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Impacts of phytoplankton availability on bigeye tuna (*Thunnus obesus*) recruitment in the Indian Ocean

Yang Wang[1], Yuying Zhang[2], Zhe Geng[1,3,4] and Jiangfeng Zhu[1,3,4]*

[1]College of Marine Living Resource Sciences and Management, Shanghai Ocean University, Shanghai, China, [2]Department of Biological Sciences, Florida International University, Miami, FL, United States, [3]Key Laboratory of Oceanic Fisheries Exploration, Ministry of Agriculture and Rural Affairs, Shanghai, China, [4]National Engineering Research Centre for Oceanic Fisheries, Shanghai Ocean University, Shanghai, China

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EDITED BY
Fabio Fiorentino,
National Research Council (CNR), Italy

REVIEWED BY
Bernardo Patti,
National Research Council (CNR), Italy
Johanna Lk Wren,
National Oceanic and Atmospheric Administration, United States

*CORRESPONDENCE
Jiangfeng Zhu
jfzhu@shou.edu.cn

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Introduction: A sustainable fishery relies on consistent and substantial recruitment. There is, however, considerably high mortality among fish larvae during their early development. One of the most important factors determining larval survival is foraging success. Bigeye tuna is among the most important commercial species in the Indian Ocean. Despite being routinely researched and assessed, it remains unclear how food availability affects the recruitment success of bigeye tuna.

Methods: In this study, we used phytoplankton size (M_{D50}) as an indicator of prey availability and investigated the connection between M_{D50} and bigeye tuna recruitment from 2000 to 2018 through the Beverton-Holt stock-recruitment function. The Indian Ocean was divided into four regions to accommodate spatial differences.

Results: As a result, larger M_{D50} could bring higher recruitment, particularly in the eastern and southern Indian Ocean. Based on the analysis, we inferred that for bigeye tuna, the eastern Indian Ocean is the primary spawning ground, and the peak spawning period falls in Season 2 (April-June).

Discussion: The conclusions provide valuable insights for understanding the recruitment characteristics of bigeye tuna in the Indian Ocean.

KEYWORDS
recruitment, larvae survival, phytoplankton, bigeye tuna, Indian Ocean

1 Introduction

The Indian Ocean ranks second after the Pacific Ocean in terms of tuna fishing, accounting for 22% of the global tuna catches in 2020 (ISSF, 2022). Bigeye tuna (*Thunnus obesus* Lowe, 1839), a vital commercial tuna species in the Indian Ocean, has witnessed a surge in commercial value over the past few decades (Zudaire et al., 2022). In 2020, bigeye tuna catches amounted to 84,388 tonnes (in live weight), representing about 7.5% of the total catches in the Indian Ocean (data from FAO FishStat database, accessible at https://www.fao.org/fishery/statistics-query/en/capture/capture_quantity, retrieved on February 2, 2023). Historically, the major portion of catches came from the longline fleets, but there was a dramatic drop due to piracy activities in 2004 (ISSF, 2022). In the last decade, purse seiners and longliners are the two major fisheries comprising 80% of the catches (Secretariat, 2022). According to the stock assessment of bigeye tuna conducted by the Indian Ocean Tuna Commission (IOTC), the stock was considered to be overfished and had been subject to overfishing (Fu, 2019).

Although bigeye tuna has been regularly assessed in the Indian Ocean, the precise timing and location of recruitment are still uncertain (Fu, 2019). Recruitment, being a critical process in population dynamics, plays a vital role in ensuring the sustainability of fisheries. Despite intensive fishing, fish populations may still persist or even be maintained at sustainable levels due to substantial compensatory and density-dependent mortality (Camp et al., 2020). A better understanding of the recruitment characteristics could enhance the efficiency of fishery management and provide useful information for stock assessment and projection.

The spawning of bigeye tuna exhibits both seasonal and year-round characteristics (Muhling et al., 2017). It occurs in tropical and sub-tropical waters when the surface water temperature exceeds 24°C (Nishikawa and Kenkyūjo, 1985; Schaefer, 2001). Eggs laid typically hatch into larvae (about 3 mm in length) in a few days, develop foraging and swimming organs quickly, and then grow into juveniles within the first month of life (Miyashita et al., 2001; Reglero et al., 2014). It is worth noting that the recruits experience exceedingly high mortality throughout the hatching and early life stages (Anderson, 1988; Russo et al., 2022; Shropshire et al., 2022). The biotic and abiotic conditions (e.g., temperature, zooplankton biomass, and eddies) in the water column, especially the surface layers, could strongly affect fish larval distribution and abundance, thereby impacting the reproduction of the species (Cuttitta et al., 2018; Russo et al., 2022). The feeding success of larvae is one of the most important processes in their survival (Anderson, 1988; Llopiz and Hobday, 2015). In particular, for species such as bigeye tuna, which primarily spawn in tropical regions, prey availability is more relevant than temperature to larvae (Reglero et al., 2014; Shropshire et al., 2022). To meet their metabolic requirements, tuna larvae hinge on the zooplankton availability after the yolk sack absorption (Llopiz and Hobday, 2015; Shropshire et al., 2022). They have a very narrow diet and are highly selective in their consumption of limited species of zooplankton inhabiting the shallow mixed layer (such as appendicularians, cladocerans, and cyclopoid copepods in the genera *Farranula* and *Corycaeus*) (Llopiz and Hobday, 2015; Artetxe-Arrate et al., 2021).

After transitioning from endogenous to exogenous nutrition, the larvae are most vulnerable to environmental factors, particularly food availability. High mortality rate often follows the strictly endogenous yolk feeding period as well as the first exogenous feeding phase. This period has been hypothesized as a "critical period" (Hjort, 1914) that determines recruitment success, but the hypothesis remains controversial (Sifa and Mathias, 1987; Robert et al., 2013). As a highly migratory species in the open seas, the recruitment of bigeye tuna is difficult to monitor by fishery-independent methods (Kolody et al., 2019). Thus, only a limited amount of research has been conducted to explore the influence of larval foraging success on the recruitment of bigeye tuna, with most information being related to tuna recruitment and reproduction confined to the Pacific Ocean (Langley et al., 2009; Zhu et al., 2010; Muhling et al., 2018; Woodworth-Jefcoats and Wren, 2020). Owing to this research gap, we developed a new method to explore the validity of the "critical period" hypothesis for bigeye tuna in the Indian Ocean. The median phytoplankton size (M_{D50}) was used as a proxy for the larval food quality (Barnes et al., 2011). A higher M_{D50} signifies larger phytoplankton and, in turn, more food available for the zooplankton upon which larval bigeye tuna feed. Since it is unclear whether the relationship between food availability and recruitment can be explained by linear or nonlinear regression due to the complexity of the real world, we examined the relationship between M_{D50} and the environment-related parameter, β, of the Beverton–Holt stock–recruitment function (B–H function) (Beverton and Holt, 1957). If there was a relationship between M_{D50} and the parameter β, the B–H function could describe the relationship between food availability and recruitment of bigeye tuna. Regional differences in the relationship were also considered based on the spatial stratification of the stock assessment model for bigeye tuna (Fu, 2019). The findings of this study could refine the estimation of bigeye tuna recruitment and elucidate the factors affecting its variation, thereby advancing stock assessment and management practices.

2 Materials and methods

2.1 Study region

Spatial structures, critical in stock assessments and fisheries management, take into account the differences in exploitation levels and fishery operations (Vincent and Hampton, 2018). The research area of this study spans the entire Indian Ocean and was divided into four regions based on the spatial structure used in the current bigeye tuna stock assessment (Figure 1): the south-western equatorial region (R1S), the north-western equatorial region (R1N), the eastern equatorial region (R2), and the southern region (R3) (Fu, 2019).

2.2 Beverton–Holt stock–recruitment function

The B–H stock–recruitment function describes the relationship between the recruit abundance and the spawning biomass of the stock (Miller and Brooks, 2021). The basic function is as follows:

$$\frac{R}{S} = \frac{1}{\alpha S + \beta} \tag{1}$$

where R represents the number of recruits, and S is the spawning stock biomass. The parameters α and β are related to two types of mortality: α is mainly linked to density-dependent mortality rates, whereas β pertains to the mortality caused by

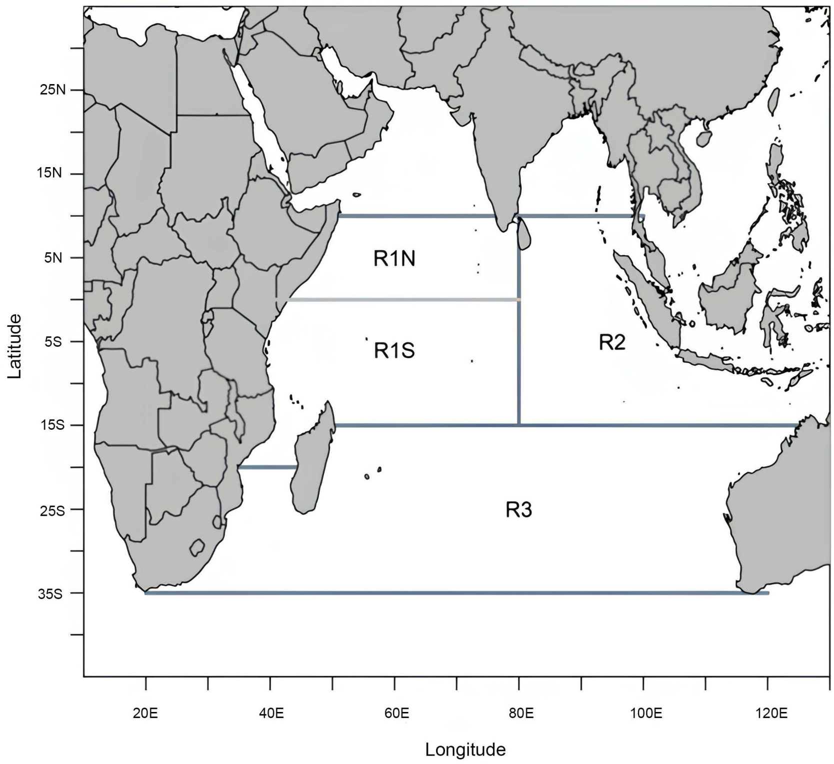

FIGURE 1
Study area of the stock assessment of the bigeye tuna in the Indian Ocean (Fu et al., 2019).

external (or density-independent) factors, such as temperature, wind, currents, and food availability (Beverton and Holt, 1957; Miller and Brooks, 2021). This study focuses on the relationship between M_{D50} and β; if there is any monotonic relationship between the two, the B–H function may be used to describe the relationship between M_{D50} and recruitment.

An alternative form of the B–H function was introduced by Mace et al. (1988) in terms of steepness Δ, equilibrium unexploited recruitment R_0 or spawning biomass S_0, and the unexploited spawning biomass per recruit S_0/R_0 (also defined as φ_0). Francis (1992) denoted the steepness as h, which is more frequently used nowadays. The parameters h, R_0, and S_0 were extracted from the bigeye tuna stock assessment, conducted by the Stock Synthesis model version 3.24z (SS3) (Fu, 2019). The B–H function was defined in the SS3 model as follows:

$$\frac{R_y}{S_y} = \frac{1}{\frac{5h-1}{4hR_0} \cdot S_y + \frac{(1-h)\ S_0}{4hR_0}} \tag{2}$$

where S_y and R_y are the spawning stock biomass and the recruitment in season y, respectively. Comparing Equation (2) to the basic function Equation (1), α can be calculated as (Equation 3):

$$\alpha = \frac{5h-1}{4hR_0} \tag{3}$$

Assuming that β is a vector of random effects, its seasonal values can be back-calculated according to the observed S_y and R_y time series (Equation 4).

$$\beta = \frac{S_y}{R_y} - \alpha S_y \tag{4}$$

The seasonal S_y and R_y data from 1975 to 2018 have been estimated in the stock assessment model (Fu, 2019). To be consistent with the stock assessment, the same seasonal setting was used in the present study: January–March (season 1), April–June (season 2), July–September (season 3), and October–December (season 4). The spatial structure of SS3 allows the calculation of β for each region and season from 1975 to 2018.

2.3 Environmental data

The M_{D50} (cell size) in equivalent spherical diameter in µm is derived from the cell mass (M_{B50}), which is calculated as follows (Equation 5):

$$\log_{10}(M_{B50}) = 0.929(\log_{10}(chla)) - 0.043(SST) + 1.340 \tag{5}$$

where *chla* denotes chlorophyll-a in mg/m^3, while *SST* is sea surface temperature in °C (Barnes et al., 2011). Then, M_{B50} can be converted to M_{D50} as follows (Equation 6):

$$M_{D50} = 2.138(M_{B50})^{0.355} \tag{6}$$

(Menden-Deuer and Lessard, 2000; Polovina and Woodworth, 2012).

Since there was limited continuous chlorophyll-a record before the year 2000, monthly chlorophyll-a data from 2000 to 2018 were obtained from NASA's Moderate-resolution Imaging Spectroradiometer (MODIS) Terra Chlorophyll Data (Terra/MODIS) with a 9-km spatial resolution (NASA Goddard Space Flight Center, 2018) (https://oceandata.sci.gsfc.nasa.gov/directdataaccess/). Therefore, the research period covered the years from 2000 to 2018. The monthly SST data with 1° resolution from 2000 to 2018 were sourced from NOAA Extended Reconstructed SST v5 (Huang et al., 2017) (https://psl.noaa.gov/data/gridded/data.noaa.ersst.v5.html). The chlorophyll-a and SST data were then computed seasonally and averaged over each region to calculate the M_{D50}, aligning with the spatial and temporal stratifications of β. The quarterly M_{D50} and β from 2000 to 2018 for four regions were then used to analyze the relationship between food availability and recruitment of bigeye tuna.

2.4 Statistical analysis

As the variables followed normal distributions, linear regression analysis was used to evaluate the relationship between M_{D50} and β. As previously stated, tuna larvae demonstrate a rapid growth in their early life history, becoming juveniles within the first month of life. To validate the significance of food availability at the egg-hatching stage, the time-lag effects were disregarded in this study since new recruitments were defined in the stock assessment model as occurring every season (Fu, 2019).

2.5 Z score transformation

Given that the metrics of the data sets are distinct, Z-score standardization was applied to normalize individual distributions. The Z-score formula is (Equation 7):

$$Z = \frac{X - \overline{X}}{s} \tag{7}$$

where X is the original data value, $\overline{X}$ and s are the mean and the standard deviation, respectively. A converted Z will result in a distribution with a mean of 0 and a variance of 1.

3 Results

The distributions of β and M_{D50} for each region can be visualized in Figure 2. Given that β represents density-independent mortality in the B–H function, the negative monotonic relationship observed between β and M_{D50} implies that lower food availability would lead to higher mortality and, consequently, diminished recruitment levels. According to Figure 2, the majority of M_{D50} is negatively related to β as hypothesized, although there are some outliers. The outliers with lower M_{D50} values but still lower β mean that there is less food availability but higher recruitment compared to other points. When plotting β against M_{D50} by season, it appears that most outliers arise from the same season. In the regions R1N, R2, and R3, outliers predominantly occurred in season 2 (April–June). In the region R1S, outliers were primarily attributed to season 3 (July–September). We referred to these seasons as anomalous seasons, which make it more difficult to find mean patterns. Therefore, for each area, two comparisons were carried out between β and M_{D50} time series: one using the original datasets and the other with the anomalous seasons associated with the outliers removed and only containing the normal season. In all regions, the time series of β and M_{D50} have significant opposite trends, especially when the anomalous seasons were excluded (Figure 3).

Model 1 was developed using data from all seasons, while model 2 utilized the data excluding anomalous seasons. The results of linear regression are presented in Table 1, and the Pearson correlation coefficients are shown in Table 2. According to model 1, M_{D50} showed significant negative linear relationships with β in regions R1S (p = 0.003, r = -0.333), R2 (p < 0.001, r = -0.371), and R3 (p < 0.001, r = -0.546). However, no significant correlation was found in region R1N (p = 0.152, r = -0.166). Upon the removal of the anomalous season, model 2 exhibited enhanced correlations. β and M_{D50} had significant correlations (p < 0.001) in all regions, with correlation coefficients being -0.544 in R1N, -0.561 in R1S, -0.665 in R2, and -0.677 in R3, respectively. The residual diagnostics of the linear regression models were shown as Q–Q plots in Figure 4.

4 Discussion

The results highlight that food availability plays a crucial role in bigeye tuna recruitment, thereby supporting the hypothesis of the "critical period", which posits that the survival rate of newly hatched larvae is highly sensitive to feeding conditions during the first feeding stage (Hjort, 1914). A noteworthy negative relationship is observed between β and M_{D50} fit across all regions. It is generally believed that the eastern Indian Ocean (R2) serves as the principal spawning area, and the temperate region (R3) functions as the feeding grounds for bigeye tuna (Reglero et al., 2014; Muhling et al., 2017; Fu, 2019). Accordingly, the highest values of correlation coefficients were discovered in the R3 and closely followed by R2. It is worth mentioning that tuna larvae exhibit a marked preference for warmer waters (García et al., 2013; Alvarez et al., 2021), and R3 is located in the temperate Indian Ocean where the temperature is presumably cooler for bigeye tuna spawning or larval survival. The high correlation coefficient in R3 could be ascribed to the increased metabolic demands in lower-temperature environments. The results of this study indicate that, in addition to temperature reported by literature, food availability also strongly influences recruitment success. The "critical period" hypothesis was also borne out in the study of Woodworth-Jefcoats and Wren (2020). In their study, M_{D50} was identified as an environmental driver of bigeye tuna recruitment and can be an informative predictor of bigeye tuna catch rates in Hawaii's deep-set longline fishery with a 4-year forecast window, aligning with the results of our study. The importance of food availability on recruitment is also found in other

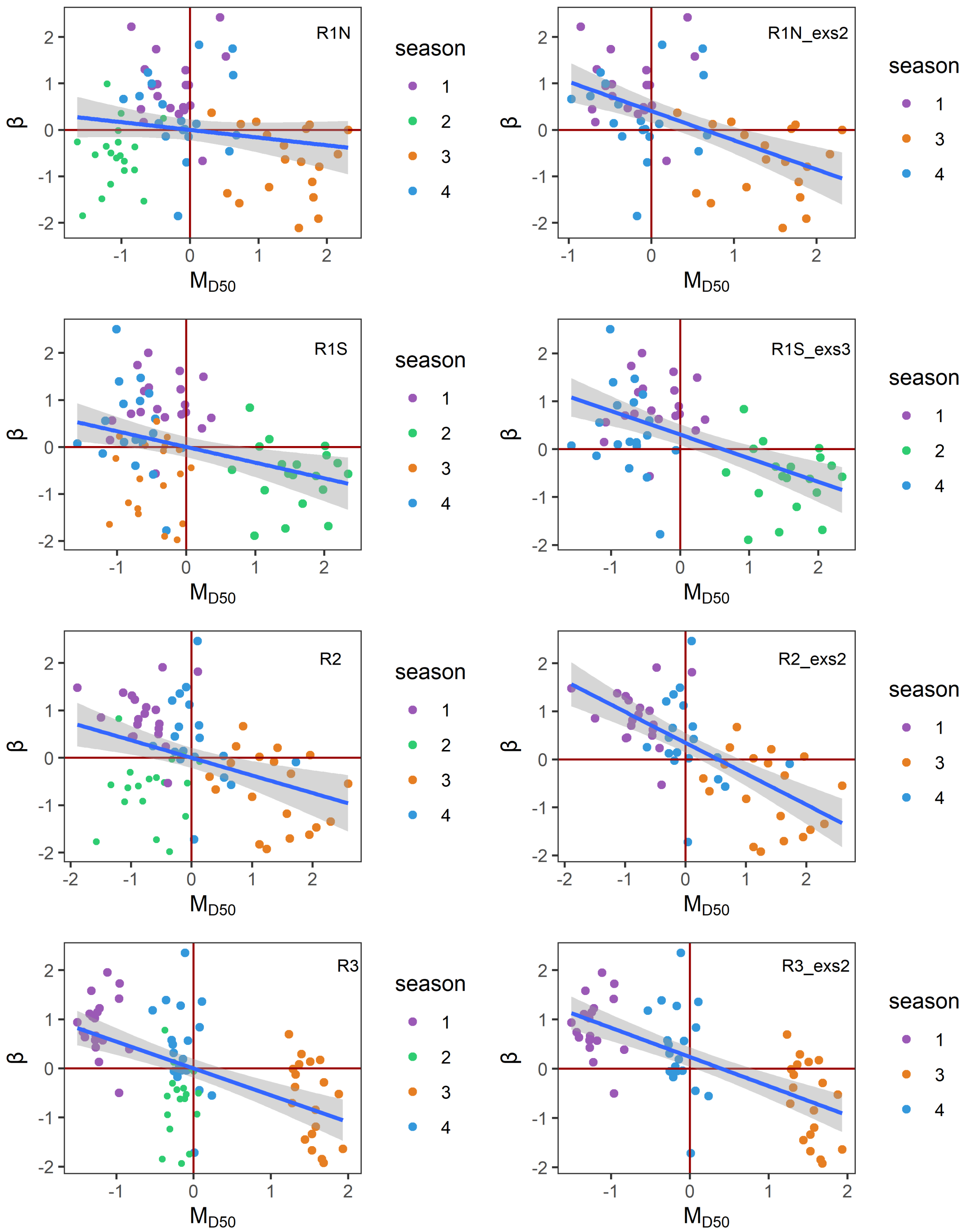

FIGURE 2
Scatter plots of Z-transformed M_{D50} and β with fitted linear regression lines in four regions. The figures on the left include all-season data, while the figures on the right exclude anomalous seasons. R1N_exs2, excluding season 2 data in R1N; R1S_exs3, excluding season 3 data in R1S; R2_exs2, excluding season 2 data in R2; R3_exs2, excluding season 2 data in R3.

marine fishes, e.g., *Pomacentrus amboinensis* (Jones, 1986), *Sardina pilchardus* (Guisande et al., 2001), and North Sea cod (Olsen et al., 2011). Regional differences should also be noticed in this study. Across the four regions, we observed different correlation coefficients between food availability and recruitment. This heterogeneity emphasized the importance of spatially structured stock assessment. Accurately accounting for population structure in stock assessments can improve model performance and reduce bias (Punt, 2019).

A strong seasonal pattern was evident in the results. The recruitment is lower during seasons 1 and 4 and corresponds to the lower M_{D50} in all regions. Recruitment is higher during seasons 2

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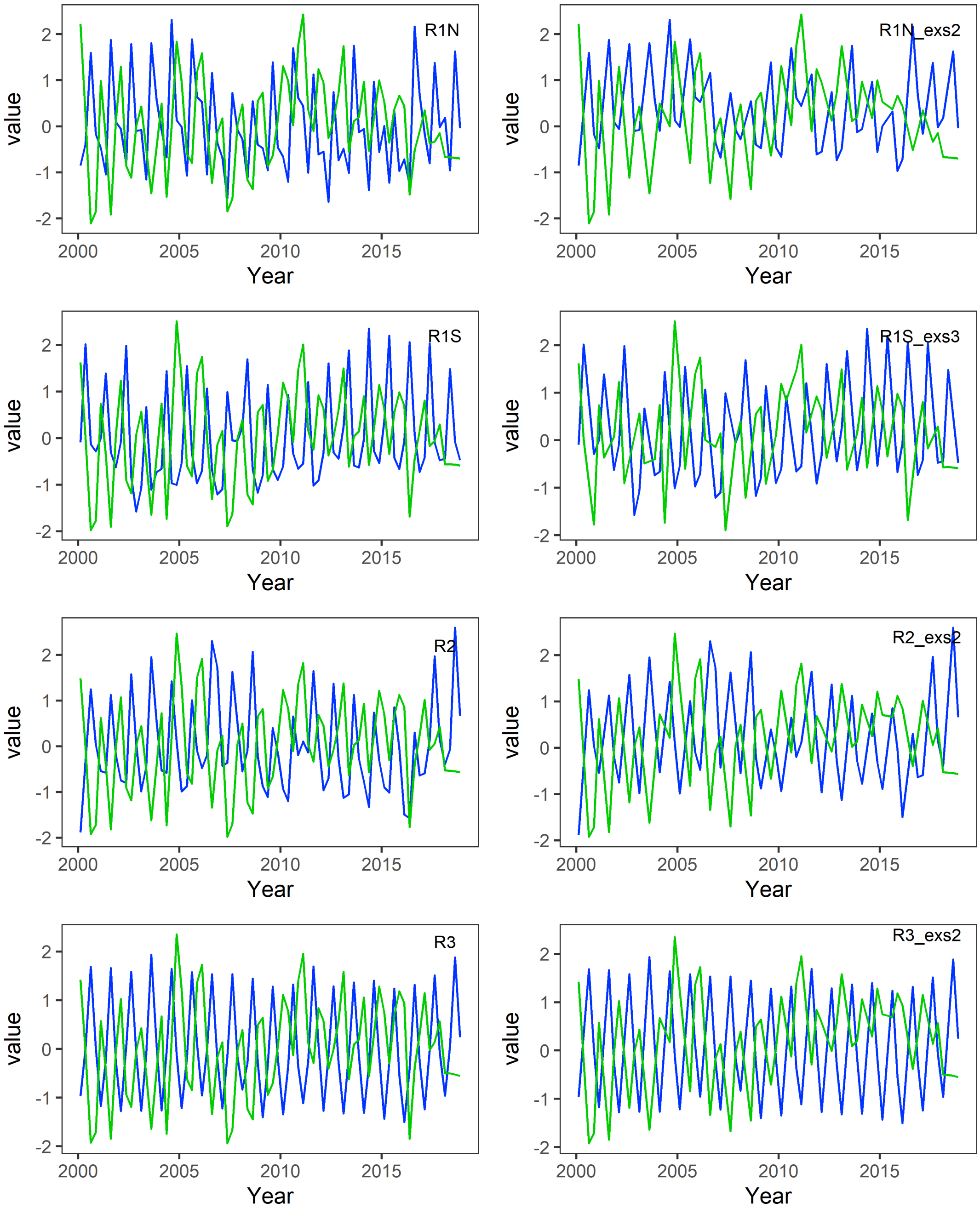

FIGURE 3
Time series of Z-transformed M_{D50} (blue) and β (green) from 2000 to 2018. The figures on the left include all-season data, while the figures on the right exclude anomalous seasons. R1N_exs2, excluding season 2 data in R1N; R1S_exs3, excluding season 3 data in R1S; R2_exs2, excluding season 2 data in R2; R3_exs2, excluding season 2 data in R3.

and 3. However, M_{D50} are relatively lower in season 2 in R1N, R2, and R3. Based on the previous hypothesis that more food could bring more recruitment, season 2 with opposite trends may be anticipated to be the spawning season. Despite the insufficient food supply, numerous eggs may also contribute to higher recruitment. Besides this, spawning seasons often coincide with optimal environmental conditions that support egg development and survival. Some researchers have shown that the lipid composition of egg improved due to the alteration of habitat that adults are exposed to during the spawning seasons (Navas et al., 1997; Yanes-Roca et al., 2009). A higher lipid composition of fish eggs enhances their survival and development by providing energy reserves, essential fatty acids for structural integrity, and resilience against environmental stressors (Singh et al., 2021). Consequently, high-quality eggs generally lead to higher hatching rates, improving the recruitment success (Kjørsvik et al., 2003; Ienaga et al., 2021). However, very limited studies verified

TABLE 1 Summary of regression analysis on β and M_{D50} in four regions.

	Model 1					Model 2				
	Regression equation	SE	DF	*p*	Adjusted-r^2	Regression equation	SE	DF	*p*	Adjusted-r^2
R1N	$\beta = -0.17M_{D50}$	0.11	74	0.152	0.014	$\beta = -0.63M_{D50} + 0.4$	0.13	55	< 0.001	0.28
R1S	$\beta = -0.33M_{D50} - 0.9$	0.11	74	0.003	0.1	$\beta = -0.49M_{D50} + 0.3$	0.1	55	< 0.001	0.31
R2	$\beta = -0.37M_{D50} + 0.16$	0.11	74	< 0.001	0.13	$\beta = -0.64M_{D50} + 0.35$	0.09	55	< 0.001	0.43
R3	$\beta = -0.55M_{D50} + 0.14$	0.09	74	< 0.001	0.29	$\beta = -0.59M_{D50} + 0.24$	0.08	55	< 0.001	0.45

SE, standard error; DF, degrees of freedom. Data in model 1 covered all-seasons data, and in model 2 the anomalous season was removed.

the egg quality of bigeye tuna in the Indian Ocean, more efforts still need to be conducted. It is also challenging to explain why the spawning season in R1S deviates from expectations. Furthermore, previous studies have demonstrated that bigeye tuna spawn in the western Indian Ocean between January and April and in the eastern Indian Ocean from December to January and in June (Nootmorn, 2004; Zudaire et al., 2022), which is not consistent with the findings of this study. Given that the model time step is arbitrarily divided, it may lack the flexibility to accurately reflect the complex spawning behavior in nature. In addition, if there are inaccuracies in the growth function estimation, the recruitment timing may also be biased.

There is also considerable uncertainty associated with recruitment estimates obtained from tuna stock assessment models. While growth, selectivity, and natural mortality are typically assumed to be constant over time in stock assessments, recruitment exhibits considerable temporal variations owing to the egg production and the subsequent larvae survival being highly sensitive to both biotic and abiotic factors (Maunder and Thorson, 2019). Most tuna stock assessments (including the Indian Ocean bigeye tuna stock assessment) recognize the concurrent existence of the process and observation errors. The Stock Synthesis model modeled recruitment deviations as log-normally distributed and estimated based on a stationary B–H relationship using a penalized likelihood approach. However, researchers have found that, compared to the penalized likelihood approach, the marginal likelihood approach possesses superior statistical properties (Maunder and Deriso, 2003; Valpine and Hilborn, 2005). Apart from that, estimating the parameters and variance of the stock–recruitment remains a complex task. In the Indian Ocean bigeye tuna stock assessment, the steepness is usually set at 0.7, 0.8, and 0.9, and the CV (σ_R) is fixed at 0.6. Several studies have pointed out that σ_R is frequently overestimated, and there are still controversies regarding the setting of σ_R in tuna stock assessments (ISSF, 2011; Kolody et al., 2019). Fishery-independent recruitment monitoring programs are desirable to increase the precision of population estimation and reduce management uncertainty and risk. However, due to the high cost and logistical challenges, they remain rare in tuna management (Kolody et al., 2019).

TABLE 2 Correlation coefficients between β and M_{D50} in four regions.

	Dataset 1 (*r*)	Dataset 2 (*r*)
R1N	-0.166	-0.544
R1S	-0.333	-0.561
R2	-0.371	-0.665
R3	-0.546	-0.677

Dataset 1 covered all-seasons data, and in dataset 2 the anomalous season was removed.

Environmental covariates have been integrated into recruitment estimation in various ways. Galindo-Cortes et al. (2010) explored the effect of environmental variables on the Pacific sardine (*Sardinops sagax*) stock–recruitment (S–R) relationship by incorporating these variables into the S–R function as the additive random errors. Crone et al. (2019) proposed including environmental information in the integrated stock assessments to inform the S–R dynamics. Both methods generated relatively high-quality estimates, either by including environmental covariates as an additional component of the S–R function or by fitting covariates in the model as a survey index of recruits outside the S–R function. These methods could potentially pave the way for incorporating chl-a data into the bigeye tuna S–R function.

More and more research continue to illustrate that the effects of climate change and environmental drivers on fisheries cannot be overlooked. There has been an increased interest in incorporating environmental factors in recruitment forecasting models (Haltuch et al., 2019), and a variety of models have been developed to explore the feasibility of the approach—for example, Langley et al. (2009) developed a generalized linear model (GLM) to predict the variation in yellowfin tuna (*Thunnus albacares*) recruitment across the western and central Pacific Ocean in relation to a multitude of environmental variables. They reported that integrating the recent GLM recruitment indices into stock assessment may enhance the precision of estimates of the current and projected (in the next 1 to 2 years) biomass and exploitation. Miller et al. (2016) proposed a state-space approach that treats environmental covariates (the mid-Atlantic cold pool) as stochastic processes and estimated the effects of the environment variables on southern New England yellowtail flounder (*Limanda ferruginea*) recruitment. Although the results suggest that the cold pool was an important predictor of recruitment, the projections were less than ideal due to the uncertainty associated with the projected cold pool. Haltuch et al. (2019) suggested that environmentally informed recruitment forecasting would be more successful for species whose population dynamics are dominated by recruitment and where recruitment is driven by strong environmental factors. Since the results of this study indicated a strong correlation between food

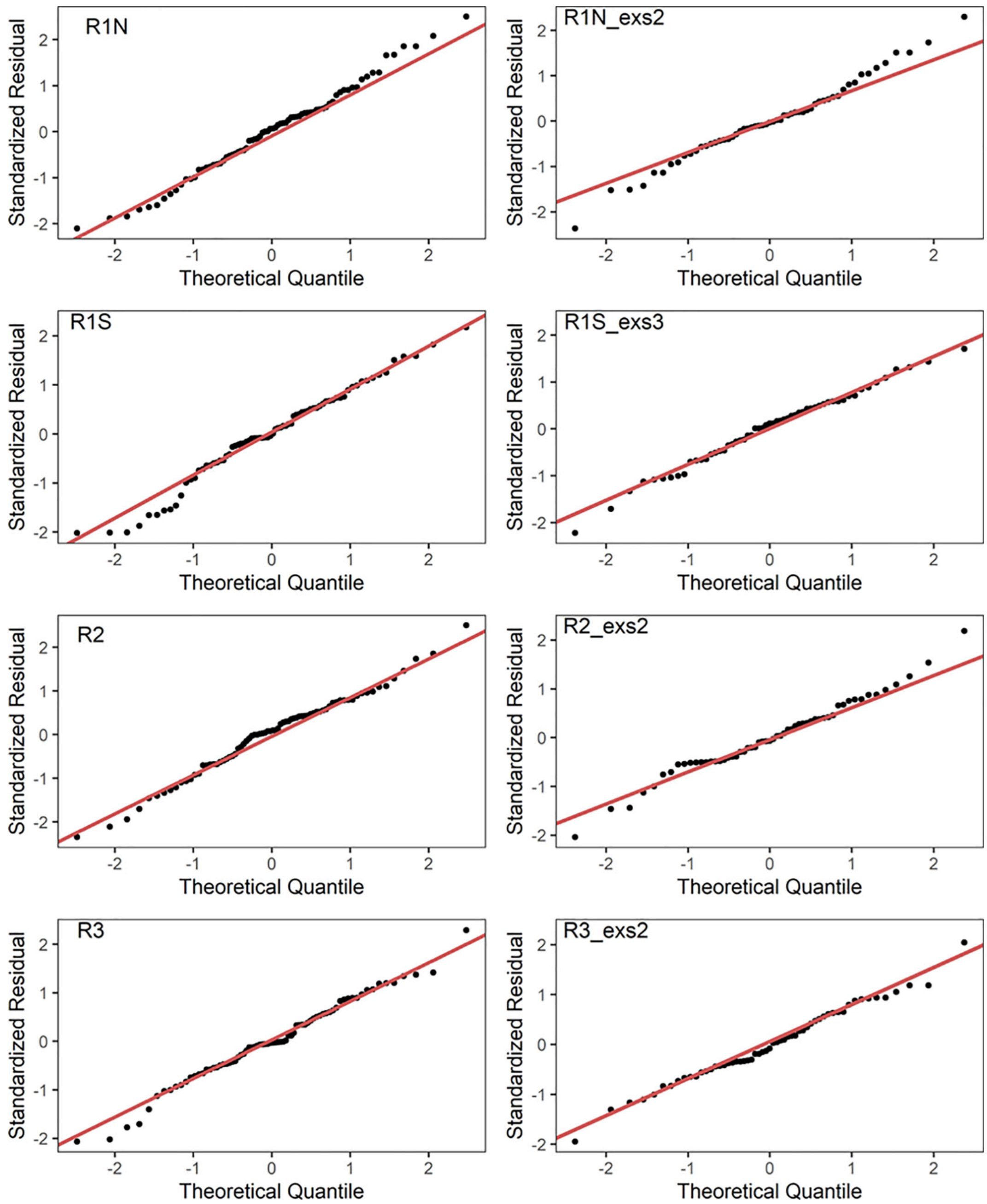

FIGURE 4
Residual diagnostics of linear regression models as Q–Q plots. R1N_exs2, excluding season 2 data in R1N; R1S_exs3, excluding season 3 data in R1S; R2_exs2, excluding season 2 data in R2; R3_exs2, excluding season 2 data in R3.

availability and bigeye tuna recruitment, future research could concentrate on forecasting recruitment by incorporating M_{D50} data and identifying more informative environmental predictors.

5 Conclusion

This paper attempts to investigate the relationship between food availability and the recruitment success of bigeye tuna in the Indian Ocean based on the available data of IOTC. The median phytoplankton size (M_{D50}) was used as a proxy for the larval food quality. We examined the connection between M_{D50} and the environment-related mortality parameter (β) of the Beverton–Holt stock–recruitment function and also considered the spatial differences in the Indian Ocean. We observed that the time series of β and M_{D50} exhibits significant opposite trends. M_{D50} was negatively related to β, suggesting that larger M_{D50} could bring lower mortality and therefore higher recruitment. This research strongly suggests the importance of incorporating environmental oceanographic variables, such as those related to pre-recruit feeding, into recruitment estimates in the stock assessment of bigeye tuna in the Indian Ocean.

Data availability statement

The datasets presented in this article are not readily available because the authors do not have permission to share the stock assessment data. Environmental data will be made available on request. Requests to access the datasets should be directed to YW, shouwyh@163.com.

Author contributions

YW: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. YZ: Conceptualization, Methodology, Supervision, Writing – review & editing. ZG: Data curation, Methodology, Writing – review & editing. JZ: Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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