

Original Articles

Fitting methods and seasonality effects on the assessment of pelagic fish communities in Daya Bay, China

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ABSTRACT

The general relationship indicating that biomass decreases with individual body size is referred to as size spectra. This is consistent with the power law that characterizes size frequency distributions. While many previous studies have used the estimated exponent in size spectra as a metric to assess external perturbations, limited empirical studies have focused on the fitting methods. Here, we compared the effects caused by fitting methods and distribution models based on one-year pelagic fish data from Daya Bay, China. Our empirical results showed that maximum likelihood estimation (MLE) is more suitable than traditional normalized biomass spectra (NBS), and that a power law is not always the best model when using MLE. Moreover, we found significant size structure variation in different seasons. Principal component analysis (PCA) and linear mixed effects model (LMM) results showed that temperature was the major factor in seasonal environmental variation, and fish migration might be the essential response strategy causing size structure changes. The estimated exponents and nonlinear structure indicated that the Daya Bay is under intensive human impact. Our results suggest that MLE methods are recommended in future size-based studies, and that environmental variation and migration patterns are crucial in understanding seasonal community structure changes.

1. Introduction

Organism size is a “master trait” in ecological studies (Horne et al., 2016), allowing ecologists to understand the organism’s physiological processes (e.g., growth, metabolism, and mortality rate), population interactions and ecosystem processes (Brose et al., 2016; Brown et al., 2004; Trebilco et al., 2013). Size structure, or how body size is distributed, has also been increasingly recognized as important to study the community structure and function (Genner et al., 2010; Yvon-Durocher et al., 2011). Traditional food web models focus on inter-specific relationships without considering individual size, although the latter may determine feeding interactions or predator-prey relationships (Brose et al., 2016). On a global scale, size distributions have been used as a metric to indicate warming effects (Yvon-Durocher et al., 2011); in regional studies, such information helps to predict the effect of external factors, such as fishing pressure or environmental fluctuation (García-Comas et al., 2014; Graham et al., 2005). In general, size-based models have become a powerful approach to the study of ecological communities, especially in aquatic ecosystems (Dulvy et al., 2004; Genner et al., 2010). However, more attention should be paid to

the theories and methods of size distribution to ensure consistency in future studies.

A general size distribution rule states that small-size individuals aggregate the largest biomass in a community and that abundance decreases sharply in higher trophic levels. This is referred to as a power law rule in natural phenomena (Savage et al., 2004). The rule could be explained by “allometric scaling” between metabolic rate and body mass at the individual level (Brown et al., 2004), or by ecological pyramids at the community level (Trebilco et al., 2013). A power law relation could be transformed to a typical size spectra model through a logarithmic transformation. Since power law distributions have been found in many studies, including analysis of oceans, freshwater lakes, rivers, and terrestrial ecosystems (Benejam et al., 2018; Gaedke, 1992; Hatton et al., 2015; Yurista et al., 2014), the exponent of linear pattern has become an important indicator to quantify size structure changes. The quantification of the exponent is based on the predator-prey mass ratio (PPMR) and trophic transfer efficiency (TTE), an ideal value of the exponent is exactly -1.0 when the TTE is 10% and PPMR equals 10^4 (Mehner et al., 2018). However, empirical studies have shown that the community distribution tends to be steeper and that exponent is lower

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than -1.0 (Mehner et al., 2018; Sprules et al., 2016), owing to the effects of external perturbation. For example, excessive human fishing could cause substantial biomass loss of large fish and higher abundance of small-size individuals through trophic cascading, leading to steeper slopes of the biomass spectra than those communities that are less exploited (Robinson et al., 2017; Sweeting et al., 2009). In addition to fishing pressure, climate change is also a major driving factor in shifts of community size distributions. Consistent warming in the North Sea has resulted in declines in body size and abundance of larger fish individuals (Genner et al., 2010). A warmer environment also increased the steepness of freshwater plankton size spectra (Yvon-Durocher et al., 2011), which provided essential insight into climatic effects on the global ocean community. Moreover, the size spectra are not consistently linear and environmental deviations such as habitat complexity might cause nonlinear relationships between biomass and body size (Rogers et al., 2014). All these results concerning the size distribution have prompted new understanding of the environmental effects on marine ecology and fishery conservation.

Although deviation of spectral exponents driven by direct interference have been examined in previous studies (Duplisea and Kerr 1995; Niels Daan et al., 2005; Sweeting et al., 2009; Yvon-Durocher et al., 2011), limited empirical work has focused on the effects of fitting methods. Recently, Edwards et al. (2017) have tested the accuracy of several bin-based methods, including 4 methods fitting regression with log (abundance) against log (size bin) and 2 methods fitting regression with log (biomass) against log (size bin). The former methods appeared to underestimate exponent value, and the latter methods have less than 95% (74–90%, depend on the maximum value) confidence intervals including the true exponent value. The main reasons are that these models binned the data and assumed that individual size distribution is power law (Edwards et al., 2017), although the choice of bin widths might cause biased estimates of the slope (Vidondo et al., 1997; White et al., 2008) and the size distributions also require more validity test. Hence, White et al. (2008) and Edwards et al. (2017) have proposed that the term “probability density of body size” is more suitable in describing size structure. Consequently, the uses of explicit likelihood-based methods should be also more recommended. However, maximum likelihood estimation (MLE) is not usually applied in aquatic research, and only few tests employed empirical data (Reuman et al., 2008). Therefore, it is necessary to expand the usage of MLE from simulation to empirical studies.

It is well known that environmental variation affects species composition and body size (Akin et al., 2005; Maestri et al., 2016), but how community size structure responds to abiotic factors and nutrient availability is still unclear (dos Santos et al., 2017; Mulder et al., 2018). Marcolin et al. (2015) reported that nutrient-rich oceanic intrusions induced steeper zooplankton size compositions, while García-Comas et al. (2014) suggested that slopes of mesozooplankton size spectra were unrelated to environmental factors. According to Edwards' et al. (2013) study, how species responded to environmental fluctuation is related to their functional traits. Limited resources, such as light irradiance and nutrients, are key for phytoplankton growth rates, light capture and carbon fixation, and can affect energy flows towards the whole community (Edwards et al., 2015). The physiological processes, predator-prey relationships and community function of species in higher trophic levels are also directly affected by environmental variables (Dobashi et al., 2018; Montero-Serra et al., 2015; Yeager et al., 2017), which are mainly affected by seasonality (Tonkin et al., 2017). Besides, the intra-annual trawl frequency could also affect the size structure (Duplisea et al., 2002). All these factors contribute significantly to the shifts in the size distribution and may provide an explanation of seasonal effects on size structure.

Here, we examined the effects of fitting methods and seasonality on community size structure of pelagic fish in Daya Bay, China. The pelagic fish community is an essential functional group that links primary producers and carnivorous predators (Peck et al., 2013). Due to their

high recruitment rates and rapid responses to changes, the pelagic fish had been widely used as indicators of environment effects and climate change (Lefort et al., 2015; Montero-Serra et al., 2015). Fish data were collected through intra-annual trawl surveys in Daya Bay, South China Sea, a typical closed gulf subjected to long-term anthropogenic activities and environmental eutrophication (Wang et al., 2011). Therefore, the gulf is a justified region to study the effects of human activities on fish community size distributions. In this study, we aimed to (1) compare fitting methods effects and usability of different methods in the estimating of fish size spectra to validate the results of Edwards et al. (2017); (2) to describe spatial and temporal variation in fish size spectra exponent; (3) to determine the major factors related to the seasonal changes in fish size distributions.

2. Materials and methods

2.1. Sampling and data

Fish data were collected through an intra-annual trawl survey in Daya Bay, a gulf between Shenzhen City and Huizhou City in Guangdong Province, China ($22^{\circ}30' - 22^{\circ}50' \text{ N}$, $114^{\circ}30' - 114^{\circ}50' \text{ E}$). Trawl surveys were conducted seasonally (November in 2017, January, April, and July in 2018, representing autumn, winter, spring and summer, respectively). Pair trawls with the power levels of 125 kw were employed to collect pelagic fish. Simultaneously, larval fish was collected horizontally using plankton net (length: 145 cm, inner diameter: 50 cm, net mesh: 0.505 mm). The trawling at each station lasted 30–50 min, and larval fish sampling costed 15 min.

The 16 sampling stations were divided into 4 sampling line, which is Daya Bay east (DE), Daya Bay west (DW), Daya Bay mouth (DM) and Daya Bay south (DS). Each sampling line include 4 stations (Fig. 1). The stations were selected to cover the different region of Daya Bay as far as possible, although the stations were not evenly distributed due to the complex factors of sites. Fish samples were identified to species level and the density, individual body mass and length of each species were counted on site based on random sampling. Finally, 123 species were collected in the trawl surveys. Identification of species and relative feeding habits were done using <http://www.fishbase.com>.

Environmental variables including sea surface temperature (SST), dissolved oxygen content (DO), Chemical Oxygen Demand (COD), inorganic nitrogen (DIN), and phosphorus (PO_4^{3-}) were measured. Among them, SST and DO were measured on site using thermometer and iodimetry method, respectively. A total of 1000 mL water sample was collected for COD, DIN and PO_4^{3-} -P measurement. The sampling water was stored in polyethylene bottles and sulfuric acid was added as a fixative. All the samples were kept under 4°C and transported to the laboratory. The measurement of COD, DIN, PO_4^{3-} was using basic potassium permanganate, hypobromite oxidation and molybdenum blue spectrophotometric method respectively. Method detection limits (MDL) are 0.15 mg/L for COD measurement, 0.0004 mg/L for DIN measurement and 0.0014 mg/L for PO_4^{3-} measurement. All the measurements were according to the National Standard of China (GB 17378.4-2007).

2.2. Fitting methods

2.2.1. MLE

MLE has long been used for estimating power law distributions in other natural phenomena (Edwards et al., 2007; Serra and Corral, 2017). Here, we simulated 4 data sets (each data set represents a season) according to our summary statistics from fish sampling and assumption that body sizes followed a normal distribution. The simulated data were generated by encapsulated R function `rnorm()`, which based on the Mersenne Twister algorithm. The data sets contained 150661, 916501, 79533, and 1470774 individual body masses. Based on the large data sets, we tested how the fish community would fit six

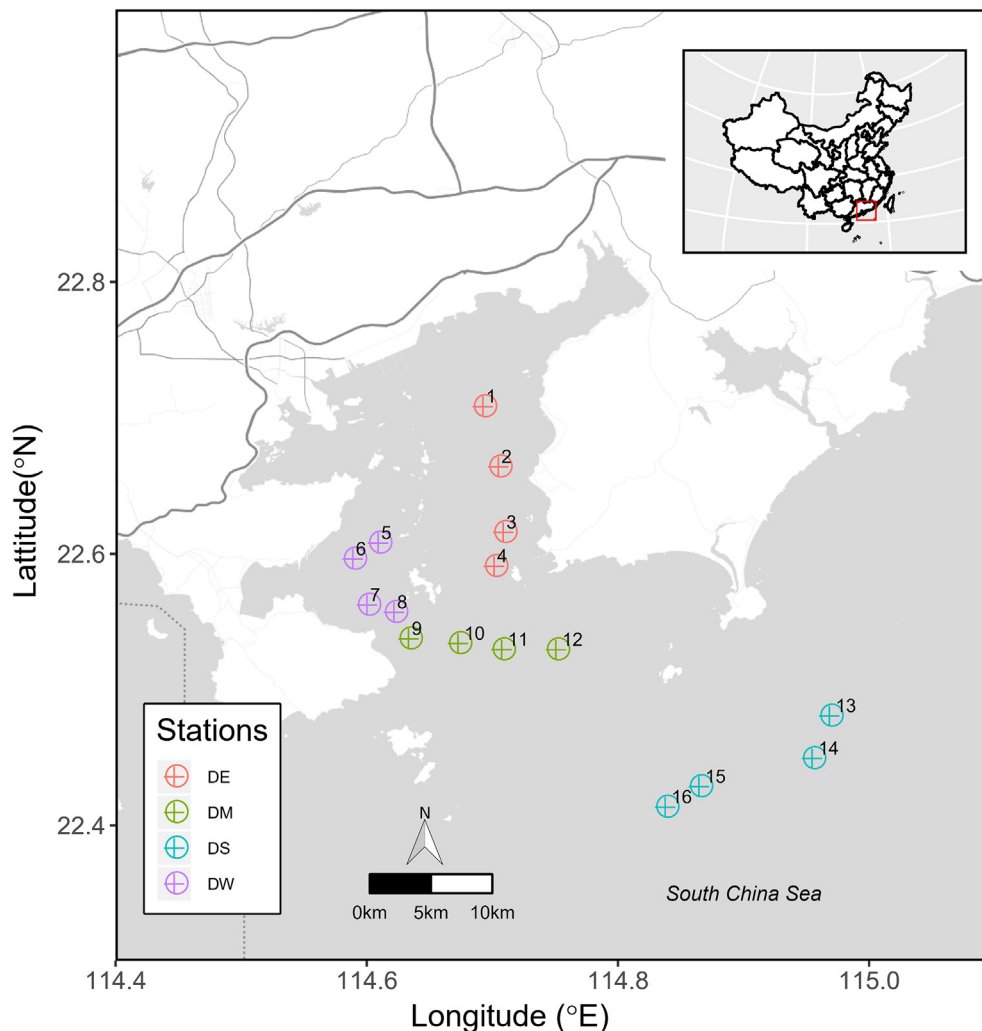


Fig. 1. The map of 16 Sampling stations in Daya Bay, China. All the stations were divided into 4 sampling lines, which is DE (Daya Bay east), DW (Daya Bay west), DM (Daya Bay mouth), DS (Daya Bay south).

specific distributions (i.e., power law, Pareto type I, exponential, logistic normal, Pareto type II and Burr distributions). All the distribution functions are included in Table A.1. Cumulative density functions (CDF) of body size were plotted to visualize the results.

2.2.2. Normalized biomass spectra

This method used data of biomass (kg) at size (the body mass in g), and binned the individuals into several intervals with same width (1 on \log_2 scale here) after a \log_2 transformation of individual size. Then the regression of \log_2 (normalized biomass with each size bin) against \log_2 (midpoint of the size interval) was fitted and plotted. The biomass was normalized by dividing the total biomass within every interval by bin width Platt and Denman (1977). Here we also fitted a quadratic model to compare with the linear model, since the quadratic model has provided a better description in previous studies (Sprules and Goyke, 1994).

2.2.3. Normalized biomass spectra without binning

As White et al. (2008) and Edwards et al. (2017) reported, binning-based methods often perform poorly. They are sensitive to bin width and are prone to bias. We thus constructed normalized biomass spectra without binning (NBS-2 hereafter) to demonstrate the effect of size bin width. More specifically, we plotted the fitted spectra as above, but without summarizing each bin size. This was done in view of the mathematical limit; we believed that every species could be assigned an

independent size. Points were grouped by feeding habit to indicate distributions of different trophic levels, and body size of every species was the mean value of population. Actual body size of individuals should cover several size classes, and this is one reason why we do not consider this result to be completely credible.

2.3. Data analyses

To indicate goodness of fit in NBS, Akaike information criterion (AIC) was calculated. Models with lower AIC values using the same method are recognized as better. Goodness-of-fit (GoF) tests were made to compare models in the MLE method while Kolmogorov-Smirnov statistics (KS statistic) was used to quantify differences between empirical data and the reference distributions (Clauset et al., 2009). Larger values of the KS statistics mean larger discrepancies with the observed distribution. According to the model comparison results, we also estimated the exponents of the size distributions. Two-way ANOVA and multiple comparisons were made to show the effects of season and station on size structure changes.

The principal component analysis (PCA) to the environmental variables was applied to reduce the dimensionality and extract the dominant factors. PCA of the original environmental variables could avoid multicollinearity in building a linear model. Correlation coefficients between each variable and principal component are known as loadings; these explain the correlativity of the original variables and the

principal components. Cos^2 values were used to visualize the representation of variables on principal components. A higher cos^2 value means a better quality of representation.

Based on the exponent data sets and the results of the PCA, we applied linear mixed effects models (LMM) with environmental variables, fishing interference, and migration. To avoid conflicts with the assumptions of LMM, we tested the normality of our data and calculated the VIF (Variance Inflation Factor) to test for multicollinearity and found our data met the assumption. Thus we used PC1 and PC2 to replace the original multidimensional environmental variables. The migration effects were also quantified by the abundance of larval fish at each station. To consider the effect of the summer fishing moratorium, we also added fishing as a binary categorical variable in the linear mixed effects model. Comparison of the models was made through the AIC and Akaike weights (ω_i), which represent the “weight of evidence” for the optimal model (Wagenmakers and Farrell, 2004).

To further examine the specific interactions between factors and size structure and to visualize the complex mixed model, we performed linear regression analyses of SST and maximum body size, SST and exponent, and exponent and maximum body size, because temperature was a major factor among the environmental variables. Furthermore, we used bar plots to illustrate the occurrence frequency of four species (*Stolephorus chinensis*, *Thryssa dussumieri*, *Sardinella lemuru*, and *Sardinella melanura*).

All the statistical analysis was carried out by statistical software R v3.5.1 (R Core Team, 2018).

3. Results

3.1. Model fitting results

As shown in Fig. 2 and Table 1, the shape of the community size distribution is generally domed using NBS. Slopes of linear regression results were not significant ($P > 0.05$). The quadratic model had a lower AIC value than the linear model in fitting the empirical data, meaning that the quadratic model is “better” than the linear model in this case. Normalized biomass also displays seasonal dynamics. In spring and summer, normalized biomass was higher than in autumn and winter. Normalized biomass during these two seasons are both less than 400 km^{-2} .

For NBS-2, linear regression results show that estimated slopes were significant ($P < 0.01$), which is contrary to NBS. This indicates that the effect of size classification is large in fitting biomass spectra. As shown in Fig. 2, species in lower body size bins are basically planktivores, indicating that these species belong to lower trophic levels in the marine community. Slopes by NBS-2 from autumn to summer were -1.19 , -0.72 , -0.43 , and -0.60 .

Fitting results of the six models using MLE performed differently as well. According to GoF test results and the AIC values, comparison of the six models reflected the general rule that models with more parameters fit better (Table 1). Burr distribution models had the lowest values of the KS statistics and can be regarded as the best model fitting the empirical data. The power law and Pareto type I distributions, which was the most frequently used in the size distributions, yielded the worst performance. The exponential model was the best one-parameter distribution, indicating that the exponents in an exponential distribution are more meaningful. The overall estimated exponents of the power law distributions were 1.13, 1.09, 1.13, and 1.11, and the estimated exponents of the exponential model were 0.07, 0.41, 0.07, and 0.28 for four seasons. Exponents for autumn and spring were similar and were also the lowest among the four seasons; the exponents in winter were the highest, showing that its size structure distribution was the most even.

3.2. PCA of environmental variables and seasonal exponent variation

The results of the PCA indicated that the environmental variables were grouped by season. Summer caused the highest discrepancy compared to the other three seasons, and environmental conditions in winter and autumn were similar (Fig. 3.A). The first principal component explained 57.2% of the overall variance, and the first two principal components explained 77.7% collectively. The two principal components were considered sufficient in reducing dimension and avoiding multicollinearity. For the environmental variables, SST had the highest cos^2 value, and the contributions of the other environmental variables were similar (Fig. 3.B).

Two-way ANOVA found no significant differences among stations. The exponents were significantly different between seasons except for autumn and winter (Fig. 4.A). In four seasons, the summer owns the highest exponent and the spring owns the lowest.

3.3. Linear mixed effects model

Comparison of seven linear mixed effects models showed that M5 = environment + migration was optimal (Table 2). M6 was not preferred, probably due to the collinearity between PC1 and fishing factor (both $\text{VIF} > 8$). This might result in the strong seasonal dynamics for both environment and fishing s in summer. ANOVA for the linear mixed effects model M5 showed that environmental factors PC1, PC2 and migration had significant influence on the community size structure (Table 3).

Regarding the specific effects of environmental factors, SST had a positive relationship with both maximum body size and the size distribution exponent. This indicated that the increased temperature related to seasonality leads to larger body size and improves the evenness of the community size distribution. The exponent of size structure is also strongly correlated with the maximum body size, indicating that changes in size structure might be caused by increased abundance of larger individuals (Fig. 5).

4. Discussion

Based on empirical data of the fish community size distribution, we built and compared different methods and models. Our analysis has confirmed the results of Edwards et al. (2017) that the widely used regression-based methods are deficient and the estimated slopes in size spectra are not always comparable due to different methods. Our study also tested and confirmed the validation whether the individual size distribution is power law. The estimation results are highly affected by different fitting distributions and different approaches might cause some subjective deviation. For example, the regression-based method is inappropriate to describe the nonlinear size structure, while the MLE method does not have the limitation.

Beyond this, our studies demonstrated the effects of seasonality on size structural changes. Exponents used to indicate size structure display significant differences in different seasons, similar to the variation observed for environmental variation and migration. Our analysis confirmed that environmental variation and responses of fish assemblages are both major factors in seasonal oscillations of size spectra.

4.1. Nonlinear structures between body size and biomass

Our results displayed visibly nonlinear relationships between body size and biomass. While a large number of prior studies have shown that linearity was the most likely relationship in normalized biomass spectra, nonlinear patterns have increasingly been observed in studies of freshwater fish, coral reef fish, and plankton communities (Arranz et al., 2018; Chang et al., 2014; Rogers et al., 2014). Multiple explanations for such patterns have been offered. Chang et al. (2014) have proposed a generalized MTE (metabolic theory of ecology) model that

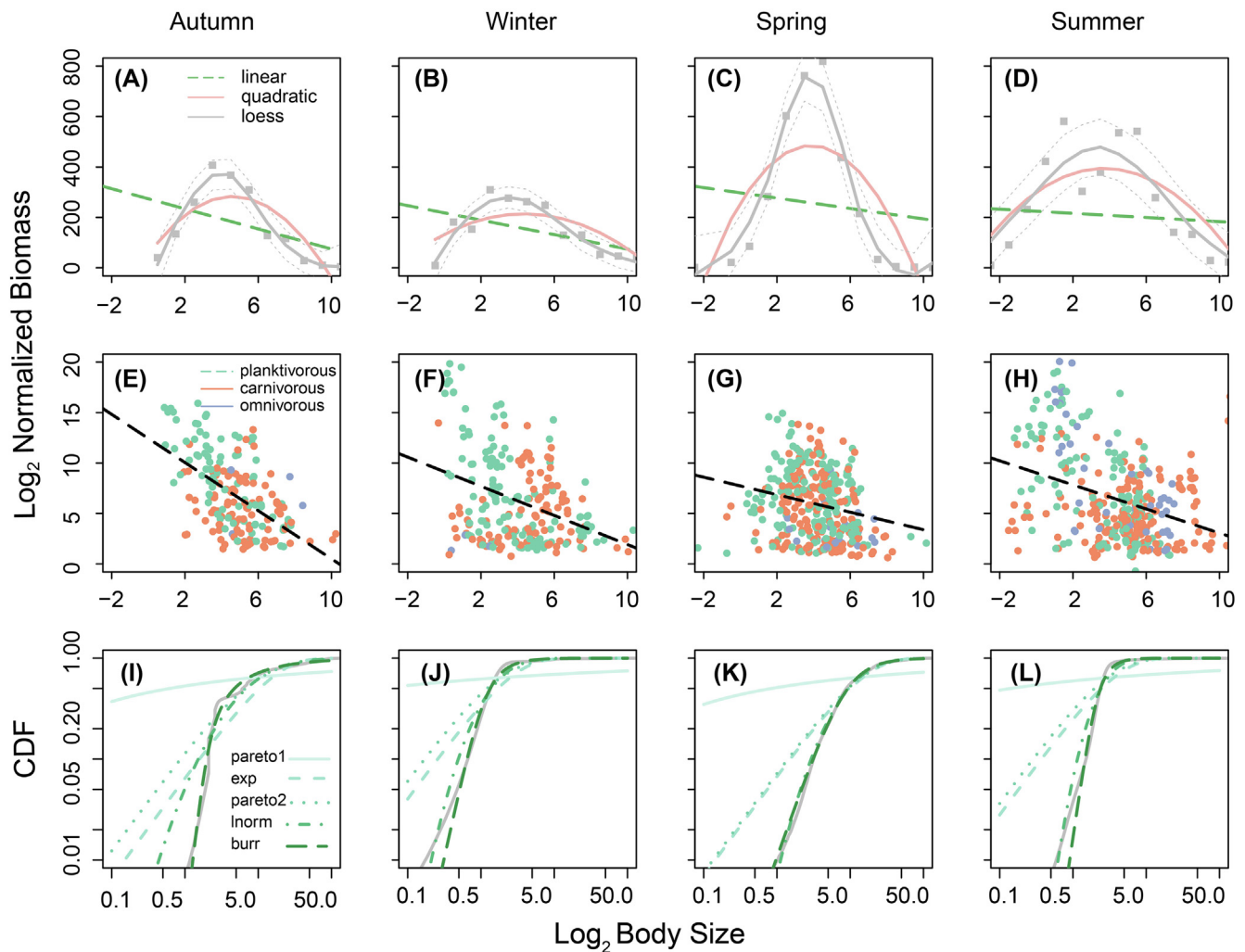


Fig. 2. Fitting result of three kinds of fitting methods. A–D): NBS, orange solid line means fitting result of quadratic model, green dotted line means linear regression result, grey solid and dotted line means loess model fitting result and 95% confidence intervals. Loess (locally estimated scatterplot smoothing) curve here is used to indicate a rough tendency. E–H): NBS-2, every point represents a species with similar size, they are grouped by feeding diets. Green, orange and blue dots mean planktivorous, carnivorous and omnivore species. I–L): MLE model results, different colors and lines mean different models, deeper green line represents better performance. X-axis of all subplots are body size in log-scale, but labels of I–L) display untransformed values. In I–L), y-axis is mean cumulative distribution function (CDF), a rapid rise on cumulative density curve means a large amount of biomass exists in relative individual size level.

Table 1
Main coefficient(s) of six fitting models.

Seasons	Autumn	Winter	Spring	Summer	Tendency
NBS					
Linear	−19.9 ^{ns}	−14.4 ^{ns}	−10.3 ^{ns}	−4.1 ^{ns}	linear < quadratic
Quadratic	−11.0 ^{**}	−4.3 ^{**}	−15.3 ^{**}	−6.9 ^{**}	
NBS-2					
Linear	−1.19 ^{***}	−0.72 ^{***}	−0.43 ^{***}	−0.60 ^{***}	
MLE					
Power law	1.13	1.09	1.13	1.11	one-parameter
Pareto I	0.13	0.09	0.13	0.11	
Exponential	0.07	0.41	0.07	0.28	< two-parameter
Log-Normal	1.9/1.2	0.3/0.8	2.3/0.9	0.9/0.6	
Pareto II	2.0/15.9	4.1/6.5	14.1/188.6	7.3/19.6	< three-parameter
Burr	0.1/6.4/0.5	0.6/3.3/0.9	0.9/2.1/0.1	0.6/5.0/0.5	

Notes: Coefficients of linear models are slope of regression results. Coefficients of quadratic models are parameter c in equation $a + bx + cx^2$. In MLE method, parameters mean a in power law, a and θ in pareto distribution, a and γ and θ in burr distribution sequentially. All the MLE models calculated the tendency of fit goodness rather than significance. Tendency is according to AIC value and KS statistics (Table A.2), the one to the right of less than symbol is preferred.

** $P < 0.01$

*** $P < 0.001$, ns: not significant

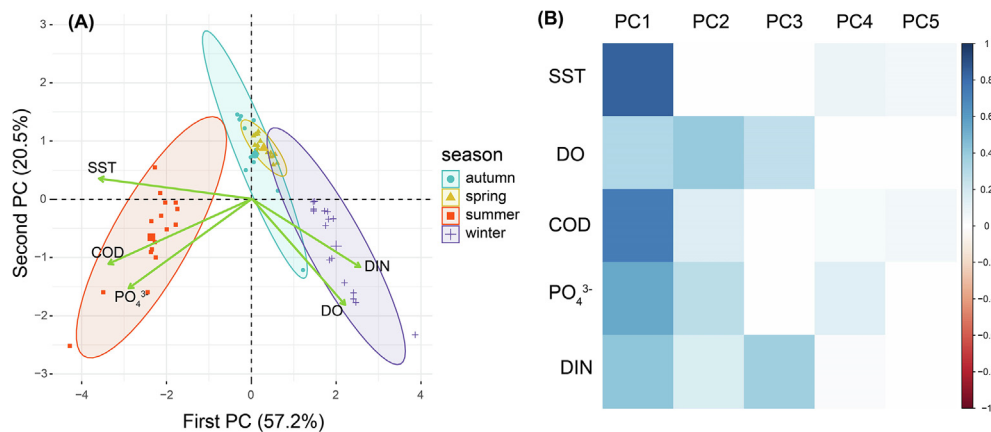


Fig. 3. (A) Principal component analysis of environmental variables and (B) \cos^2 value of different variables, blue indicate positive relationship with principal components, deeper color means better quality of representation.

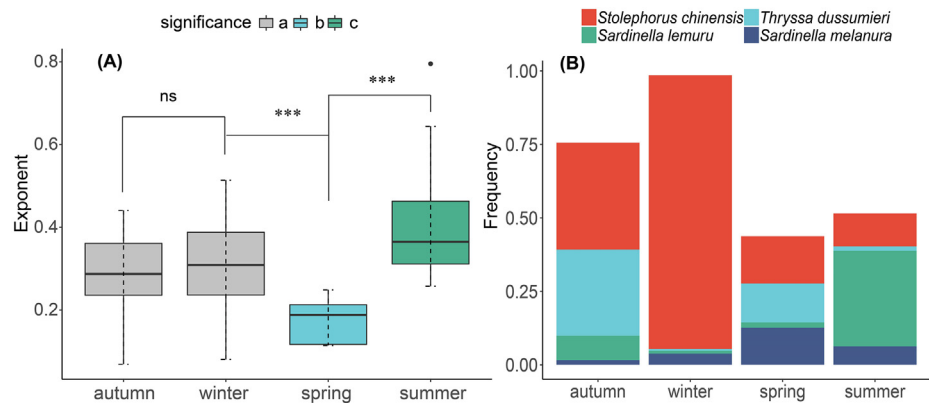


Fig. 4. (A) Comparison of exponent among different season, different color of the column indicated differences at $P < 0.001$; and (B) occurrence frequency variation of 4 representative species (*Stolephorus chinensis*, *Thyssa dussumieri*, *Sardinella lemuru*, and *Sardinella melanura*) in each season.

Table 2
Summary statistics of comparison of linear mixed effect models.

Model	Formula	Log-likelihood	ΔAIC	ω_i
M1	PC1 \times Migration	43.431	17.243	0.000
M2	PC2 \times Migration	43.431	17.245	0.000
M3	PC1 \times Migration + PC2 \times Migration	51.580	2.946	0.133
M4	PC1 \times Migration + PC2 \times Migration + Fishing	51.614	4.877	0.051
M5	PC1 + PC2 + Migration	52.053	0.000	0.582
M6	PC1 + PC2 + Fishing	48.423	7.26	0.015
M7	PC1 + PC2 + Migration + Fishing	52.073	1.959	0.218

Notes: Effects of environment (PC1, PC2), migration and fishing were used as fixed effect and effect of station as random effects. The M5 having the lowest AIC and highest Akaike weights is the preferred model.

Table 3
ANOVA of linear mixed effect model M5.

Factor	d.f.	P-value	VIC
PC1	1	< 0.001	1.02
PC2	1	< 0.001	1.04
Migration	1	< 0.01	1.06

linked size distributions and food webs from the perspective of trophic interactions. The dynamic models have predicted that the PPMR (predator-prey mass ratio) is not constant, in contrast to the key assumption in linear size-TL (trophic level) relationships (Fuchs and Franks, 2010). The impact of trophic interactions should be crucial for a gulf influenced by long-term human impacts, the abundant prey fish community

leads to a low PPMR, which makes size spectra sensitive and showed large oscillations or travelling waves (Datta et al., 2011). Recent empirical observations in lakes have also showed strong nonlinearity associated with the low PPMR (Arranz et al., 2018). Other than fishing intensity, fishing pattern is also important for size structure. Unselective fishing (as in our study) produced low yields of large fish, and thus individuals from 10 to 1000 g became dominant (Jacobsen et al., 2014). This is consistent with our findings for individual size (2–10 in \log_2 scale are major). Thus it is suggested that the unselective fishing patterns increase the mortality of juvenile fish, and caused the nonlinear structure (less juvenile fish and less large fish). However, in a diverse environment, there are multiple factors influencing the instability of the ecosystem and nonlinear patterns. How the secondary structure is shaped and affected is still an open question and requires more

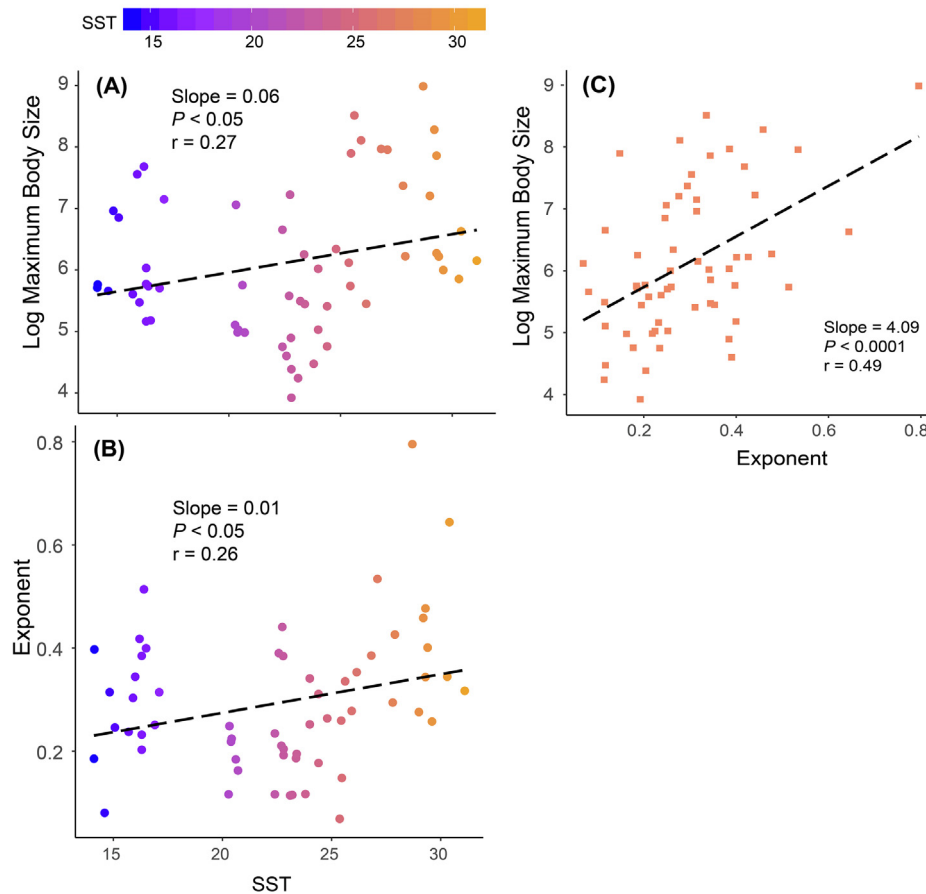


Fig. 5. Correlation between (A) SST and maximum body size, (B) SST and exponent, (C) exponent and maximum body size.

theoretical and empirical studies.

4.2. Deviation of size spectra caused by methods

Despite of the wide use in ecological studies, regression-based spectra were proposed to have methodological shortcomings (Sims et al., 2007; White et al., 2008; Edwards et al., 2017). And the keys of the deficiencies are: (i) inconsistent method; (ii) binning and (iii) regression.

Many size-based patterns were studied, including biomass size spectrum, abundance-size relationship and diversity size spectrum (Scott et al., 2014; White et al., 2007; Reuman et al., 2014). However, the estimated slopes of different methods are not comparable owing to the confusing definition of size spectrum (one parameter mapping on many patterns) (White et al., 2007) and different stability and accuracy of methods themselves (Edwards et al., 2017).

Methods involving binning and regression are also problematic and are not applicable when describing nonlinear structure or when the regression result are not significant. Moreover, the interval widths can affect the assessment precision (White et al., 2008). When size bin width was limited to zero, the NBS-2 yielded results contrary to spectra with binning in our study. In addition, logarithmic transformation may lose much of the available information in low-size bins. For example, a log-2 transformation converts individuals ranged from 0.125 to 1.000 g into three intervals even though their size does not vary largely. These individuals of low biomass are mainly planktivores and low trophic level organisms, as a result, the unreasonable partition may amplify the differences within similar functional groups (Pikitch et al., 2014).

Consequently, the term “probability density of body size” and MLE method, both of which avoid binning and regression, are suggested in our study. But when the MLE method was applied, further test of the

individual size distribution was necessary. In addition to power law distribution, Pareto distribution or exponential was also likely to be appropriate in ecological studies (Newman, 2005; Edwards et al., 2007; Humphries et al., 2010). For example, the Pareto type II distribution has been suggested as a better model for nonlinear structures (Vidondo et al., 1997). However, owing to the difficulty of interpreting the features of the model from an ecological perspective, there existed a tradeoff between availability and accuracy in multiple models. So model selection is critical and could be done using AIC weights or goodness-of-fit test. In our study, the exponential model was the most suitable, consistent with the study of Humphries et al. (2010) for marine predator study. Hence, the MLE is a better method and is recommended for size spectra construction, and the fitting distribution should not be limited to a power law.

4.3. Effects of seasonality on the biomass-size distribution

We generated size spectra and obtained the relevant exponents for each station and season. When the overall community was considered, the power law results yielded exponents less than -1 (from -1.13 to -1.09). This indicates that our results followed the general tendency of biomass-size relationships (Sprules et al., 2016). When every station is taken into consideration, environmental variables or migration ratios make no difference in the spatial scale. Therefore, it is reasonable to regard the whole gulf as a homogeneous habitat (Thrush et al., 2006). However, for the temporal scale, size structure, environmental variables, and migration all displayed differences to the extent as predicted. This suggested that seasonal dynamics played an important role in size distribution variations.

Understanding within-year fluctuation is fundamental for interpretation of fish assemblage behavior. A recent study has shown that

seasonal processes induced time-varying behavior for individuals, including growth rate and spawning strategy; thus, the spectral slope was more variable in seasonal systems (Datta et al., 2016). Similar results had been found in our empirical observations that the spectral exponent displayed significant changes with seasonality (Fig. 4.A), and both migration movement and environmental factor were significantly related to such variation (Table 3). As a major influencing factor for structural change, fish response strategy (e.g., spawning period or location) was driven by resource limitation (Albo-Puigserver et al., 2017; Datta et al., 2016). These response patterns are not consistent and depend on the species (Fig. 4.B). This also explained why the exponents and migration movements are not totally correlated with environmental variation.

In the other influencing factor, temperature was the most typical variable (Fig. 3). It has long been regarded as important factor related to animal biological processes. Both temperature and dissolved oxygen were the principal drivers of the zooplankton biomass distribution (Lucas et al., 2014). For pelagic fish, oceanic warming has induced their spatial shift towards colder region (Fossheim et al., 2015). The fish life histories are highly dependent on environmental temperature including their embryonic viability (Janhunen et al., 2010), growth rate (Benoît et al., 2000), and migration period (Jansen et al., 2012). Our study showed that higher temperature was significantly related to increased body size and fish stocks, which is consistent with earlier studies (Sabatés et al., 2006). Although this seem to be conflict to the report of Genner et al. (2010) that increased temperature led to decreased body size owing to long term effects of global warming, our study provided information about the fittest temperature for fish growth and reproduction, which is caused by seasonal dynamic in regional scale. In short, pelagic fish search for an optimal or sub-optimal temperature for a better growth environment (Peck et al., 2013). The pattern of energy allocation and energy utilization efficiency is directly influenced by temperature (Albo-Puigserver et al., 2017).

In this study, we did not describe the effects of fishing perturbation precisely due to the lack of related technology. Some methods used to quantify fishing intensity in previous studies like human population density or the region area were not preferable in this case (Dulvy et al., 2004; Robinson et al., 2016). Because these methods focus on the spatial variance rather than temporal changes as in our study. However, some technology like geographical information system (GIS) techniques and vessel monitoring systems (VMS) might be helpful in future studies for their preciseness (Lambert et al., 2012; Waluda et al., 2002) to provide better estimates of temporal and spatial fishing impacts and to expand research scale from region to globe.

5. Conclusions

Our empirical study confirmed our hypothesis that size-based approaches and seasonality exert subjective and objective influences on the assessment of community size structure. We suggest that (1) the MLE method is more accurate and is recommended for describing size structure; (2) the fish community size distribution has a strongly seasonal dynamic, temperature and spawning migration were the major driving factors; (3) human activity like unselective fishing patterns have affected the stability of the whole fish community in Daya Bay. The size spectrum model provides valuable ecological insights for the analysis of regional fishery resources and their variation. Future researches should include analyses using quantitative approaches to study community size distributions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.04.042>.

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