

Temporal variations of food web in a marine bay ecosystem based on LIM-MCMC model

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Abstract

Climate change has led to significant fluctuations in marine ecosystems, including alterations in the structure and function of food webs and ecosystem status. Coastal ecosystems are critical to the functioning of the earth's life-supporting systems. However, temporal variations in most of these ecosystems have remained unclear so far. In this study, we employed a linear inverse model with Markov Chain Monte Carlo (LIM-MCMC) combined with ecological network analysis to reveal the temporal variations of the food web in Haizhou Bay of China. Food webs were constructed based on diet composition data in this ecosystem during the year of 2011 and 2018. Results indicated that there were obvious temporal variations in the composition of food webs in autumn of 2011 and 2018. The number of prey and predators for most species in food web decreased in 2018 compared with 2011, especially for *Trichiurus lepturus*, zooplankton, *Amblychaeturichthys hexanema*, and *Loligo* sp. Ecological network analysis showed that the complexity of food web structure could be reflected by comprehensive analysis of compartmentalized indicators. Haizhou Bay ecosystem was more mature and stable in 2011, while the ecosystem's self-sustainability and recovery from disturbances were accelerated from 2011 to 2018. These findings contribute to our understanding of the dynamics of marine ecosystems and highlight the importance of comprehensive analysis of marine food webs. This work provides a framework for assessing and comparing temporal variations in marine ecosystems, which provides essential information and scientific guidance for the Ecosystem-based Fisheries Management.

Key words: LIM-MCMC, ecological network analysis, marine ecosystem, food web

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1 Introduction

Increasing human activities exert great influence on marine ecosystem, especially in coastal ecosystem (Anh et al., 2015). Climate changes, environment pollution, overfishing and many other aspects not only lead to the decline of fishery resources, but also destroy the marine ecological environment (Lin et al., 2016; Yang et al., 2018). Since the beginning of the 21st century, it is noteworthy that continuous high-intensity fishing pressure and climate changes have caused the unprecedented extinction rate of global fisheries (Ceballos et al., 2015). However, the impacts on marine ecosystems are generally not well known (Griffiths et al., 2010). Analysis of temporal variations in ecosystems can help to understand the effects of climate change and fishing pressure on food web characteristics and ecosystem status (Cloern et al., 2016; Wu et al., 2019; Li et al., 2021).

Food webs provide tractable representations of species interactions (Eskuche-Keith et al., 2023), which are the key to understand ecosystem dynamics. Examinations of the structural properties (Rooney and McCann, 2012), topological structure, and

stability of the food web (Layman et al., 2015) are essential to reveal the status of marine ecosystems. Many ecosystem models have been used for understanding ecosystem dynamics, including the Atlantis model (Rose et al., 2010), OSMOSE (Xing et al., 2022), Ecopath model (Han et al., 2017; Yin et al., 2021), size-spectrum model (Yvon-Durocher et al., 2011), Linear inverse model (LIM) (Xu et al., 2021), and so on. Among these models, LIM is a valuable ecosystem modeling tool for describing the structure and function of food webs at the ecosystem level due to its moderate data requirements and flexibility to accommodate future updates (Leguerrier et al., 2007). Initially, Vézina and Platt (1988) adopted it from the physical sciences to ecology, and subsequently used for reconstruction of food webs (Van Oevelen et al., 2010) and ecological modeling (De Laender et al., 2010). The limitations in the model, such as underestimating the scale and complexity of food webs, can be effectively resolved by combining Markov Chain Monte Carlo (MCMC) algorithms (Johnson and McElhane, 2009). Linear inverse model with Markov Chain Monte Carlo (LIM-MCMC) can estimate food webs from incom-

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plete data sets (Marquis et al., 2007; Olsen et al., 2007; van Oevelen et al., 2010), allowing estimation of difficult-to-measure processes in the food web (Anh et al., 2015), and has been successfully applied in different regions (Daniels et al., 2006; Savenkoff et al., 2007; Chaalali et al., 2015; Xu et al., 2021).

Ecological network analysis (ENA) has been widely used to assess the status of ecosystems (Fetahi and Mengistou, 2007). ENA describes the function of trophic networks and emergent properties linked with species interactions, being capable of assessing complex interactions within ecosystems (Horn et al., 2019). In recent years, ENA has been widely used to identify key components (Borrett, 2013), stress characterization (Bondavalli et al., 2006), and define ecosystem health indicators (Fath et al., 2019; Safi et al., 2019). Ecological network analysis can provide a holistic representation of the food web including all system components, and assess the status of ecosystems (Mukherjee et al., 2015; Horn et al., 2019). Meanwhile, ENA can also be used to reveal the underlying responses of ecosystems to various pressures (Dubois et al., 2019; Wang et al., 2019), and provide a theoretical basis for the understanding and protection of marine ecosystems.

Haizhou Bay is a typical open bay ecosystem in the southern Yellow Sea, which is an important fishing ground and spawning habitat in the Yellow Sea (Zhang et al., 2015). However, intensive fishing pressure and climate changes have caused remarkable changes in fishery resources, including species community structure and biodiversity (Wu et al., 2019; Li et al., 2021). This study analyzed changes in the composition of food webs and diets in autumn of 2011 and 2018. The LIM-MCMC and ENA were combined to evaluate the status and temporal variations of the ecosystem in Haizhou Bay. This study helps construct a framework for assessing and comparing marine ecosystems and provide essential information and scientific guidance for the Ecosystem-based Fisheries Management (EBFM).

2 Methods

2.1 Study area

The survey area is in Haizhou Bay of China, ranging from

34°20'N to 35°40'N and 119°20'E to 121°20'E (Fig. 1). Bottom trawl surveys were conducted in autumn (September) of 2011 and 2018 using stratified random sampling. Detailed description of the survey design is available in the research of Xu et al. (2015). The trawl was towed for about 1 h at a speed of 2–3 kn. Catch data were standardized to 1 h haul at 2 kn.

2.2 The data

In this study, diet composition of marine organisms was obtained mainly from stomach contents analysis of samples collected from Haizhou Bay in autumn of 2011 and 2018, combined with some data from FishBase and related literatures (Xue, 2005; Sheng et al., 2009; Zhang et al., 2011; Xu et al., 2018; Song et al., 2020; Liu et al., 2021; Froese and Pauly, 2023). The biomasses [$t/(km^2 \cdot a)$] of fish, cephalopods, and crustaceans were estimated using the sweep area method based on bottom trawl surveys conducted during autumn of 2011 and 2018, and the biomass of phytoplankton, zooplankton and detritus was based on references in Haizhou Bay and its adjacent waters (Nuttall et al., 2011; Lin et al., 2013; Han et al., 2017; Yuan et al., 2018). Environmental variables, such as temperature and salinity, were measured during bottom trawl surveys with probes equipped in a CTD recorder (CTD75M/1167) (Li et al., 2020). Moreover, parameters such as production/biomass (P/B), consumption/biomass (Q/B), respiration/biomass (R/B) and unassimilated/biomass (U/B) were sourced from published literatures (Lin et al., 2009, 2018; Li et al., 2010; Feng et al., 2010; Wang et al., 2018; Liu et al., 2019; Xu et al., 2019; Ren et al., 2020) (Table S1).

2.3 LIM-MCMC model

The LIM can be used to quantify a large number of unknown processes between compartments in the food web by combining a small amount of experimental data with parameters in the literature (van Oevelen et al., 2010; De Laender et al., 2011). This represents a key advantage of the LIM-MCMC model (i.e., its potential in under-sampled environments) (Kones et al., 2009). The general structure of a LIM consists of mass-balance equations

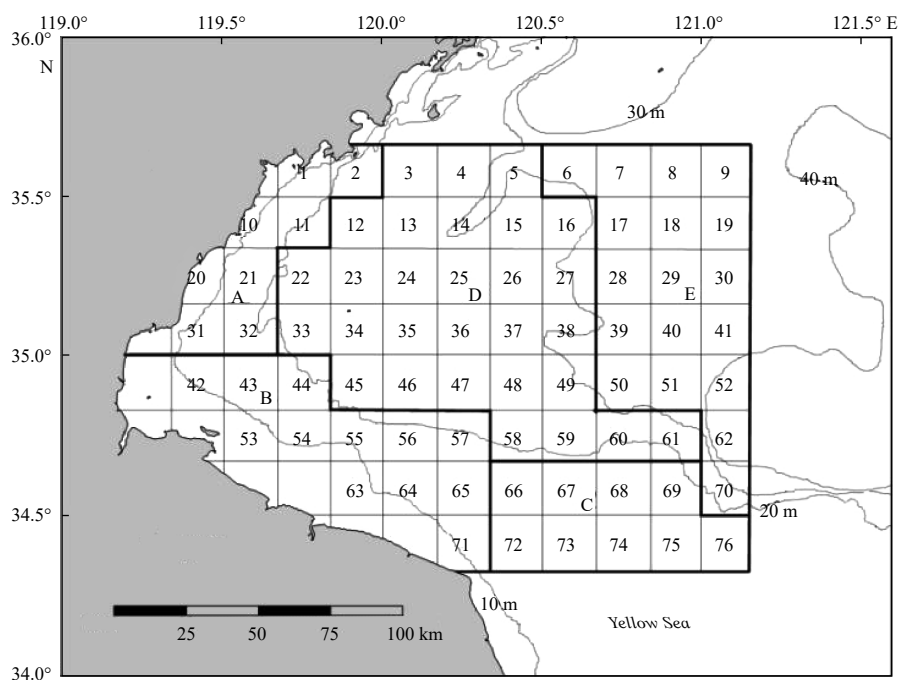


Fig. 1. Sampling areas in Haizhou Bay, China.

(Equality) and constraints (Inequality). Their specific formulas are as follows (van Oevelen et al., 2010):

$$\text{Equality: } E(m \times n) \times x = F, \quad (1)$$

$$\text{Inequality: } G(c \times n) \times x \geq h, \quad (2)$$

where $E(m \times n)$ and $G(c \times n)$ are energy flow path coefficient matrices, and m is the mass balance of each compartment or the known energy flow path data measured by experiment. c represents the number of inequalities added to the model, and n is the number of energy flow paths (x_1, x_2, \dots, x_n), F is the matrix of equation values ($m \times 1$), and h is the value of inequalities.

Furthermore, with the further development of the model, researchers have proposed combining it with the MCMC method to solve the limitations of underestimating the scale and complexity of the food web (Johnson and McElhane, 2009). Thus, LIM-MCMC produces many potential solutions that satisfy the balance of the food web rather than a single food web. The model is developed by means of “Lim” and “LimSolve” (Soetaert and van Oevelen, 2009; Soetaert et al., 2009) and implemented in R (version 3.5.2). In this study, we calculated 1 000 possible solutions to sample the entire solution space sufficiently using the function X-sample (Kones et al., 2009), and to calculate the average value, providing a more realistic estimate of the food web.

2.4 Ecological network analysis

In this study, we evaluated 26 indicators based on LIM-MCMC model outputs, reflecting the properties of the food web and the status of the ecosystem (Mukherjee et al., 2015). Specifically, these indicators were grouped into five categories (Kones et al., 2009; Yin et al., 2021), including (i) general measures, which consider a number of general properties of ecosystem; (ii) pathway analysis, which identifies the direct and indirect pathways in a network; (iii) network uncertainty, which are related to the whole network interactions; (iv) system development and growth, including ascendancy (A), development capacity (DC), overhead (Φ) and extent of development (AC) to imply the development and growth of ecosystem; (v) environment analysis, including homogenization (HP), synergism index (b/c) and dominance indirect effects (i/d).

In this study, the relevant ENA indices were shown in Table 1, and the details are described in Latham (2006) and Julius et al. (2009). All indices were directly realized by NetMatCale-X software. In addition, the annual differences between 2018 and 2011 are reflected by relative percentage changes, which can effectively eliminate differences between indicators.

3 Results

3.1 Temporal variations in food webs composition

The food web of Haizhou Bay in autumns of 2011 and 2018 consisted of 78 and 59 species or taxa, respectively (Table 2), with the number of food web components decreasing significantly in 2018 compared to 2011. Notably, *Lophius litulon* and *Liparis* sp., were two species only appearing in the food web of 2018.

Changes in the composition of the food web are critical to the impact of diet composition. The results showed that food web diet composition of Haizhou Bay were markedly different between 2018 and 2011. The number of prey and predators for the same species in Haizhou Bay food web reduced in 2018 compared with 2011 (Fig. 2 and Table 3), especially for species of

Table 1. Ecological network analysis (ENA) indices analyzed in this study

ENA	Name of indices	Abbreviation	
General measures	Number of compartments	N	
	Total system throughput	T	
	Total system throughflow	TST	
	Link density	LD	
	Number of links	L	
	Average compartment Throughflow	TST'	
	Connectance	C	
	Average link weight	T_{ij}	
	Compartmentalization	C'	
	Pathway analysis	Total system cycled throughflow	$TSTc$
		Total system non-cycled Throughflow	$TSTs$
		Finn's cycling index	FCI
		Average path length	PL
–		–	
Network uncertainty	Average mutual information	AMI	
	Statistical uncertainty	HR	
	Conditional uncertainty	DR	
	Realized uncertainty	RUR	
	Network constraint	HC	
System development and growth	Constraint efficiency	CE	
	Ascendancy	A	
	Development capacity	DC	
Environment analysis	Overhead	Φ	
	Extent of development	AC	
	Homogenization	HP	
	Synergism index	b/c	
	Dominance indirect effects	i/d	

Trichiurus lepturus, zooplankton, *Amblychaeturichthys hexanema*, and *Loligo* sp. Notably, *Syngnathus acus* and *Sepia esculenta* remained relatively consistent among a large number of species or taxa.

3.2 Temporal variations in ENA indices

The specific results of ENA in the Haizhou Bay ecosystem in autumn of 2011 and 2018 are shown in Table 4. When paired with the relative percentage change in ENA (Fig. 3), clear temporal variations can be seen in the ENA indices. Temporal variations had a negative impact on general measures like N , T , TST , LD , and L , and but a positive effect on TST' , C , T_{ij} , and C' . Pathway analysis showed negative effects on $TSTs$ and positive effects on $TSTc$, FCI , and PL . Notably, the impacts on all network uncertainty, system development and growth indicators were negative. In addition, the impact on the environment analysis was relatively low, especially the negative impact on HP (Fig. 3).

4 Discussion

4.1 Changes in food web composition

In the context of climate change, continuous high fishing pressure causes drastic variations in the ecosystem, which bring great challenges to EBFM (Zhang et al., 2011). Understanding changes in ecosystems and their responses to climate changes is critical. Based on LIM-MCMC model and ENA, this study comprehensively evaluated the temporal variations in Haizhou Bay ecosystem.

The quantitative changes in food web composition may be the result of a combination of continued high-intensity fishing and climate change. Continuous high-intensity fishing is bound to cause over-exploitation of resources, which not only destroys the marine ecological environment, but also leads to the reduction or even extinction of fishery resources (Lin et al., 2016; Yang et al., 2018). In this study, the food web compositions in Haizhou Bay decreased from 78 to 59, which reflected the effects of high-in-

Table 2. Food web composition in Haizhou Bay in autumn of 2011 and 2018

Code	Species or taxa	2011	2018	Code	Species or taxa	2011	2018
G1	<i>Eualus sinensis</i>	√	–	G41	<i>Johnius belangerii</i>	√	√
G2	<i>Pennahia argentata</i>	√	√	G42	<i>Amoya pflaumi</i>	√	√
G3	<i>Pampus</i> sp.	√	√	G43	Other gobies	√	√
G4	<i>Thryssa kammalensis</i>	√	√	G44	Other shrimps	√	√
G5	<i>Hexagrammos otakii</i>	√	√	G45	<i>Loligo</i> sp.	√	√
G6	<i>Protosalanx hyalocranius</i>	√	–	G46	<i>Sardinella zunas</i>	√	√
G7	<i>Trichiurus lepturus</i>	√	√	G47	<i>Alpheus japonicus</i>	√	√
G8	<i>Metapenaeopsis dalei</i>	√	√	G48	<i>Scomber japonicus</i>	√	√
G9	<i>Coilia nasus</i>	√	–	G49	<i>Charybdis japonica</i>	√	√
G10	Benthos	√	–	G50	<i>Soleidae</i> sp.	√	√
G11	<i>Pagrus major</i>	√	√	G51	<i>Charybdis bimaculata</i>	√	√
G12	<i>Cottus</i> sp.	√	√	G52	<i>Sepiolo birostrata</i>	√	–
G13	<i>Octopus ocellatus</i>	√	√	G53	Bivalvia	√	√
G14	<i>Enedrias fangi</i>	√	√	G54	<i>Euprymna morsei</i>	√	√
G15	<i>Coilia mystus</i>	√	√	G55	<i>Azuma emmion</i>	√	–
G16	Zooplankton	√	√	G56	<i>Engraulis japonicus</i>	√	–
G17	Phytoplankton	√	√	G57	<i>Thamnaconus modestus</i>	√	–
G18	Gastropods	√	√	G58	<i>Sillago sihama</i>	√	√
G19	<i>Syngnathus acus</i>	√	√	G59	<i>Leptochela gracilis</i>	√	–
G20	<i>Metanephrops Challengeri</i>	√	–	G60	<i>Jaydia lineata</i>	√	√
G21	<i>Sebastes marmoratus</i>	√	–	G61	<i>Alpheus distinguendus</i>	√	√
G22	<i>Paralichthys olivaceus</i>	√	–	G62	<i>Callionymus</i> sp.	√	√
G23	Annelida	√	–	G63	<i>Eupleurogrammus muticus</i>	√	–
G24	<i>Nibea albiflora</i>	√	–	G64	<i>Larimichthys polyactis</i>	√	√
G25	<i>Setipinna tenuifilis</i>	√	√	G65	<i>Chelidonichthys spinosus</i>	√	√
G26	Echinodermata	√	√	G66	Other crabs	√	√
G27	<i>Crangon affinis</i>	√	–	G67	<i>Conger myriaster</i>	√	√
G28	<i>commersonii</i>	√	–	G68	<i>Sebastes schlegelii</i>	√	√
G29	<i>Pleuronichthys cornutus</i>	√	√	G69	<i>Trachypenaeus curvirostris</i>	√	√
G30	<i>Sepia esculenta</i>	√	√	G70	<i>Platycephalus indicus</i>	√	–
G31	<i>Sebastes hubbsi</i>	√	√	G71	<i>Sphyræna pinguis</i>	√	√
G32	<i>Raja porosa</i>	√	–	G72	<i>Ammodytes personatus</i>	√	√
G33	<i>Oratosquilla oratoria</i>	√	√	G73	<i>Palaemon gravieri</i>	√	√
G34	<i>Decapterus maruadsi</i>	√	–	G74	<i>Octopus variabilis</i>	√	√
G35	<i>Amblychaeturichthys hexanema</i>	√	√	G75	<i>Saurida elongata</i>	√	√
G36	<i>Acetes</i> sp.	√	√	G76	<i>Myersina filifer</i>	√	√
G37	<i>Chaemrichthys stigmatias</i>	√	√	G77	<i>Thryssa mystax</i>	√	√
G38	<i>Collichthys</i> sp.	√	√	G78	<i>Tridentiger barbatus</i>	√	√
G39	<i>Erisphex pottii</i>	√	–	G79	<i>Lophius litulon</i>	–	√
G40	<i>Miichthys miiuy</i>	√	√	G80	<i>Liparis</i> sp.	–	√

Note: √ indicates the presence of the species or taxa. – represents non-presence of species or taxa.

tensity fishing pressure on the structure of marine ecosystems (Griffin et al., 2021). Moreover, the impacts of climate changes on biological and ecological systems are incontrovertible (Doney and Sailley, 2013; Beaugrand et al., 2015). Species can adapt to climate change by changing suitable habitats, which is also an important factor affecting the composition of food webs. Evidence for a shift in species distribution to deeper or higher-latitude waters has been widely documented (Perry et al., 2005; Dulvy et al., 2008). However, the addition in food web composition of Haizhou Bay in 2018 may be caused by the migration of species (such as *L. litulon*) in time or space. Yuan et al. (2023) found that the environmental factors that most affect the suitable habitat of *L. litulon* in autumn is sea bottom temperature. Meanwhile, the suitable temperature of this species in the central and southern Yellow Sea is low and narrow (Li et al., 2015). In addition, *L. litulon* has obvious migration ability (Yoneda et al., 2001) and mi-

grates to higher latitudes to adapt to temperature changes caused by climate change (Cheung et al., 2009; Li et al., 2015).

4.2 Temporal variations in diet composition

Changes in the species composition and biomass of the food web will inevitably have an impact on diet composition. The number of food web components in 2018 was significantly less than that in 2011, which may be related to the increased fishing intensity. Overfishing is the pervasive human disturbance to coastal ecosystems, causing resource depletion or removal of target species and affecting biological communities at all trophic levels (Vasseur and McCann, 2005; Cloern et al., 2016). The loss of high-trophic level predators could reduce the predation mortality of low-trophic level species, allowing the increase of their biomass (Casini et al., 2008). Meanwhile, the diet structure of the entire food web is also affected through trophic cascading effects

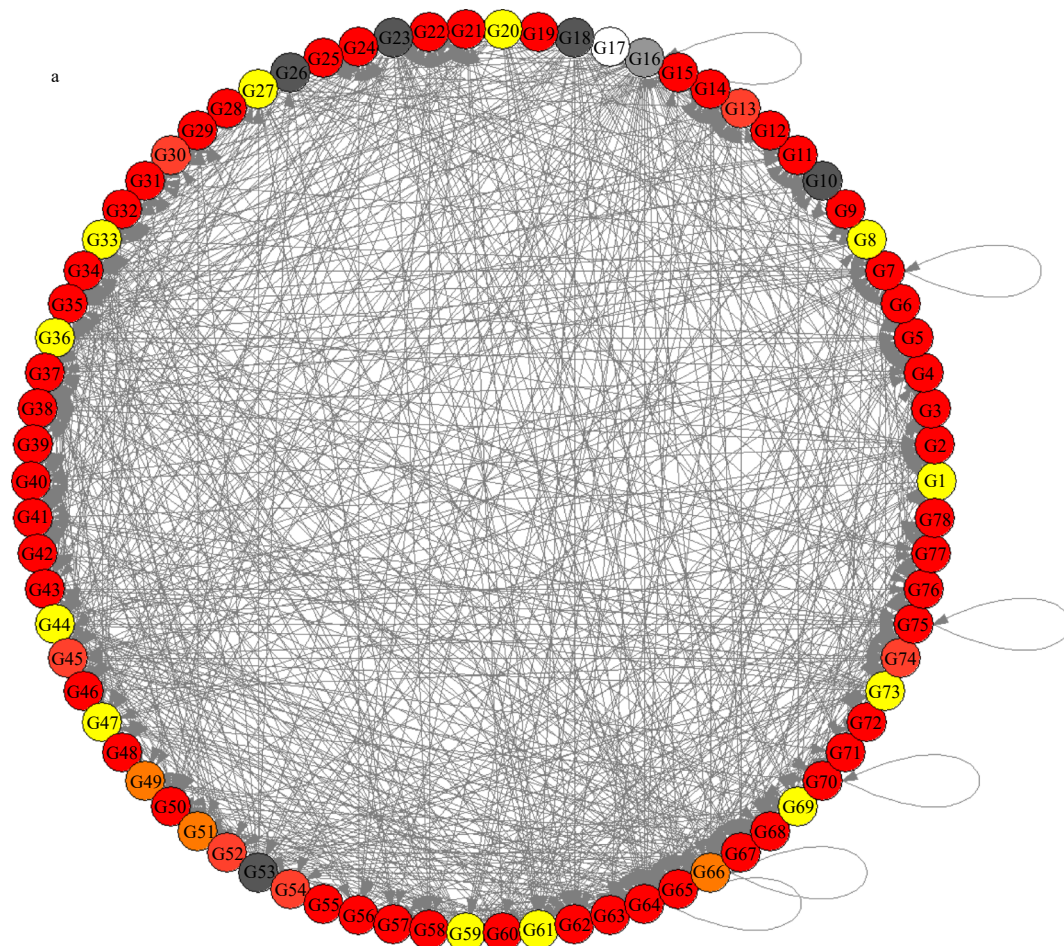
(Vasseur and McCann, 2005).

Ocean warming is the most intuitive manifestation of climate changes, which is one of the main drivers of variations in abundance and distribution of marine species (Perry et al., 2005; Poloczanska et al., 2013; Cloern et al., 2016). Ocean warming could result in the decline in phytoplankton biomass (Fernández-González et al., 2022) and decrease in the body size of zooplankton (Forster et al., 2012), which will affect energy transfer efficiency between different trophic levels. Meanwhile, changes in species distribution may alter the probability of encounters between predators and prey (Friedland et al., 2020). In this study, the reduction and increase of species or taxa directly affects the diet composition, requiring adjustment of feeding relationships to maintain the energy balance of the food web, which plays an important role in maintaining the stability of the ecosystem (Navia et al., 2019). Wei (2015) showed that the temperature rise under climate change was more sensitive to the metabolic activities of heterotrophs (Allen et al., 2005). The mean sea surface temperature (SST) during autumn of Haizhou Bay has increased by about 2.78°C from 2011 to 2018 (Fig. S1). However, higher temperatures may cause fish to consume more food resources and excrete excess nutrients to maintain increased respiration (Hessen and Anderson, 2008). Therefore, whether the fish species have changed or are present in the composition of the food web, the diet composition needs to be adjusted to maintain the homeostasis of the food web.

4.3 Temporal variations of ecosystem based on ENA

Ecological network analysis can effectively reflect the properties of food web and the status of ecosystem (Mukherjee et al., 2015). Both the whole ecosystem and its individual compartments could serve as reference to reflect the structural characteristics of the food web. Krause et al. (2003) pointed out that the structural complexity of food webs reflected by wholes and compartments is different, and compartments can theoretically increase the stability of the network. In this study, N , LD , and L generally reflect the complexity of the structure of the food web (Latham, 2006), while TST' , C , T_{ij} , C' , and PL are often used to determine the complexity of compartments (Pimm and Lawton, 1980; Rybczyk and Elkaïm, 2003; Latham, 2006; Dunne, 2009). In particular, C and C' of the compartments in this study reflect the module, which are critical for the stability of the food web. The change in these indices in 2018 was caused by a decline in the composition of the food web and diet. Notably, the reduced species were at less connected nodes at the periphery of the network (e.g., *Protosalanx hyalocranius*, *Coilia nasus*, *Sebastes marmoratus*, *Paralichthys olivaceus*). In the process, the reduction of these species increases the complexity of compartments, although it reduces the overall complexity of the food web (Krause et al., 2003). Modularity has been suggested as a key structural feature linked to food web stability (Eskuche-Keith et al., 2023). Thus, to capture the intricacy of the food web structure, both the overall and compartmental indices should be taken into account.

However, functional properties of food webs are usually reflected by T , TST , $TSTc$, $TSTs$, and FCI (Vasconcellos et al., 1997;



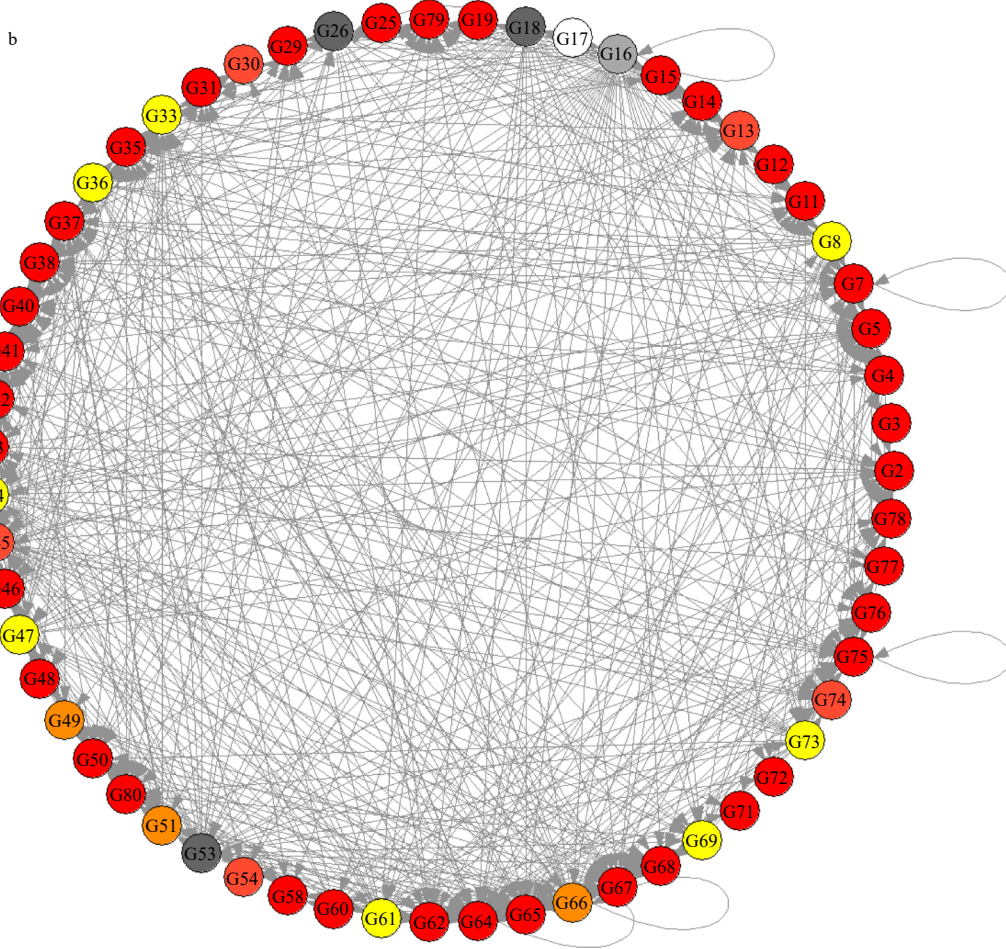


Fig. 2. Diet composition of species in Haizhou Bay food web in 2011 (a) and 2018 (b). The codes of G1–G80 are shown in Table 2. Different colors represent different groups, which are white (phytoplankton), gray (zooplankton), grayish (others), yellow (shrimps), orange (crabs), tomato (cephalopods), and red (fish).

Table 3. Changes in the number of prey and predators for each species in the food web of Haizhou Bay in autumn of 2011 and 2018

Code	Prey		Predators		Code	Prey		Predators	
	2011	2018	2011	2018		2011	2018	2011	2018
G1	4	/	19	/	G41	19	15	10	9
G2	20	16	3	4	G42	5	4	6	6
G3	3	2	0	0	G43	12	9	9	6
G4	5	4	9	9	G44	7	5	38	33
G5	31	24	0	0	G45	16	11	27	24
G6	1	/	0	/	G46	5	4	5	4
G7	28	20	2	1	G47	10	7	26	22
G8	4	3	18	20	G48	9	6	0	0
G9	4	/	0	/	G49	7	6	4	3
G10	7	/	2	/	G50	16	13	7	6
G11	15	12	1	0	G51	6	6	9	10
G12	1	1	0	0	G52	6	/	13	/
G13	16	11	1	1	G53	2	2	41	36
G14	16	12	4	4	G54	6	4	1	1
G15	5	3	4	3	G55	1	/	0	/
G16	2	2	62	52	G56	5	/	21	/
G17	0	0	8	4	G57	9	/	0	/
G18	2	2	35	31	G58	10	7	4	3
G19	1	1	0	0	G59	2	/	43	/
G20	2	/	20	/	G60	2	1	20	18

to be continued

continued from Table 3

Code	Prey		Predators		Code	Prey		Predators	
	2011	2018	2011	2018		2011	2018	2011	2018
G21	12	/	1	/	G61	9	6	24	21
G22	17	/	0	/	G62	15	11	7	6
G23	2	/	37	/	G63	5	/	0	/
G24	14	/	0	/	G64	30	23	11	10
G25	4	3	4	1	G65	32	26	0	0
G26	4	3	21	18	G66	7	6	34	30
G27	4	/	21	/	G67	33	26	0	0
G28	1	/	0	/	G68	16	12	1	1
G29	9	8	0	0	G69	12	8	15	12
G30	5	5	0	0	G70	5	/	2	/
G31	9	6	0	0	G71	5	3	2	0
G32	15	/	0	/	G72	4	3	2	1
G33	18	15	22	18	G73	5	3	23	23
G34	17	/	1	/	G74	16	11	2	2
G35	20	13	15	13	G75	22	19	4	3
G36	2	2	26	21	G76	10	8	5	5
G37	18	13	16	14	G77	5	4	3	4
G38	17	13	6	4	G78	13	9	2	2
G39	4	/	0	/	G79	/	14	/	0
G40	21	17	0	0	G80	/	16	/	0

Note: Italics indicate a change (decrease) of greater than 7 in the number of prey and predators of a species or taxa compared to 2011, and bold fonts indicate an increase in the number of predators. / represents no until.

Table 4. Temporal variations in ecological network analysis (ENA) indices in Haizhou Bay in autumn of 2011 and 2018

ENA	Abbreviation	Value	
		2011	2018
General measures	<i>N</i>	78	60
	<i>T</i>	30 070.17	24 662.32
	<i>TST</i>	43 535.31	35 441.45
	<i>LD</i>	12.12	10.87
	<i>L</i>	945	652
	<i>TST'</i>	558.15	590.69
	<i>C</i>	0.14	0.16
	<i>T_{ij}</i>	31.82	37.83
	<i>C'</i>	0.23	0.27
Pathway analysis	<i>TSTc</i>	937.56	1 081.01
	<i>TSTs</i>	42 597.96	34 360.44
	<i>FCI</i>	2.15	3.05
	<i>PL</i>	2.71	2.78
Network uncertainty	<i>AMI</i>	2.70	2.48
	<i>HR</i>	5.44	5.18
	<i>DR</i>	2.74	2.70
	<i>RUR</i>	0.50	0.48
	<i>HC</i>	306.00	241.57
	<i>CE</i>	0.62	0.60
System development and growth	<i>A</i>	81 230.64	61 263.66
	<i>DC</i>	246 482.26	194 203.61
	<i>Φ</i>	165 251.63	132 939.95
	<i>AC</i>	0.33	0.32
Environment analysis	<i>HP</i>	2.15	2.11
	<i>b/c</i>	0.97	1.00
	<i>i/d</i>	6.83	7.12

Julius et al., 2009). Most of these functional indicators declined in 2018 (with the exception of *TSTc* and *FCI*), indicating a reduction in the scale of the food web. *FCI* is an important indicator of food web function, reflecting the recovery time of the food web (Finn, 1980). In this study, *FCI* of Haizhou Bay food web were 2.15% (2011) and 3.05% (2018) respectively, which were relatively low. *FCI* increased slightly, mainly due to differences in food web and diet composition. In 2018, there was a decrease in overall complexity and an increase in compartment complexity associated

with a decrease in the number of food web components in Haizhou Bay. After external disturbance, it is easier to return to a relatively stable status through the regulation of the food web compartment (Navia et al., 2019).

In addition, the status of Haizhou Bay ecosystem is comprehensively reflected through network uncertainty, system development and growth, and environment analysis. Compared with 2011, both network uncertainty (*AMI*, *HR*, *DR*, *RUR*, *HC*, and *CE*) and system development and growth (*A*, *DC*, *Φ*, and *AC*) in 2018 showed varying degrees of decline (Fig. 2). The temporal variations in these indicators indicate a decrease in uncertainty of the ecosystem in 2018, with lower system development and growth. The difference is that the 2018 environment analysis (*HP*, *b/c*, and *i/d*) increased slightly from 2011, indicating that the ecosystem is dominated by indirect effects and has a high degree of self-sustainability (Fath and Patten, 1998, 1999b; Latham, 2006; Kones et al., 2009). Notably, the variation trends of *HP* and *FCI* in this study are opposite, which is inconsistent with Fath and Patten (1999a) proposal that cycles are related to *HP* because cycles generally increase the evenness of flow in the network. Previous studies have shown that these modifications in ecosystem status are associated with obvious changes in low-trophic functional groups (Chaalali et al., 2016), such as primary producers, primary consumer, or plankton in ecosystems (Parmesan and Yohe, 2003; Parmesan, 2006). In addition, climate change tends to reduce the body size of zooplankton (Yvon-Durocher et al., 2011; Forster et al., 2012), which may lead to a weakening of the influence of their top-down effect on primary producers (DeLong et al., 2015). In this study, a decline in *HP* (i.e., evenness) was observed under temporal variation, possibly due to the increased *TSTc* was not effectively transferred to higher trophic levels, but mainly concentrated at low trophic levels.

The ENA indices showed that the Haizhou Bay ecosystem was more mature and stable in 2011, while the ecosystem's self-sustainability and recovery from disturbances were accelerated in

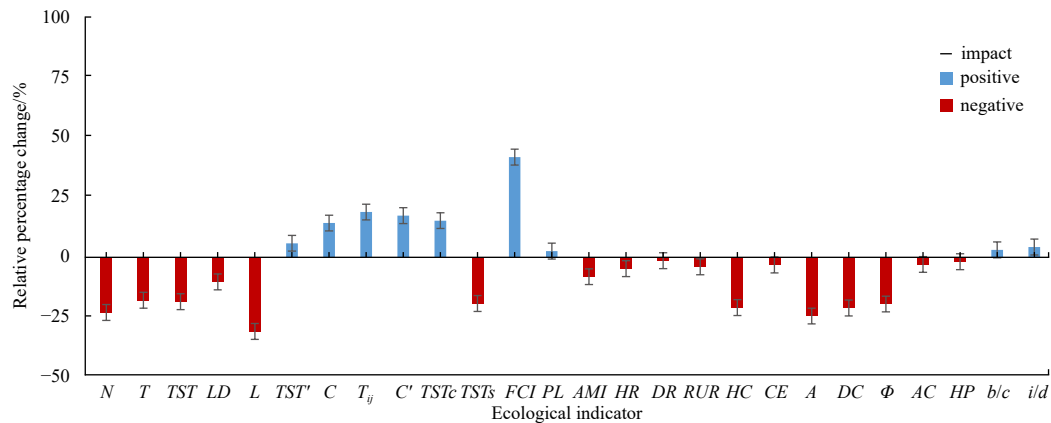


Fig. 3. Percentage change of ecological indicators in Haizhou Bay in autumn of 2011 and 2018. Notes: the negative impacts indicate decreased indices in 2018 and positive impacts indicate increased indices.

2018. These findings will enhance our understanding of the ecosystem responses and can inform the application of ENA indicators in EBFM. It also helps to understand the temporal variations in marine ecosystems, contributing to biodiversity conservation. In the future, the study of food web should pay more attention to the compartment-related indices, which is irreplaceable for the food web structure.

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Supplementary information:

Table S1. Parameters and sources of LIM-MCMC model construction in Haizhou Bay.

Figure S1. Mean sea surface temperature (SST) of Haizhou Bay during autumn in 2011 and 2018.

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