Indian J. Fish., 69(1): 45-53, 2022
DOI: 10.21077/ijf.2022.69.1.117781-05

Role of species associations and environmental variables in structuring the coastal fish community: A case study in Leizhou Bay, northern South China Sea

KUN LIN[1], SHAOLIANG LYU[1], KEXIN DING[1], JIAWEI ZENG[1,2], SHIYUAN PAN[1], XUEFENG WANG[1,2] AND ZI YANG[1]
[1]Fisheries College, Guangdong Ocean University, Zhanjiang, 524088, China
[2]Southern Marine Science and Engineering Guangdong Laboratory, Zhanjiang - 524025, China
e-mail: xuefeng1999@126.com

ABSTRACT

The objective of this study was to understand how the biological and environmental factors affect fish community structures. Using the data of fish communities in Leizhou Bay waters, northern South China Sea, this study built an ecological network based on the model niche overlap between species. The effects of biological and environmental factors on the fish community structure complexity were analysed using principal component analysis (PCA) and generalised linear model (GLM), of which the complexity was represented with a global weighted clustering coefficient (*mCw*) of the network. Results showed that the fish community structure was highly complex with significant seasonal variations ($mCw = 0.821 \pm 0.081$, $p<0.01$) and it was dominated by the strong interspecific associations ($mCw>C$). A large quantity of species associations decreased the chances of the cascading species extinction in terms of the magnitude of direct (k_i) and indirect (*tris*) species associations. The direct species associations (k_i: Estimate = -4.23, $p<0.01$) and the indirect species associations (*tris*: Estimate =3.12, $p<0.01$) were the primary factors, accounting for 89.92% of the variations of the first principal components and then the three factors (the number of species, water depth and the positions of sampling sites) contributed to 83.1% variations of the second principal components. In all, the species associations directly affected the fish community in Leizhou Bay, which were influenced by the species abundance under the driving of environmental factors.

Keywords: Ecological network, Fish community, Leizhou Bay, Species associations, Structure complexity

Introduction

As a self-organizing system, an ecosystem maintains a complex state between order and chaos (Tzafestas, 2018) due to the adaptions and species interactions (Tansley, 1935; Zhang *et al.,* 1998). There has been considerable debates regarding relationships between complexity and stability of community or ecosystem (Pimm, 1984; Cohen and Newman, 1985; Haydon, 1994; Christianou and Kokkoris, 2008; Demongeot and Demetrius, 2015; van Altena *et al.,* 2016; Landi *et al.,* 2018). Most of the previous studies aimed to solve ecological or evolutionary problems through the knowledge of complexity. However, considerable attention has been paid to understand species interactions (Landi *et al.,* 2018; Li *et al.,* 2021) and less effort has been invested in how species interactions affect community complexity (Banasek-Richter *et al.,* 2009; Lin *et al.,* 2020). Very little is known about species interactions at community-level (Benedek *et al.,* 2007), despite interactions between individuals in population-level can form complex spatial structure in small scales (Plank *et al.,* 2020). The community is essentially a complex ecological network with species interactions (Montoya *et al.,* 2006; Gu *et al.,* 2017), which are usually determined by field sampling (Silknetter *et al.,* 2020). However, even in small scale ecosystems, species interactions were affected by species abundance (Morales-Castilla *et al.,* 2015).

Interspecific association, a form of species interaction, reflects the spatial relationships between species within a community (Sfenthourakis *et al.,* 2006) and is a driving force in community succession (Maihaiti and Zhang, 2014). Analysis of associations is an effective way to identify community structure (Zbinden, 2021), especially when experiments cannot detect the spatiotemporal variation in species interactions (Chamberlain *et al.,* 2014). Interspecific associations are usually categorised to be positive, negative and neutral (Diekmann *et al.,* 2003; Sfenthourakis *et al.,* 2006; Maihaiti and Zhang 2014; Calatayud *et al.,* 2020). However, these studies neglected the latent effects of pair-association between species (Morueta-Holme *et al.,* 2016). Ecological network analysis can quantify these latent effects as indirect association between species, improves understanding of processes involved in ecological succession and has been performed on a wide range of communities from bacteria

(Zhao *et al.,* 2016), plants (Gu *et al.,* 2017), birds (Rasool *et al.,* 2021), freshwater fishes (Zbinden 2021) and marine fishes (Albouy *et al.,* 2019).

The complexity of biological communities varies in time and space (Ushio *et al.,* 2018), with biological processes at scales of thousands of miles being driven by the smaller local scales (hundreds of miles or even smaller scales) (Barbier, 2017). Spatial patterns in fish population were reported to be significantly influenced by environmental factors (Zeng *et al.,* 2019), but further study on the effects of biological interactions on the community structure is needed to gain deeper insights into development of community complexity (Maihaiti and Zhang, 2014). Using fish communities as an example, we aimed to monitor how the biological and environmental factors affect local marine ecosystem at community level.

Methods and model building

Study area and data collection

Fish community data were collected from eight fishery resource surveys in April (Spring), August (Summer) and November (Autumn) of 2016, February (Winter), April (Spring), August (Summer) and November (Autumn) of 2017 and January (Winter) of 2018 (Fig. 1). Sampling was undertaken from as much as 20 stations during monthly survey, except in February 2017, where only 19 stations were available. Fish samples were collected during day time using bottom trawls from the same fishing boat from all the sampling sites. The trawls, with the minimum mesh size of 25 mm in cod end, were towed about 45 to 60 min along the bottom, maintained at 3 knots at each sampling site. The data included the number of fish species (*N*) and the number of associations (*L*). For each station, water depth (*Depth*) and dissolved oxygen (*DO*), latitude (*lat*) and longitude (*lon*) and season (*month*) were recorded.

After eliminating species occurring at <10% of stations [to reduce the impact of rare species on ecological community (Zeng *et al.,* 2019)], data for 206 species remained for ecological network modeling.

Establishing a species association network

Three hypotheses were established to perform species associations in network analysis:

(1) The rate of emigration equals that of immigration (*i.e.* the community is in a state of equilibrium);

(2) No significant seasonal or annual variation in anthropic impact on fish community exists during the period of study;

(3) The community complexity is the sum of species-association complexity (*i.e.* the global weighted complexity in a community is the sum of local weighted complexity).

Interspecific associations occur with niche overlap between two species (Helaouet and Beaugrand, 2009). A temporal and spatial niche overlap model treats each fish species as a subunit and assumes that interspecific association occurs when two species are caught together at

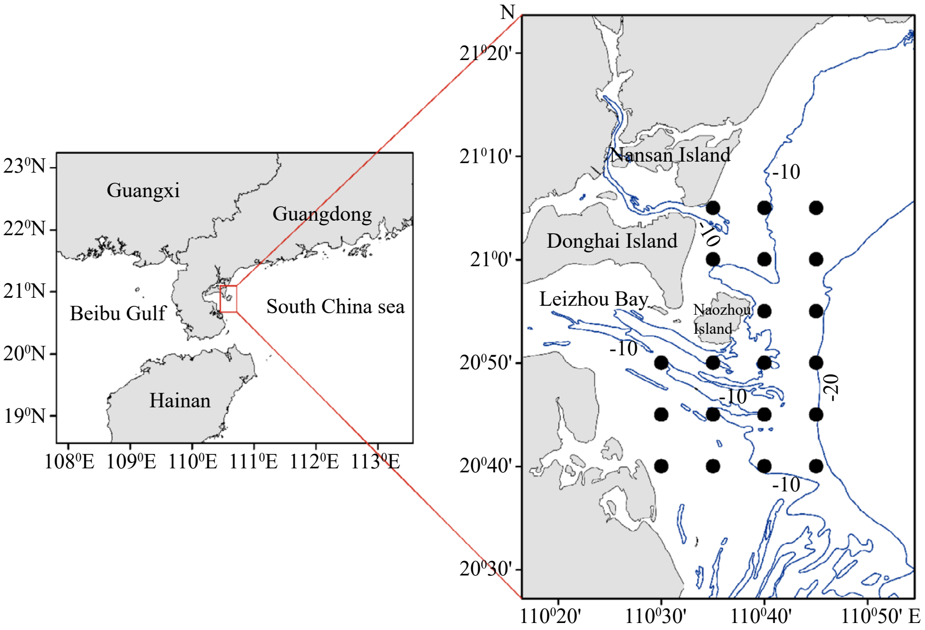


Fig. 1. Study area and sampling sites. The blue lines are isobaths with the numbers showing the water depth

a sampling site. The intensity of interspecific associations is quantified by species overlap (Schoener 1974):

$$W_{ij} = 1 - \frac{1}{2} \sum |p_i - p_j| \tag{1}$$

where w_{ij} is the intensity of an interspecific association between species *i* and species *j*, p_i and p_j are the abundance's percentages of species *i* and *j* in the total abundance of a sampling site.

Calculating community complexity

Determining the complexity of community structure (hereinafter complexity) involves calculating local weighted complexity (Cw_i), global weighted complexity (*mCw*) and global unweighted complexity (*C*). Cw_i explains the change in complexity from the perspective of species. *mCw* reflects seasonal and annual differences in complexity. If $mCw>C$, the community is more likely formed by the edges of the interconnected triples in the network, which means that the topological clustering is generated with larger weights. On the contrary, $mCw<C$ denotes a network that formed with low weight (Boccaletti *et al.,* 2006).

A local-weighted clustering coefficient is used to reflect the local complexity (the contribution of each species to complexity) (Barrat *et al.,* 2004; Emmert-Streib, 2013).

Local weighted complexity, Cw_i:

$$Cw_i = \frac{1}{Si\,(k_i - 1)} \sum_{j,k} \frac{w_{ij} + w_{ik}}{2} a_{ij}\, a_{jk}\, a_{ki} \tag{2}$$

$$S_i = \sum a_{ij}\, w_{ij} \tag{3}$$

Global unweighted complexity, C:

$$C = \frac{1}{N} \sum_i \frac{2 a_{ij} a_{jk} a_{ki}}{k_i (k_i - 1)} \tag{4}$$

where S_i is the strength of association between species *i* and other species in the community; k_i is the number of direct associations of species *i;* w_{ij} is the niche overlap value of species *i* and *j; a_{ij}* is 1 when species *i* associated with species *j* (or 0 otherwise) and *N* is the number of species. Triplets (*tris*) representing the number of indirect associations of species *i*, are formed by $a_{ij}\, a_{jk}\, a_{ki}$, count as 1 when species *i*, *j* and *k* are associated with each other or otherwise 0.

As the global weighted complexity is difficult to measure, so 1000 Monte Carlo sampling of the local weighted complexity was carried out and its mean value (*mCw*) is used to reflect the global complexity of community structure (Mcassey and Bijma, 2015), with standard deviations (*sdCw*). The temporal change of global complexity for the eight surveys were shown in seasonal and annual differences.

Relationship between complexity and influencing factors

Because a two-dimensional image does not exhibit the relationship between more than two variables and complexity at the same time and to prevent the over-fitting phenomenon of general linear models (GLM), principal component analysis (PCA) was used to identify the main factors which influence complexity (Facchinelli *et al.,* 2001). The biotic variables k_i, S_i, *tris* and *abundance*, as well as the abiotic variables *Depth* and *DO* were standardised using the Z score transformation (Cheadle *et al.*, 2003). The PCA results were screened by Kaiser-Guttman criterion for principal components and variables and the first several principal components with eigenvalues greater than 1 were retained (Kaiser, 1991). The average contribution rate of each variable to the principal component was then calculated and variables with a contribution rate >the average were retained (Yeomans and Golder, 1982).

Variables screened by PCA were used as predictive variables and Cw_i was used as a response variable. The relationship between complexity as well as biotic and abiotic variables was fitted by GLM model and factors influencing community complexity were derived. A gaussian method was selected for the link function (McCullagh and Nelder, 1989). A stepwise regression method was used to identify the best model *i.e.* "Step model" which was used to represent the results.

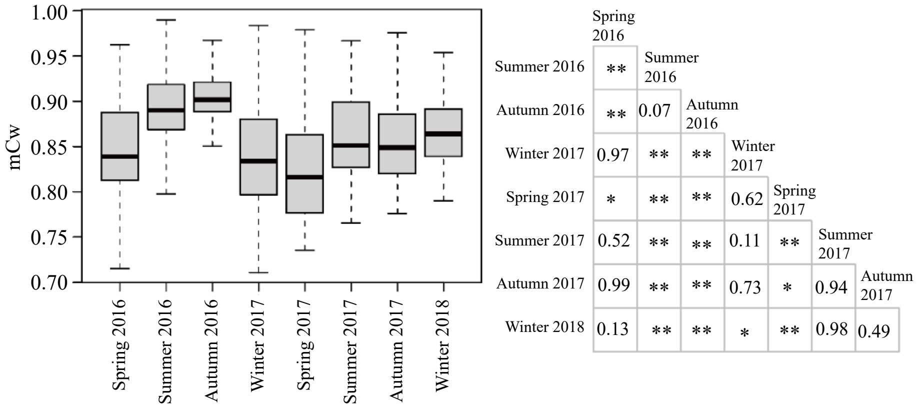
The map of the study area and sample sites was generated using ArcGIS 10.2 and the network construction, complexity analysis, PCA and GLM were performed by R version 3.5.1 with SPAA (Zhang, 2016), iGraph (Csardi and Nepusz, 2006) PSYCH (Revelle, 2020) Factoextra (Kassambara and Mundt, 2020) and FactoMineR (Le *et al.*, 2008).

Results

Community complexity

The fish community in Leizhou Bay was found to be highly complex, with *mCw* values of 0.821±0.081. The seasonal variation was significant (Fig. 2) and the community was mainly formed by the edges of the interconnected triples ($mCw>C$, Table 1), denoting stronger species association.

The complexity showed significant (winter, spring) or extremely significant (summer, autumn) differences within a season in different years and the *N* values and *L* values



	Spring 2016	Summer 2016	Autumn 2016	Winter 2017	Spring 2017	Summer 2017	Autumn 2017
Summer 2016	**						
Autumn 2016	**	0.07					
Winter 2017	0.97	**	**				
Spring 2017	*	**	**	0.62			
Summer 2017	0.52	**	**	0.11	**		
Autumn 2017	0.99	**	**	0.73	*	0.94	
Winter 2018	0.13	**	**	*	**	0.98	0.49

(a) (b)

Fig. 2. (a) Seasonal fluctuation in global complexity of fish communities in Leizhou Bay; (b) Result of one-way ANOVA for the complexity of each season. Significance levels: *<0.05, **<0.01

Table 1. Seasonal variation of fish community ecological network in Leizhou Bay

Season	Weighted global complexity		Unweighted global complexity		N	L
	mCw	sdCw	C	sdC		
Spring 2016	0.849	0.049	0.839	0.073	80	2139
Summer 2016	0.894	0.034	0.879	0.055	113	5078
Autumn 2016	0.907	0.025	0.889	0.046	73	2198
Winter 2017	0.838	0.056	0.827	0.080	69	1653
Spring 2017	0.823	0.059	0.811	0.079	83	2328
Summer 2017	0.863	0.042	0.850	0.069	114	4832
Autumn 2017	0.857	0.047	0.844	0.070	77	2177
Winter 2018	0.870	0.036	0.857	0.051	71	1948
All	0.821	0.081	0.809	0.121	206	11602

did not change significantly. In different seasons within a year, complexity did not differ significantly between summer and autumn, or between winter and spring, but differences were extremely significant between spring and summer. Seasonal *mCw* ranged between 0.823-0.907, and was highest in autumn of 2016 and lowest in spring of 2017. Seasonal *C* ranged between 0.811-0.889 and was highest in autumn of 2016 and lowest in spring of 2017. *N* ranged between 69-114 and was highest in summer of 2017 and lowest in winter of 2017 and *L* ranged from 1653 to 5078 and was found highest in summer of 2016 and lowest in winter of 2017.

The linear correlation between variables *abundance*, k_i, *tris* and S_i was statistically significant when only biotic variables were considered (Fig. 3). The best linear fitting was k_i and *tris* (R^2=0.99, p<0.01), followed by *tris* and S_i (R^2=0.73, p<0.01) and k_i and S_i (R^2=0.72, p<0.01). In the results for variables *abundance* with k_i *tris* and S_i, the best linear fitting was for *abundance* with k_i (R^2=0.58, p<0.01).

Local complexity was negatively correlated with *abundance*, k_i, *tris* and S_i (Fig. 3). The k_i had the highest effect on local complexity (coefficient -0.156, R^2=0.57, p<0.01), followed by *tris* (coefficient -0.0827, R^2=0.53, p<0.01), with S_i and *abundance* having a weak effect on local complexity.

Factors affecting community complexity

According to the Kaiser-Guttman criterion, the first five principal components with eigenvalues >1 explained 83.20% of variation in the indices of community complexity (Fig. 4, Table 2). In terms of the contribution of variables to principal components, the biotic k_i, S_i and *tris* were the most important, explaining 89.92% of the variation in first principal component. *Abundance*, *Depth*, *lon* and *lat* explained 83.10% of the variation in the second principal component. The seven main variables with a contribution rate higher than average were *tris*, k_i, *season*, *DO*, *year*, *lat* and S_i (Fig. 4).

Relationship between complexity and biotic/abiotic factors

The full GLM model was reconstructed from the 7 variables screened by PCA: ~ *tris* + k_i + *season* + *year* +

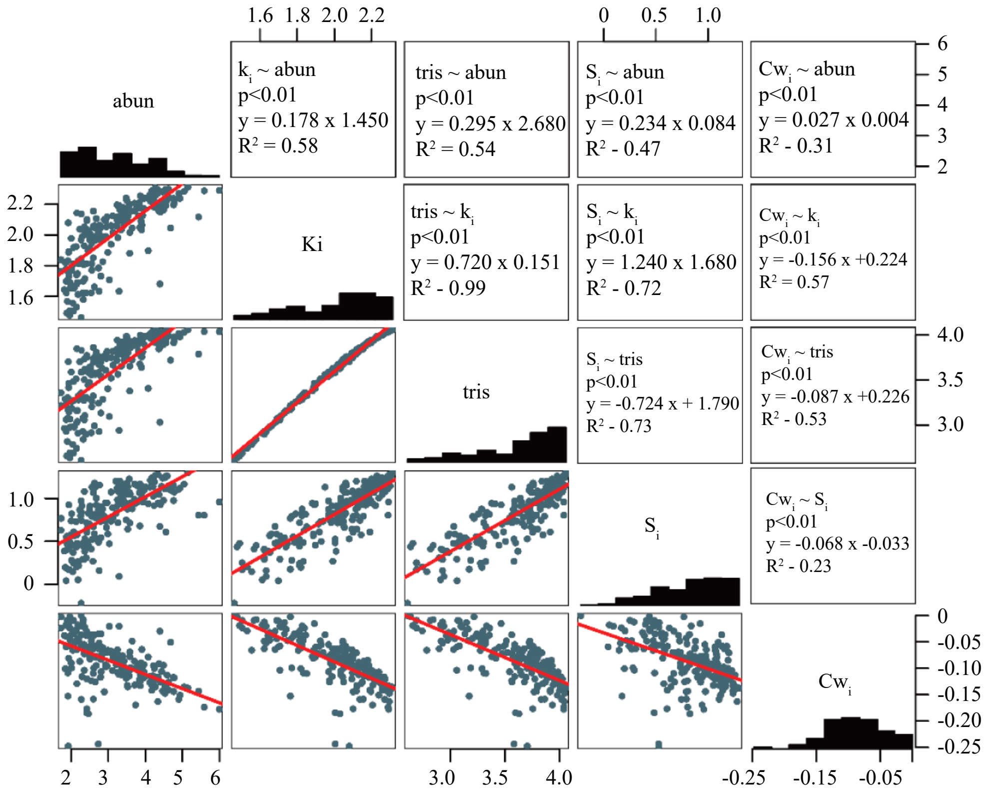
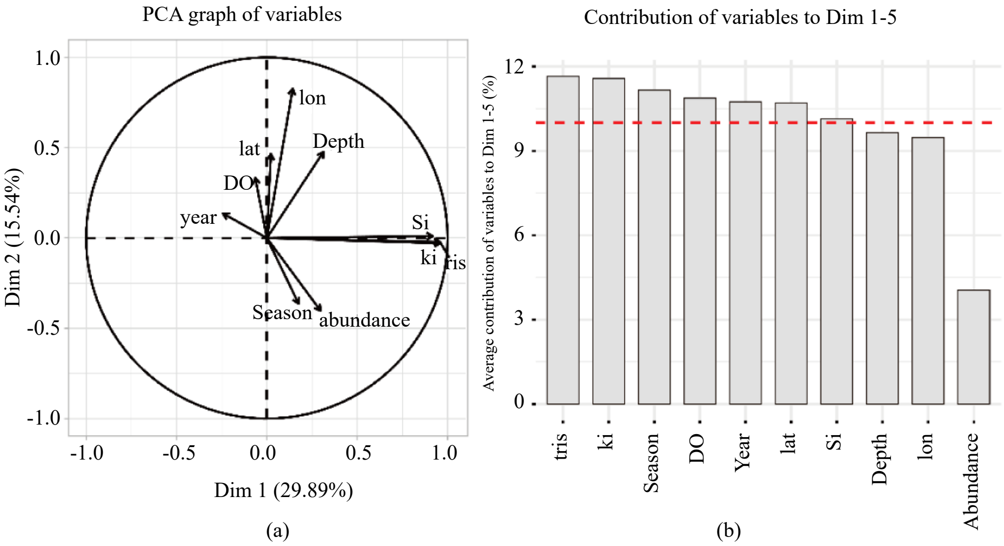


Fig. 3. Log-log plot of linear correlations between biotic variables and complexity for fish species in Leizhou Bay. *abun* - abundance; k_i - the number of direct species associations; *tris* - triplets, the number of indirect species associations; *Si* - the strength of the association between a species and others in the community; Cw_i - the local weighted complexity. The lower triangle of figure is the linear fitting plots and the upper triangle of figure is the linear fitting information between variables. The diagonal is the frequency distribution of variables. The axes represent the values of variables which were transformed by $\log_{10}$



(a) (b)

Fig. 4. (a) Principal components analysis (PCA) graph of variables affecting Leizhou Bay fish community structure (b) Result of variations filtering. k_i - the number of direct species associations; *tris* - triplets, the number of indirect species associations of species; *Si* - the strength of the association between a species and others in the community; *Depth* - the water depth; *DO* - the dissolved oxygen; *lat* - the latitude; *lon* - the longitude; “Dim” - short for “Dimension” which reflect the principal components. The horizontal red dashed line is average contribution rate of variables to the Dim 1-5

Table 2. Contributions of variations to each principal component (Dim.1~5)

Variables	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
k_i	30.75	0.03	2.77	0.11	0.00
S_i	28.20	0.01	0.00	0.01	0.03
Tris	30.96	0.05	2.79	0.05	0.00
Abundance	2.96	10.46	3.16	3.09	0.14
Lon	0.69	44.04	4.80	0.36	0.68
Lat	0.02	13.98	3.02	0.19	57.10
Depth	3.27	14.61	10.20	0.50	29.10
DO	0.14	7.11	16.20	45.28	1.11
Year	1.98	1.19	48.90	0.02	7.40
Season	1.03	8.51	8.17	50.39	4.43
Eigenvalue of Dim	2.99	1.55	1.51	1.18	1.09
Variance percent of Dim	29.89	15.54	15.06	11.77	10.95
Cumulative variance percent of Dim	29.90	45.40	60.50	72.30	83.20

lat + S_i + *DO*. Model results (Table 3) reveal: k_i (Estimate = -3.49, p<0.01) to have an extremely significant negative effect on complexity and *tris* (Estimate = 3.03, p<0.01), *season* (Estimate = 0.28, p<0.01) and S_i (Estimate = 0.13, p<0.01) to have an extremely significant positive effect on complexity. Y*ear* (Estimate = -0.08, p<0.01) had a significant negative effect on community complexity. Remaining variables had no significant effect on complexity.

The best fitting GLM model was obtained by stepwise regression method: ~ *tris* + k_i + *season* + *year* + *lat* + S_i. The influence of each variable on (estimated values) was k_i > *tris* > *season* > S_i > *year* > *lat*. The Akaike information criterion (AIC) value of the model decreased after removing *DO*, while the coefficients and significance of other variables did not change significantly; the effect of *DO* on complexity could be ignored. The negative effects of k_i on complexity may be offset by *tris* (indirect associations). Season as a variable was a secondary factor. Because the abiotic spatial variables of the environment were not significant, the impacts of abiotic variables on complexity were not significant.

Table 3. The linear relationship between each variable and the complexity of community structure

Variations	Full model estimate	Step model estimate
k_i	-3.49***	-3.50***
tris	3.03***	3.05***
Season	0.28***	0.28***
S_i	0.13**	0.13**
year	-0.08*	-0.07*
lat	0.04	0.04
DO	0.02	-
AIC	1268	1266

Notes: "*" means a significant level less than 0.05, "**" means a significant level less than 0.01 and "***" means a significant level less than 0.001.

Discussion

The closer the species associations (high niches overlap), the greater the likelihood of species extinction or niche partitioning (Bregman *et al.,* 2015), which led to the increase of competitive effects between species. The fish community in Leizhou Bay was highly complex (*mCw* values of 0.821±0.081) and the community is mainly comprised of populations with high niche overlap (*i.e.* the pair-populations). Considering all biological, environmental and spatial variables, both direct (k_i, Estimate = -3.49, p<0.01) and indirect (*tris*, Estimate = 3.03, p<0.01) species associations have sustained the complexity of fish community structure, but environmental and spatial effects were not significant (Table 3). Considering only biological interactions, complexity decreased while the indices' value increased (Fig. 3).

Direct and indirect species associations are the main contributors of high complexity in fish community structure, and play key roles in resistance to biological invasion (Li and Yu, 2015). Species with high k_i values in the community are the dominant species (Fig. 3). Dominant species in the community offer more chances for the stability of community structure when facing threats to biodiversity. The increase in direct species associations contributed to the development of triplets and the flux of energy in community, which could effectively prevent cascading extinctions (Sahasrabudhe and Motter, 2011; Li and Yu, 2015).

Capturing the global properties at community level is essential for understanding the community structure and functions. The species association is affected by the occurrence of species (Sfenthourakis *et al.,* 2006; Plank *et al.,* 2020) and the strength is affected by the spatial patterns of species and their abundance.

Results of the study showed that there were more roles of biological interactions than environmental variables in structuring the fish community of Leizhou Bay. Gallucci *et al.* (2020) reported that the spatial structure of community was usually determined by the environmental factors. The results of the study supported that the environmental variables influence directly the species association and then indirectly the community complexity. The migrating abilities of species in or out of a community needs to be considered to quantify the species associations between sampling surveys in future studies (Zhu *et al.,* 2013).

Acknowledgements

This work was supported by the Southern Marine Science and Engineering Guangdong Laboratory (Zhanjiang) (ZJW-2019-06) and the National Key Research and Development Program of China (2020YFD0901103). We are grateful for the assistance of Mr. Zhaowei Huang, Liyi Lu, Qian Liu, Shenzeng Zhang, Zhijie Chen and Lihua Lai in data analysis and drafts editing and also Liwen Bianji (Edanz) (www.liwenbianji.cn/) for editing the English text of the draft manuscript.

References

Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R., Fortin, M. -J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A. and Gravel, D. 2019. The marine fish food web is globally connected. *Nat. Ecol. Evol.,* 3(8): 1153-1161. https://doi.org/10.1038/s41559-019-0950-y.

van Altena, C., Hemerik, L. and de Ruiter, P. C. 2016. Food web stability and weighted connectance: The complexity-stability debate revisited. *Theor. Ecol.,* 9(1): 49-58. https://doi.org/10.1007/s12080-015-0291-7.

Banasek-Richter, C., Bersier, L. -F., Cattin, M. -F., Baltensperger, R., Gabriel, J. -P., Merz, Y., Ulanowicz, R. E., Tavares, A. F., Williams, D. D., Ruiter, P. C., Winemiller, K. O. and Naisbit, R. E. 2009. Complexity in quantitative food webs. *Ecology,* 90(6): 1470-1477. https://doi.org/10.1890/08-2207.1.

Barbier, E. B. 2017. Marine ecosystem services. *Curr. Biol.,* 27(11): R507-R510. https://doi.org/10.1016/j.cub.2017. 03.020.

Barrat, A., Barthelemy, M., Pastor-Satorras, R. and Vespignani, A. 2004. The architecture of complex weighted networks. *Proc. Natl. Acad. Sci.,* 101(11): 3747-3752. https://doi.org/10.1073/pnas.0400087101.

Benedek, Z., Jordán, F. and Baldi, A. 2007. Topological keystone species complexes in ecological interaction networks. *Community Ecol.,* 8(1): 1-7. https://doi.org/10.1556/ComEc.8.2007.1.1.

Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. and Hwang, D. -U. 2006. Complex networks: Structure and dynamics. *Phys. Rep.,* 424(4-5): 175-308. https://doi.org/10.1016/j.physrep.2005.10.009.

Bregman, T. P., Lees, A. C., Seddon, N., MacGregor, H. E. A., Darski, B., Aleixo, A., Bonsall, M. B. and Tobias, J. A. 2015. Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology,* 96(10): 2692-704. https://doi.org/10.1890/14-1731.1.

Calatayud, J., Andivia, E., Escudero, A., Melian, C. J., Bernardo-Madrid, R., Stoffel, M., Aponte, C., Medina, N. G., Molina-Venegas, R., Arnan, X., Rosvall, M., Neuman, M., Noriega, J. A., Alves-Martins, F., Draper, I., Luzuriaga, A., Ballesteros-Canovas, J. A., Morales-Molino, C., Ferrandis, P., Herrero, A., Pataro, L., Juen, L., Cea, A. and Madrigal-Gonzalez, J. 2020. Positive associations among rare species and their persistence in ecological assemblages. *Nat. Ecol. Evol.,* 4(1): 40-45. https://doi.org/10.1038/s41559-019-1053-5.

Chamberlain, S. A., Bronstein, J. L. and Rudgers, J. A. 2014. How context dependent are species interactions? *Ecol. Lett.,* 17(7): 881-890. https://doi.org/10.1111/ele.12279.

Cheadle, C., Vawter, M. P., Freed, W. J. and Becker, K. G. 2003. Analysis of microarray data using Z score transformation. *J. Mol. Diagn.,* 5(2): 73-81. https://doi.org/10.1016/S1525-1578(10)60455-2.

Christianou, M. and Kokkoris, G. D. 2008. Complexity does not affect stability in feasible model communities. *J. Theor. Biol.,* 253(1): 162-169. https://doi.org/10.1016/j.jtbi.2008.03.001.

Cohen, J. E. and Newman, C. M. 1985. When will a large complex system be stable? *J. Theor. Biol.,* 113(1): 153-156. https://doi.org/10.1016/S0022-5193(85)80081-3.

Csardi, G. and Nepusz, T. 2006. The iGraph software package for complex network research. *Inter J. Complex Syst.,* 1695(5): 1-9. https://igraph.org.

Demongeot, J. and Demetrius, L. A. 2015. Complexity and stability in biological systems. *Int. J. Bifurc. Chaos,* 25(7): 1540013. https://doi.org/10.1142/S0218127415400131.

Diekmann, M., Dupre, C. and van der Maarel, E. 2003. Fine-scale species associations in alvar limestone grasslands. *Nord. J. Bot.,* 23(1): 115-128. https://doi.org/10.1111/j.1756-1051.2003.tb00373.x.

Emmert-Streib, F. 2013. Structural properties and complexity of a new network class: Collatz step graphs. *PLoS One,* 8(2): e56461. https://doi.org/10.1371/journal.pone.0056461.

Facchinelli, A., Sacchi, E. and Mallen, L. 2001. Multivariate statistical and GIS-based approach to identify heavy metal sources in soils. *Environ. Pollut.,* 114(3): 313-324. https://doi.org/10.1016/S0269-7491(00)00243-8.

Gu, L., Gong, Z. W. and Li, W. Z. 2017. Niches and interspecific associations of dominant populations in three changed stages of natural secondary forests on Loess Plateau, P. R. China. *Sci. Rep.,* 7(1): 6604. https://doi.org/10.1038/s41598-017-06689-9.

Haydon, D. 1994. Pivotal assumptions determining the relationship between stability and complexity: An analytical synthesis of the stability-complexity debate. *Am. Nat.,* 144(1): 14-29. https://doi.org/10.1086/285658.

Helaouet, P. and Beaugrand, G. 2009. Physiology, ecological niches and species distribution. *Ecosystems,* 12(8): 1235-1245. https://doi.org/10.1007/s10021-009-9261-5.

Kaiser, H. F. 1991. Coefficient alpha for a principal component and the Kaiser-Guttman rule. *Psychol. Rep.,* 68(3): 855-858. https://doi.org/10.2466/pr0.1991.68.3.855.

Kassambara, A. and Mundt, F. 2020. *Factoextra: Extract and visualise the results of multivariate data analyses. R package version 1.0.7.* https://CRAN.R-project.org/package=factoextra.

Landi, P., Minoarivelo, H. O., Brännström, A., Hui, C. and Dieckmann, U. 2018. Complexity and stability of ecological networks: A review of the theory. *Popul. Ecol.,* 60(4): 319-345. https://doi.org/10.1007/s10144-018-0628-3.

Le, S., Josse, J. and Husson, F. 2008. FactoMineR: An R package for multivariate analysis. *J. Stat. Softw.,* 25(1): 1-18. https://doi.org/10.18637/jss.v025.i01.

Li, R. -H. and Yu, J. X. 2015. Triangle minimization in large networks. *Knowl. Inf. Syst.,* 45(3): 617-643. https://doi.org/10.1007/s10115-014-0800-9.

Li, X. X., Yang, W., Sun, T., Cui, B. S. and Shao, D. D. 2021. Relationship between complexity and diversity in aquatic food webs. *Acta Ecol. Sin.,* 41(10): 3856-3864. (in Chinese with English Abstract). https://doi.org/10.5846/stx202009192439.

Lin, K., Mai, G. M., Wang, L. F. and Wang, X. F. 2020. Structure and stability of the fish community in the Pearl River Estuary coastal waters from 2015 to 2018. *J. Fish. China,* 44(11): 1841-1850. (in Chinese with English Abstract). https://doi.org/10.11964/jfc.20191112081.

Maihaiti, M. and Zhang, W. J. 2014. A mini review on theories and measures of interspecific associations. *Selforganizology,* 1(3-4): 206-210.

Mcassey, M. P. and Bijma, F. 2015. A clustering coefficient for complete weighted networks. *Netw. Sci.,* 3(2): 183-195. https://doi.org/10.1017/nws.2014.26.

McCullagh, P. and Nelder, J. A. 1989. *Generalised linear models,* 2nd edn. Chapman and Hall, London, UK, 532 pp. http://dx.doi.org/10.1007/978-1-4899-3242-6.

Montoya, J. M., Pimm, S. L. and Sole, R. V. 2006. Ecological networks and their fragility. *Nature,* 442(7100): 259-264. https://doi.org/10.1038/nature04927.

Morales-Castilla, I., Matias, M. G., Gravel, D. and Araujo, M. B. 2015. Inferring biotic interactions from proxies. *Trends Ecol. Evol.,* 30(6): 347-356. https://doi.org/10.1016/j.tree.2015.03.014.

Morueta-Holme, N., Blonder, B., Sandel, B., McGill, B. J., Peet, R. K., Ott, J. E., Violle, C., Enquist, B. J., Jorgensen, P. M. and Svenning, J.-C. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography,* 39(12): 1139-1150. https://doi.org/10.1111/ecog.01892.

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature,* 307(5949): 321-326. https://doi.org/10.1038/307321a0.

Plank, M. J., Simpson, M. J. and Binny, R. N. 2020. Small-scale spatial structure influences large-scale invasion rates. *Theor. Ecol.,* 13(3): 277-288. https://doi.org/10.1007/s12080-020-00450-1.

Rasool, M. A., Zhang, X. B., Hassan, M. A., Hussain, T., Lu, C., Zeng, Q., Peng, B. Y., Wen, L. and Lei, G. C. 2021. Construct social-behavioral association network to study management impact on waterbirds community ecology using digital video recording cameras. *Ecol. Evol.,* 11(5): 2321-2335. https://doi.org/10.1002/ece3.7200.

Revelle, W. 2020. *PSYCH: Procedures for psychological, psychometric and personality research.* North-western University, Evanston, Illinois.https://CRAN.R-project.org/package=psych.

Sahasrabudhe, S. and Motter, A. E. 2011. Rescuing ecosystems from extinction cascades through compensatory perturbations. *Nat. Commun.,* 2(1): 170-177. https://doi.org/10.1038/ncomms1163.

Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science,* 185(4145): 27-39. https://doi.org/10.1126/science.185.4145.27.

Sfenthourakis, S., Tzanatos, E. and Giokas, S. 2006. Species co-occurrence: The case of congeneric species and a causal approach to patterns of species association. *Glob. Ecol. Biogeogr.,* 15(1): 39-49. https://doi.org/10.1111/j.1466-822X.2005.00192.x.

Silknetter, S., Creed, R. P., Brown, B. L., Frimpong, E. A., Skelton, J. and Peoples, B. K. 2020. Positive biotic interactions in freshwaters: A review and research directive. *Freshw. Biol.,* 65(4): 811-832. https://doi.org/10.1111/fwb.13476.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology,* 16(3): 284-307. https://doi.org/10.2307/1930070.

Tzafestas, S. G. 2018. Adaptation, complexity and complex adaptive systems. In: Antsaklis, P., Borne, P., Carelli, R., Fukuda, T., Gans, R. N., Harashima, F., Martinet, P., Monaco, S., Negenborn, R. R., Pascoal, M. A., Schmidt, G., Sobh, M. T., Tzafestas, C. and Valavanis, K. (Eds), *Energy, information, feedback, adaptation and self-organization*. Springer, Cham. p. 409-460. https://doi.org/10.1007/978-3-319-66999-1_8.

Ushio, M., Hsieh, C., Masuda, R., Deyle, E. R., Ye, H., Chang, C.-W., Sugihara, G. and Kondoh, M. 2018. Fluctuating interaction network and time-varying stability of a natural fish community. *Nature,* 554(7692): 360-363. https://doi.org/10.1038/nature25504.

Yeomans, K. A. and Golder, P. A. 1982. The Guttman-Kaiser criterion as a predictor of the number of common factors. *J. R. Stat. Soc. Ser. Stat.,* 31(3): 221-229. https://doi.org/10.2307/2987988.

Zbinden, Z. D. 2021. A needle in the haystack? Applying species co-occurrence frameworks with fish assemblage data to identify species associations and sharpen ecological hypotheses. *J. Fish Biol.,* https://doi.org/10.1111/jfb.14752.

Zeng J. W., Lin K., Wang X. F. and Li C. H. 2019. Fish community structure and its relationship with environmental factors in Leizhou Bay. *J. Fish. Sci. China,* 26(1): 108-117. https://doi.org/10.3724/SP.J.1118.2019.18378. (in Chinese with English Abstract).

Zhang, J. 2016. *SPAA: SPecies Association Analysis software.* https://CRAN.R-project.org/package=spaa.

Zhang, Z. B., Wang, Z. W. and Li, D. M. 1998. Ecological complexity-Review and prospect. *Acta Ecol. Sin.,* 18(4): 433-441 (in Chinese with English abstract).

Zhao, D., Shen, F., Zeng, J., Huang, R., Yu, Z. and Wu, Q. L. 2016. Network analysis reveals seasonal variation of co-occurrence correlations between Cyanobacteria and other bacterioplankton. *Sci. Total Environ.,* 573: 817-825. https://doi.org/10.1016/j.scitotenv.2016.08.150.

Zhu G. P., Liu G. Q., Bu W. J. and Gao Y. B. 2013. Ecological niche modeling and its applications in biodiversity conservation. *Biodivers. Sci.,* 21(1): 90-98. https://doi.org/10.3724/SP.J.1003.2013.09106. (in Chinese with English Abstract).

Date of Receipt : 10.11.2021
Date of Acceptance : 28.01.2022