were driven by keystone functional groups such as sharks and rays, large demersal fishes, and benthic fishes, which impacted entire food webs by negatively affecting a large number of low TL groups (Coll et al., 2013; Corrales et al., 2015).

The main mechanism of food web control can be represented by the impact of the first four functional groups based on KS_L and KS_V values (Lassalle et al., 2013). Regulation mechanisms in each bay were complex but, based on overall TD and BU values, top-down effects seemed to prevail in HZB (Table 3). Top-down control was prevalent in low-diversity continental shelf ecosystems, while bottom-up control was prevalent in more species-rich areas (Frank et al., 2007). Top-down effects in LZB may be weaker than those in HZB, because ranching not only increased species diversity, but also increased bottom-up control from benthos, shrimps, and zooplankton (Table 3), changing predation and food competition trophic interactions.

4.3. Ecosystem maturity

The PP/R ratio describes the relative maturity of an ecosystem (Odum, 1969). In mature ecosystems, primary production (PP) tends to be balanced by energy consumed (respiration), resulting in a PP/R ratio of 1 (Hattab et al., 2013). In younger ecosystems, PP tends to exceed R (PP/R > 1), organic matter and biomass accumulate, and nutrient cycling is lower; as the PP/R ratio increases, the PP/B ratio tends to decrease, and FCI decreases (Odum, 1969; Christensen, 1995). In mature ecosystems, path length increases (Christensen, 1995) and inner linkages are complex, leading to higher FMPL, CI, and SOI. Metrics of ecosystem maturity indicate that the system in LZB is less mature (Wilcoxon signed-rank test, $P = 0.028 < 0.05$) than in HZB with lower PP/B, FCI, FMPL, CI, SOI, and A/C values, and a higher PP/R but away from 1 (Table 2, Fig. 5). Although less mature, the higher O/C value (about 4% greater than for HZB) suggests that the food web in LZB is the more stable of the two (Pérez-España and Arreguín-Sánchez, 2001), with a greater capacity to withstand perturbations (Ulanowicz, 1986; Christensen, 1995; Angelini and Petrere, 2000). The differing maturity and stability of the two food webs may be due to ranching, which increases food-web linearity, enhancing the energy pathway from detritus, but decreases total recycling through harvest of low TL cultured species. The LZB food web may be less mature but more stable than that in HZB.

4.4. Preliminary implications for ecosystem-based approach to fisheries

Studies of homeostasis, nutrient and energetic cycling, and general interactions (ecological roles, keystone, and MTI) provide information that can be used to appraise an ecosystem's ability to withstand disturbance (Odum, 1969; Müller, 1997). This information can be used in ecosystem management (Pérez-España and Arreguín-Sánchez, 2001).

We demonstrate how ranching may enhance energy pathways from detritus, and improve the TEs of a food web through release of low TL species. Therefore, food web stability can be increased as the plasticity and resilience are enhanced by the energy pathways from detritus and primary producer, rather than via a single pathway (Moore et al., 2004;

Fetahi et al., 2011). The PP/B ratio indicates the state of eutrophication (Barausse et al., 2009); its lower value in LZB suggests that ranching in this area has reduced the risks associated with eutrophication (such as hypoxia or anoxia), despite its high primary productivity. Sea ranching also increases food security (Liao, 2004), has socioeconomic benefits (Whitmarsh, 2001), and reduces fishing pressure on natural systems (Taylor et al., 2017). However, releases of low TL species decrease the food-web complexity, as most species are not prey, and harvest decreases total recycled flow. Accordingly, ranching of low TL species may reduce system maturity. EwE does not model genetic risks associated with hatchery-produced species (Dannewitz et al., 2003; Purcell et al., 2012) or shifts in benthic community structure as a consequence of sea cucumber over-stocking (Purcell et al., 2012).

Ranching can increase ecosystem stability, and decrease fishing pressure on natural systems. Sea ranching could strengthen food-web complexity by an appropriate increase in the diversity of released species, especially of high TL species, to enhance ecosystem maturity. Therefore, integrated sea ranching measures that consider the advantages and disadvantages (genetic risk, shifts in benthic community structure) from sea ranching on the ecosystem structure and functioning should be implemented. These can lead to sustainable fisheries, and promote the ecosystem toward a mature, stable and healthy state by fishery enhancement activities in the future.

5. Conclusions

We proffer the first comparative analysis of ecosystem structure and functioning in LZB and HZB using food web models. We report both similarities and differences in ecosystem structure and functioning in these two bays. We identify zooplankton and shrimps to be important structuring functional groups connecting the pelagic and benthic realms in each food web, for which top-down effects are the main mechanism of control. Enhancement of low TL species in LZB increases ecological size, Ex/TST, and enhances TE, and renders the ecosystem less mature but more stable than that in HZB. Top-down effects in LZB are weaker, as fisheries enhancement increases bottom-up control from benthos, shrimps and zooplankton. Despite the similarities in these two bays, and their geographic proximity, the differences we describe for them indicate that different ecosystems will likely respond in different ways to the same management initiatives and regulations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2019.103238>.

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