

## Article

# Exploring the Response of the Japanese Sardine (*Sardinops melanostictus*) Stock-Recruitment Relationship to Environmental Changes under Different Structural Models

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**Abstract:** Japanese sardines (*Sardinops melanostictus*) are environmentally sensitive pelagic fish. We investigated the effects of environmental factors on the stock-recruitment (S-R) relationship of *S. melanostictus* in the Pacific Ocean from 1984 to 2018. We modeled and analyzed the recruitment of *S. melanostictus* using the Ricker model, the Ricker environment extension model (Ricker-E), and the generalized additive model (GAM). Different numbers of environmental factors were added to the models for fitting, and the Akaike information criterion (AIC) was used to select the optimal model. The results showed that the nonlinear GAM provided the best fit. The results of the GAM single factor and multifactor analysis showed that environmental factors were significantly correlated with recruitment in *S. melanostictus* ( $p < 0.05$ ). The best fitting model was the GAM, with an AIC of 57.9 and a cumulative explanation rate of 95.7%. Sea surface temperature was the most dominant environmental factor and had a negative impact on R/S. Considering both spawning stock biomass (S) and the environmental factors in the S-R relationship is important for studying the mechanisms of complementary changes and population changes in *S. melanostictus* under the influence of the marine environment.

**Keywords:** stock-recruitment relationship; environment factors; Ricker model; recruitment; *Sardinops melanostictus*



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## 1. Introduction

Fluctuations in fishery resources have been closely associated with changes in the global climate and marine environment [1]. Small pelagic fish are not only critical species in the ecosystem, but also essential economic fish, accounting for approximately 20–25% of the global catch annually [2–4]. Small pelagic fish are fast-growing and short-lived, with high natural mortality, which means that changes in their recruitment influence the size of the population. Therefore, the success rate of their recruitment is an essential factor in population dynamics and development [5,6]. However, recruitment is susceptible to changes in the complex marine environment of the waters in which they inhabit, and this responds very rapidly to changes in the climate, having a high degree of population variability. Therefore, it is necessary to investigate the effects of climate change and marine environmental changes on small pelagic fish populations.

The Japanese sardine (*Sardinops melanostictus*) is a representative species of small pelagic migratory fish that has a significant ecological and commercial value [7–9]. The species is primarily distributed in the Northwest Pacific region of China, Japan, and Korea, with spawning grounds on nearly all coastlines and adjacent water [10]. Information regarding *S. melanostictus* has previously been reported, including biological measurements [11], spawning [12], larval reproductive development [13], and environmental factors that affect

population dynamics [14]. Morimoto [15] studied the relationship between different inter-annual variables and the age, body length, and weight of *S. melanostictus*. He suggested that age and growth changes in *S. melanostictus* are among the factors affecting fluctuations of the population. The relationship between spawning stock and recruitment is crucial to investigate, since the environment in which fish live significantly impacts their spawning, development, and growth. Fishery stock assessment and management are based on the spawning stock-recruitment (S-R) relationship [16,17]. The population biomass of *S. melanostictus* has undergone dramatic fluctuations on a multidecade scale [3,18]. Wada and Jacobson [19] pointed out that the dynamics of recruitment under the influence of the environment and density are important factors in the fluctuation of the *S. melanostictus* population. Ganas [20] revealed the relationship between environmental factors (sea surface temperatures and chlorophyll-a) and the sardine spawning rate. Takasuka et al. [21] reported that sardines grow more slowly in warmer environments. The environmental changes experienced during spawning or migration are among the key reasons for reproductive failure. Therefore, environmental factors [22], such as the February Arctic Oscillation (AO) [23,24], the Pacific Decadal Oscillation (PDO), and the sea surface temperatures (SST), should also be considered in sardine population dynamics and complementary predictive modeling studies.

Many studies have investigated the effects of environmental factors on the S-R relationship of *S. melanostictus*. However, studies have focused more on the effects of a single environmental impact or a single model aspect [22,25,26]. In contrast, this study focuses on comparing multiple models with different structures under the influence of the environment, to find the best model for describing S-R relationships. To understand the recruitment of *S. melanostictus*, we assumed that biomass dynamics are the result of a combination of density-dependent and density-independent factors (changes in the marine environment). We developed the traditional Ricker model, Ricker environment extension model (Ricker-E), and generalized additive model (GAM), to explore the critical environmental factors of *S. melanostictus* biomass dynamics under different model structures. The effect of fishing is considered an important factor in the development of the population, especially in the case of low spawner levels, where fishing pressure can hinder the recovery and development of the population. Therefore, we should promptly adjust management strategies through resource assessment, to achieve the sustainable development of fishery resources. This is of great practical importance for future research on the dynamics of *S. melanostictus* populations, fisheries resource management, and conservation.

## 2. Materials and Methods

### 2.1. Data Source

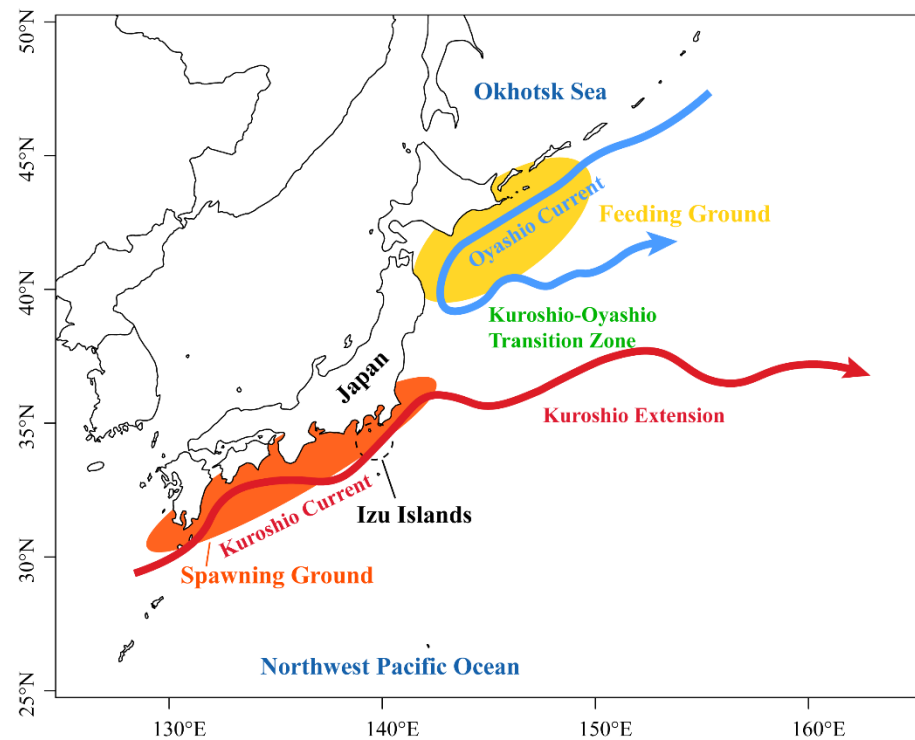
#### 2.1.1. Fishery Data

The area of this study was the Kuroshio-Oyashio system in Japanese waters of the Pacific Northwest. Our data were obtained from the Japan Fisheries Agency report of 2019, selecting biological data for *S. melanostictus* (stock spawning biomass  $10^2$  kt) and recruitment (in number/ $10^2$  million ind) from 1984 to 2018. Recruitment was taken as the number of fish aged 0 [27].

#### 2.1.2. Environmental Factors

The spawning area of *S. melanostictus* is located in the Kuroshio-Oyashio system (Figure 1), and the temperature in this area has a significant correlation with the density of sardines [28,29]. Changes in the marine environment in the Kuroshio-Oyashio area affect the reproductive success rate of sardines [30]. In this study, the sea surface temperature (SST; °C) was selected from the average autumn and winter temperature in the Kuroshio-Oyashio Transition Zone (KOTZ) ( $143.5^{\circ}$ – $155.5^{\circ}$  E,  $36.5^{\circ}$ – $39.5^{\circ}$  N) with a spatial coverage of  $1.0^{\circ} \times 1.0^{\circ}$  [31]. The average spring area of Oyashio Current (OYA,  $10^4$  km<sup>2</sup>) is the area where the water temperature is below 5 °C at a 100 m depth west of  $148^{\circ}$  E and south of  $43^{\circ}$  N. Our spring (March–May) OYA was obtained from the Japan Meteorological

Agency (JMA) [32]. The Southern Oscillation Index (SOI, May–April average), Pacific Decadal Oscillation data, and February Arctic Oscillation data were downloaded from the National Oceanic and Atmospheric Administration (NOAA) [33]. Large-scale environments including PDO, SOI, and AO have all been shown to directly or indirectly affect fish recruitment [34,35]. Watanabe et al. [36] showed that SST changes caused by interdecadal climate-ocean variability would affect the decline of sardine populations. The marine environmental time series were all from 1980 to 2018. To distinguish the descriptions in the text, Table 1 describes the abbreviations of fisheries and environmental data used in this study.



**Figure 1.** Spawning and feeding grounds of *Sardinops melanostictus* in the Kuroshio-Oyashio system.

**Table 1.** Data abbreviations used in this study.

Abbreviation	Meaning
ln(R/S)	Logarithm recruitment/spawning stock biomass
KOTZ	Kuroshio-Oyashio Transition Zone
SST	The average autumn and winter temperature in the KOTZ
PDO	Pacific Decadal Oscillation
OYA	Average spring area of the Oyashio Current
AO	Arctic Oscillation Index (February)
SOI	Southern Oscillation Index
S-R	Spawning stock-recruitment

## 2.2. Model Building Process

In order to determine the optimal fitting model for *S. melanostictus*, the influence of environmental factors on *S. melanostictus* spawning stock recruitment was investigated. We constructed and compared different S-R models: the traditional Ricker model, the Ricker environment extension model (GLM method modeling), and the GAM model. The predictors of the recruitment models included stock biomass individually and the combination of stock biomass and marine environmental factors (SST, PDO, OYA, AO, and SOI). The best model was determined by comparing the explanatory and predictive power

of the different structural candidate models (different numbers of environmental factors) against the traditional Ricker model. Through the analysis and comparison of different models, the model with the best fitting effect was selected to study recruitment. This study mainly used R (x64 version 4.1.1) and Origin for analysis.

In this study, a correlation test between environmental factors and recruitment was conducted using the Pearson correlation coefficient to screen the key environmental factors associated with recruitment. A Ricker type environmental extension model based on the traditional Ricker model was constructed using the *glm()* function and *mgcv* package. The variance inflation factor (VIF) was used to judge the collinearity numerically. Generally, a VIF <5 is considered to indicate no collinearity effect [37].

### 2.2.1. Ricker and Ricker-E Model

Both Beverton-Holt (B-H) [38] and Ricker [16] are models used to describe the S-R relationship [39,40]. However, the S-R relationship is not a simple density-dependent relationship, and researchers have gradually introduced environmental factors into the stock-recruitment model, to simultaneously consider the effects of density-dependent and environmental-dependent factors on the relationship of recruitment. The B-H and Ricker reproduction models were modified to explore the impact of the environment on the stock-recruitment relationship [41–43]. However, the latter is used more frequently, and Ricker is more appropriate for including environmental factors [44]; therefore, the Ricker model was chosen to describe the S-R relationship of *S. melanostictus* in this study.

$$R_{t+1} = \alpha S_t e^{-\beta S_t} \cdot e^{\varepsilon_t(0, \sigma^2)} \quad (1)$$

where  $R_{t+1}$  is the recruitment in the year  $t + 1$ ,  $S_t$  is the spawning stock in year  $t$ ,  $\alpha$  and  $\beta$  are parameters to be estimated, and  $\varepsilon$  is a normally distributed random error term,  $\varepsilon \sim N(0, \sigma^2)$ .

Usually, Ricker allows the model to be estimated using linear regression, and Equation (2) was used to estimate the parameters for the regression analysis:

$$\ln\left(\frac{R_{t+1}}{S_t}\right) = \ln \alpha - \beta S_t + \varepsilon_t \quad (2)$$

The mechanism of *S. melanostictus* fluctuations is complex, and the density-constrained mechanism is not the direct cause affecting population fluctuations [45]. Sakuramoto et al. [24] suggested that the fundamental cause of *S. melanostictus* fluctuations in the Northwest Pacific Ocean is related to environmental conditions. Therefore, to explore the influence of environmental factors on *S. melanostictus*, we established an S-R model of environmental influence based on the Ricker model. The Ricker model equation incorporating environmental covariates is as follows:

$$\ln\left(\frac{R_{t+1}}{S_t}\right) = \ln \alpha - \beta S_t + f(X) + \varepsilon_t \quad (3)$$

The function  $f(X)$  represents the effect of different marine environmental factors,  $f(X) = \gamma_1 X_{t,1} + \gamma_2 X_{t,2} + \dots + \gamma_n X_{t,n}$ , where  $X_{t,1}$ ,  $X_{t,2}$ , ...,  $X_{t,n}$  represent environmental variables that may impact S-R during the year. Additionally,  $\gamma_1$ ,  $\gamma_2$ , and ...  $\gamma_n$  denote the values of the corresponding environmental variable parameters.

### 2.2.2. GAM Model

The GAM is an extension of the GLM, which was used to study the environmental factors that affect the S-R of *S. melanostictus*. In general, GAM has more flexibility [46]. The GAM minimizes residuals (goodness of fit), while maximizing parsimony (lowest

possible degrees of freedom) to detect nonlinear relationships between variables [47]. The expressions is as follows:

$$g(u) = \alpha + \sum_{j=1}^p f_j(x_j) + \varepsilon_t \quad (4)$$

where  $g(u)$  is the desired response variable; (the Logarithm recruitment/spawning stock biomass in this study  $\ln(\frac{R}{S})$ ,  $f_j$  is each explanatory variable  $x_j$  ( $S_t$ ,  $SST$ ,  $PDO$ ,  $OYA$ ,  $AO$ ,  $SOI$ ) of the smoothing function), and  $\varepsilon_t$  is a residual that follows a normal distribution. The effects of the spawning stock and environmental variables on recruitment were fitted using a cubic spline  $bs = "cr"$ , and an  $s$  (smoothing spline) was used as a smoother to estimate the S-R relationship.

### 2.3. Selection Criteria and Validation of Models

The Akaike information criterion ( $AIC$ ) is essential in testing the significance of differences between models and is widely used to select optimal models [48]. Usually, the minimum value of the  $AIC$  represents a good fit for the model. The expressions is as follows:

$$AIC = 2k - 2 \ln(L) \quad (5)$$

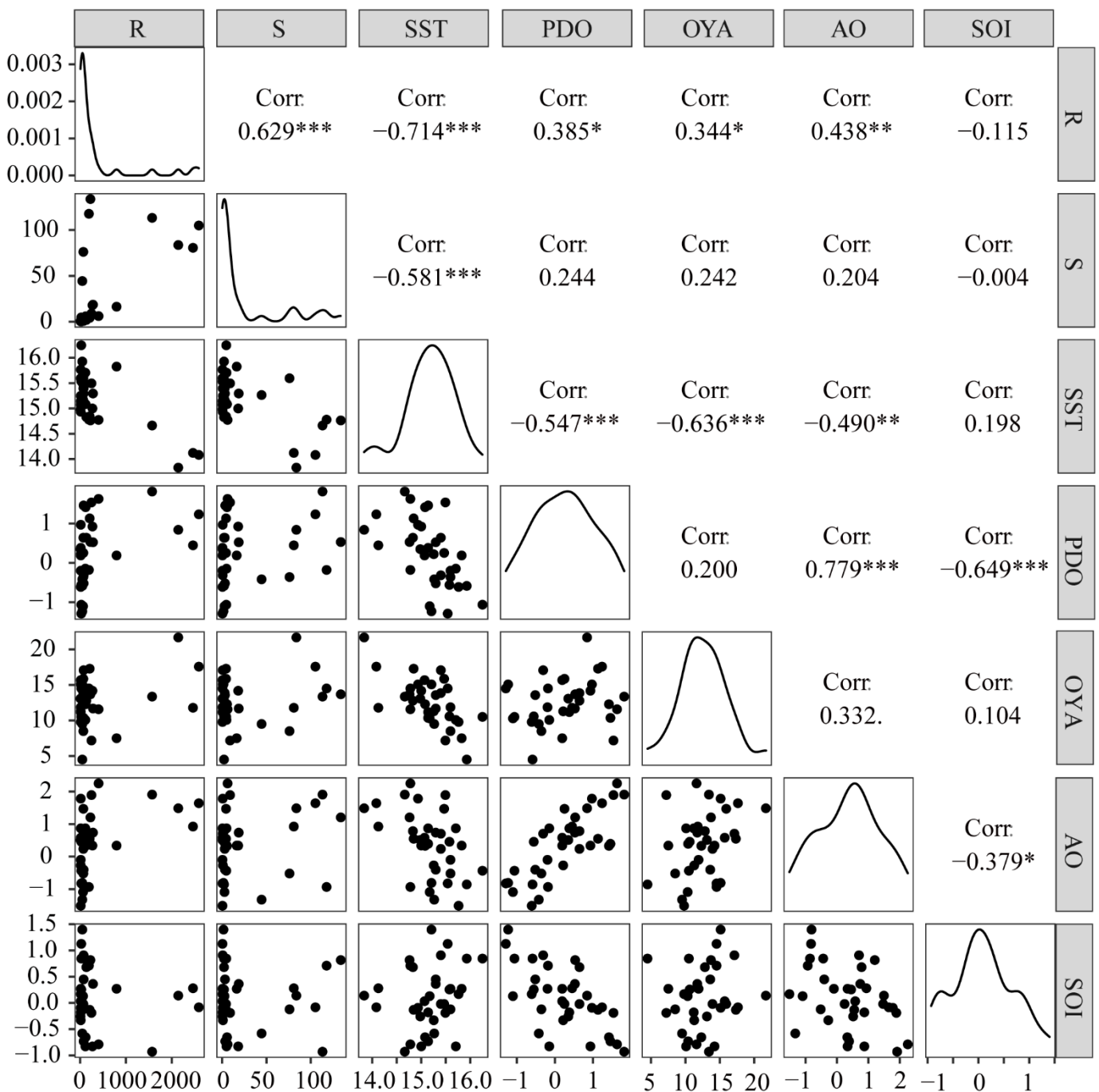
where  $k$  denotes the independent parameter format of the model and  $L$  denotes the great likelihood function of the model.

In this study, the  $AIC$  was the selection criterion for the best model. In the Ricker-E, the  $stepAIC()$  function of MASS was used to select the best model, considering various combinations of environmental factors. To improve the accuracy of the model, we used tenfold cross-validation. In the GAM, environmental factors were added to the model successively, until the  $AIC$  value was no longer decreased, and the optimal model was selected. Additionally, to ensure the accuracy of the selection results, the model was predicted for verification. Similarly, single and multivariate analyses were used separately in the GAM model building process. First, different numbers of environmental factors were added to the model successively, until the  $AIC$  value no longer decreased, and the optimal model was selected. Then, for the three S-R models with different structures,  $AIC$  was used as the judgment criterion to choose the optimal model. Lastly, we validated the model, to ensure the accuracy of the selection results.

## 3. Results

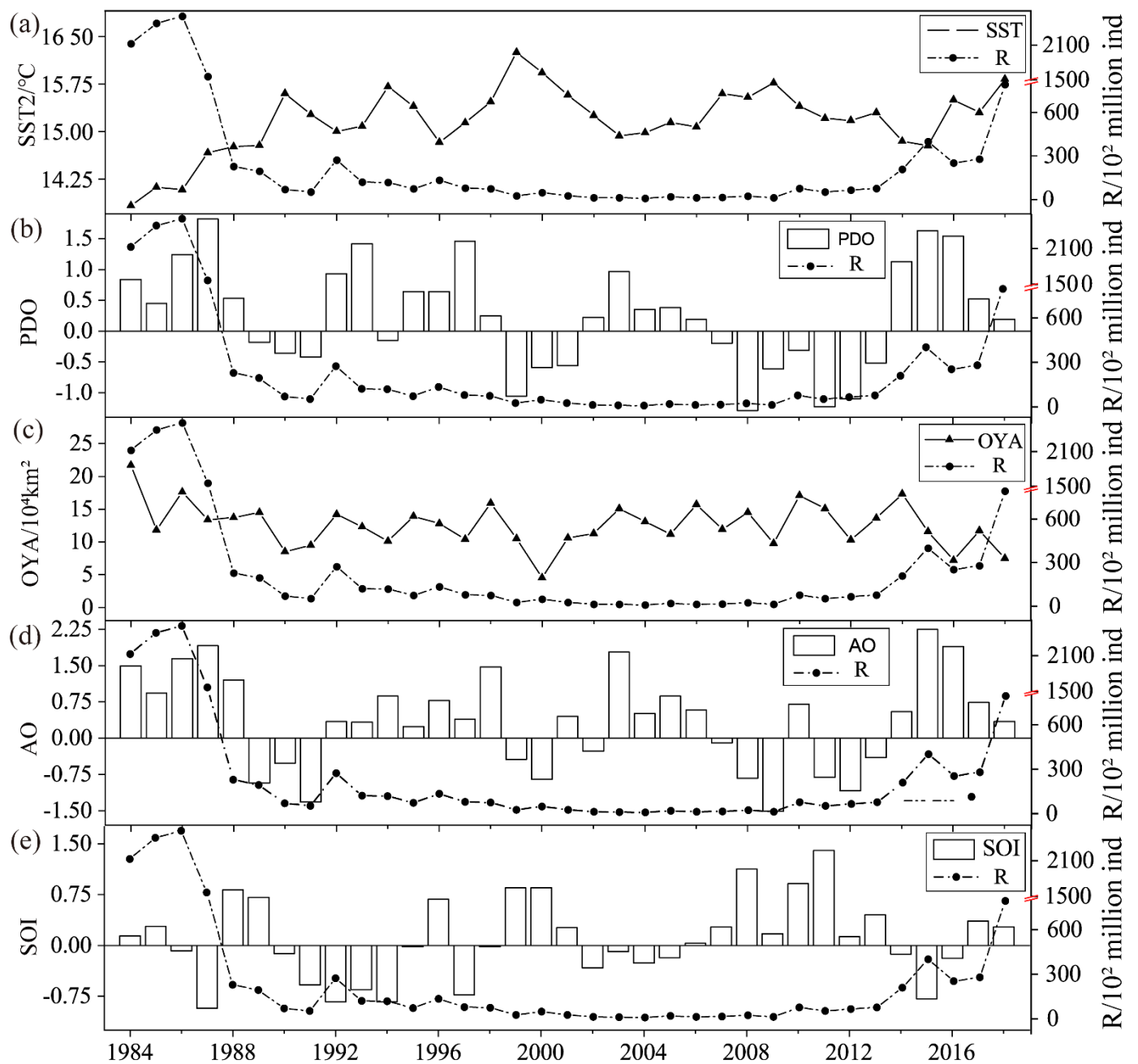
### 3.1. Screening of Environmental Factors

The results of the correlation analysis (Figure 2) showed that recruitment was significantly correlated with various environmental factors, except for  $SOI$ . At the same time, the effect of  $SST$  on recruitment showed a negative correlation ( $-0.714$ ), even higher than the correlation coefficient between spawning stock and recruitment ( $0.629$ ). On the other hand, the  $AO$  was positively correlated with recruitment, with a correlation coefficient of  $0.438$ . In addition, the  $SOI$  had the smallest relationship with the recruitment, which was negative, with a correlation coefficient of  $-0.115$ . Therefore,  $SSB$  and environmental factors should be considered when investigating the S–R relationship in *S. melanostictus* [24]. The results also indicated that there may be interactions among the environmental factors (some environmental factors had large correlation coefficients with each other, such as  $AO$  and  $PDO$ , with a correlation coefficient of  $0.779$ ).



**Figure 2.** The results of the correlation analysis between recruitment and environmental factors of *S. melanostictus* from 1984 to 2018. Signif. codes: ‘\*\*\*’ means  $p$  value  $\in [0, 0.001]$ , ‘\*\*’ means  $p$  value  $\in (0.001, 0.01]$ , ‘\*’ means  $p$  value  $\in (0.01, 0.05]$ , ‘.’ means  $p$  value  $\in (0.05, 0.1]$ , no cod means  $p$  value  $\in (0.1, 1)$ .

Figure 3 shows the overall decreasing trend in recruitment during the period of 1986–2013; after 2013, the recruitment increased under the general trend. However, the recruitment was on a downward trajectory, while the SST increased from 1986 to 1988. The SOI changed from a negative to a positive correlation from 1986 to 1988, and El Niño became La Niña during 2013–2018, with an overall fluctuating increase and a decrease in individual years.



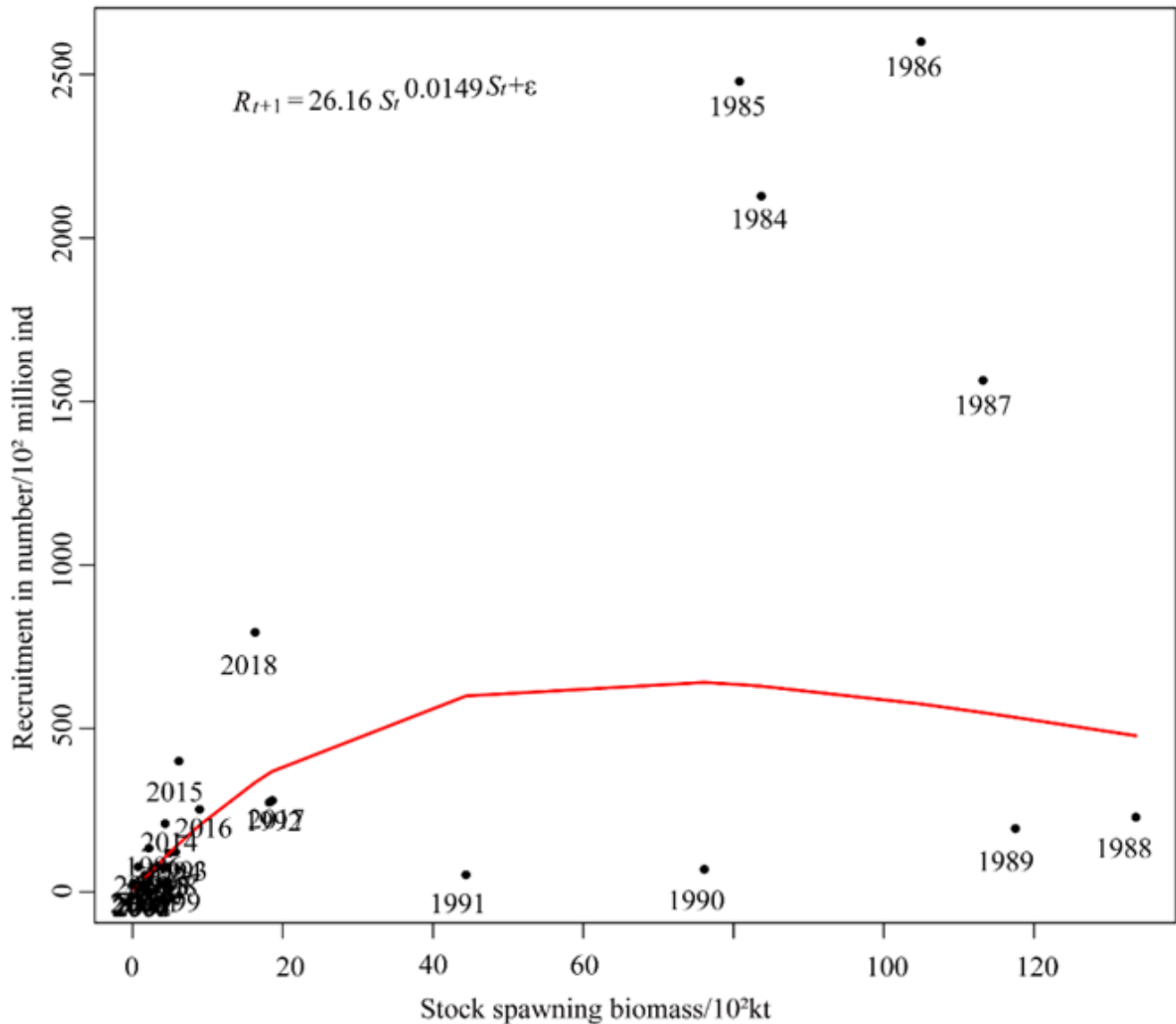
**Figure 3.** Time series plots of trends in environmental factors and recruitment during 1984–2018. (a) Trend of SST and R time series; (b) Trend of PDO and R time series; (c) Trend of OYA and R time series; (d) Trend of AO and R time series; (e) Trend of SOI and R time series.

### 3.2. Traditional Ricker Model

From 1984 to 2018, the Ricker curve of *S. melanostictus* showed the characteristics of the Ricker model dome (Figure 4). The S-R fit was satisfactory from 1992 to 2018, with observations distributed around the Ricker curve. However, before 1992, the fitted values had significant deviations, especially during the period from 1984 to 1991, in which the observed values were far from the Ricker curve, and the fit was poor. Therefore, we speculated that this might have been influenced by the marine environment. By fitting the traditional Ricker model, the AIC was 100.25, and the BIC was 104.91. The parameter

estimation results showed that the  $\alpha$  parameter was 26.16, and the  $\beta$  value was  $-0.0149$ . Therefore, the equation of the traditional Ricker model was as follows:

$$R_{t+1} = 26.16S_t e^{0.0149S_t + \varepsilon} \quad (6)$$



**Figure 4.** The relationship of *S. melanostictus* stock recruitment and the environment in 1984–2018.

### 3.3. Results of the Ricker Environment Extension Model

A stepwise regression analysis showed that the optimal Ricker-E model included three environmental variables (*SST*, *AO*, and *SOI*) that significantly affected the recruitment ( $p < 0.05$ ) (Table 2). Moreover, the results of collinearity showed that the VIF was less than 5 during the modeling process, so there was no collinearity. The *SST* had the smallest  $p$ -value (0.0079) among the environmental variables, indicating that *SST* had the most significant influence on the dependent variable. The model fit *AIC* was 84.60. The expression of the Ricker-E model with the addition of environmental factors was as follows:

$$\ln R_{t+1} - \ln S_t = 18.118 + 0.024S_t - 0.977SST + 0.4AO + 0.542SOI + \varepsilon \quad (7)$$

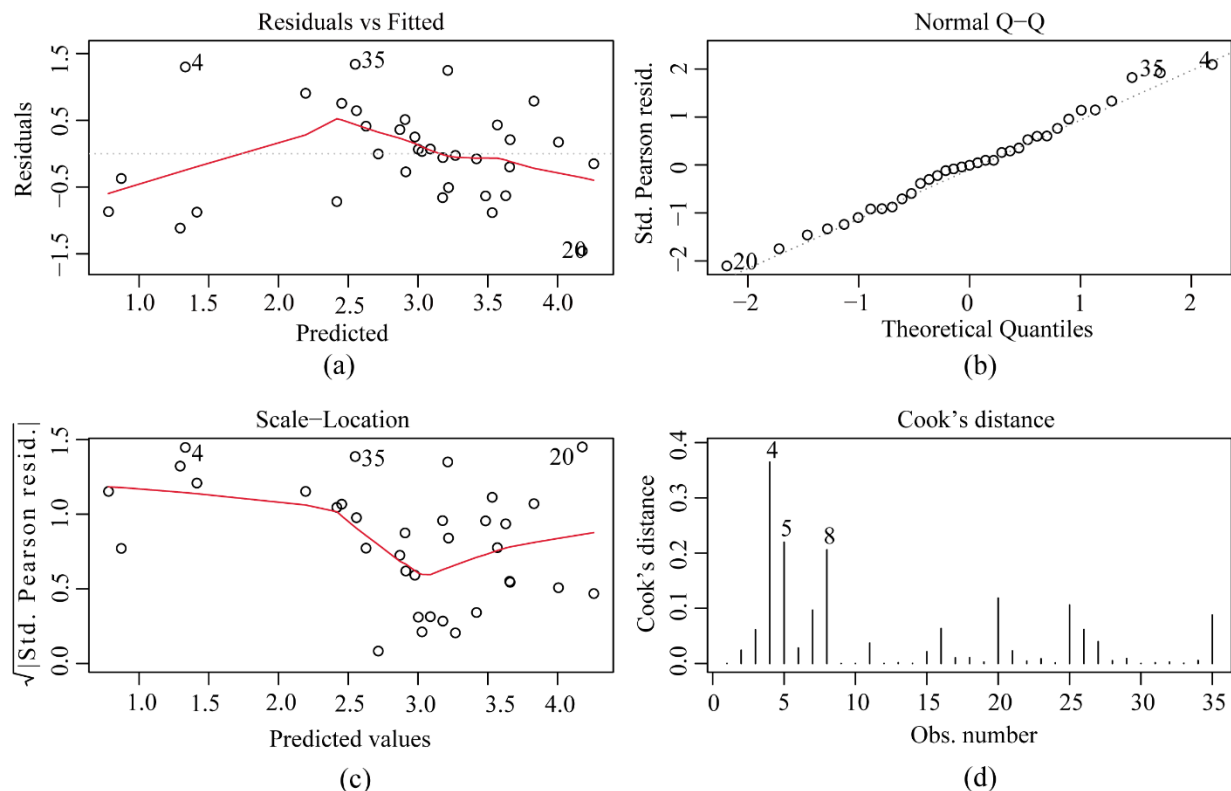


**Table 2.** Results of the best Ricker-E model with the addition of environmental factors in different numbers.

Formula	Variable	Estimate	Standard Error	t Value	Pr(> t )	VIF	AIC	BIC
$\ln(R/S) \sim S + SST$		22.087	5.149	4.290	0.0002	***	90.00	96.20
	S	−0.024	0.004	−5.640	0.0000	***		
	SST	−1.226	0.335	−3.660	0.0009	***		
$\ln(R/S) \sim S + SST + AO$	Intercept	17.293	5.645	3.060	0.0045	**	88.50	96.30
	S	−0.023	0.004	−5.600	0.0000	***		
	SST	−0.918	0.366	−2.510	0.0176	*		
	AO	0.283	0.157	1.800	0.0816	.		
$\ln(R/S) \sim S + SST + AO + SOI$	Intercept	18.118	5.287	3.430	0.0018	**	84.60	94.00
	S	−0.024	0.004	−6.206	0.0000	***		
	SST	−0.977	0.343	−2.847	0.0079	**		
	AO	0.400	0.155	2.575	0.0152	*		
	SOI	0.542	0.231	2.346	0.0258	*		

Note: Signif. codes: '\*\*\*' means  $p$  value  $\in [0, 0.001]$ , '\*\*' means  $p$  value  $\in (0.001, 0.01]$ , '\*' means  $p$  value  $\in (0.01, 0.05]$ , '.' means  $p$  value  $\in (0.05, 0.1]$ , no cod means  $p$  value  $\in (0.1, 1)$ .

The points in Figure 5a are randomly distributed; therefore, there is no heteroskedasticity. The points in Figure 5b are distributed on the 45° diagonal, indicating that the sample approximately obeyed a normal distribution. Meanwhile, the points in Figure 5c are randomly distributed, and the maximum Cook distance in Figure 5d is approximately 0.3. We typically used 0.5 and 1 as the criteria for outliers [49]; therefore, there were no outliers.



**Figure 5.** Ricker-E model validation and testing. (a) Residuals vs. Fitted; (b) Normal Q–Q; (c) Scale–location; (d) Cook’s distance.

We used tenfold cross-validation for model selection, using R-squared and RMSE as the judging criteria, and the results were the same as those of the models selected by stepwise regression. Table 2 shows the best Ricker-E models with the addition of different numbers of factors. A comparison of the best models in each group revealed that the model containing four factors had the largest R-squared (0.705) and the smallest RMSE

(0.749) (Table 3). Furthermore, when five environmental factors were added, the RMSE and RMSESD became larger, and the Required became smaller. This indicated that the Ricker-E model with four factors (*S*, *SST*, *AO*, and *SOI*) was the optimal model.

**Table 3.** Results of the tenfold cross-validation for the optimal Ricker-E model.

Nvmax	RMSE	Required	MAE	RMSESD	RsquaredSD	MAESD
1	0.931	0.686	0.747	0.334	0.338	0.277
2	0.789	0.610	0.653	0.365	0.323	0.292
3	0.935	0.653	0.781	0.299	0.282	0.264
4	0.749	0.705	0.617	0.264	0.297	0.235
5	0.806	0.641	0.668	0.331	0.295	0.286
6	0.820	0.656	0.687	0.299	0.285	0.263

Note: Nvmax represents the number of different factors added to the model.

### 3.4. Analysis Results of GAM

#### 3.4.1. Single Factor Analysis of the GAM

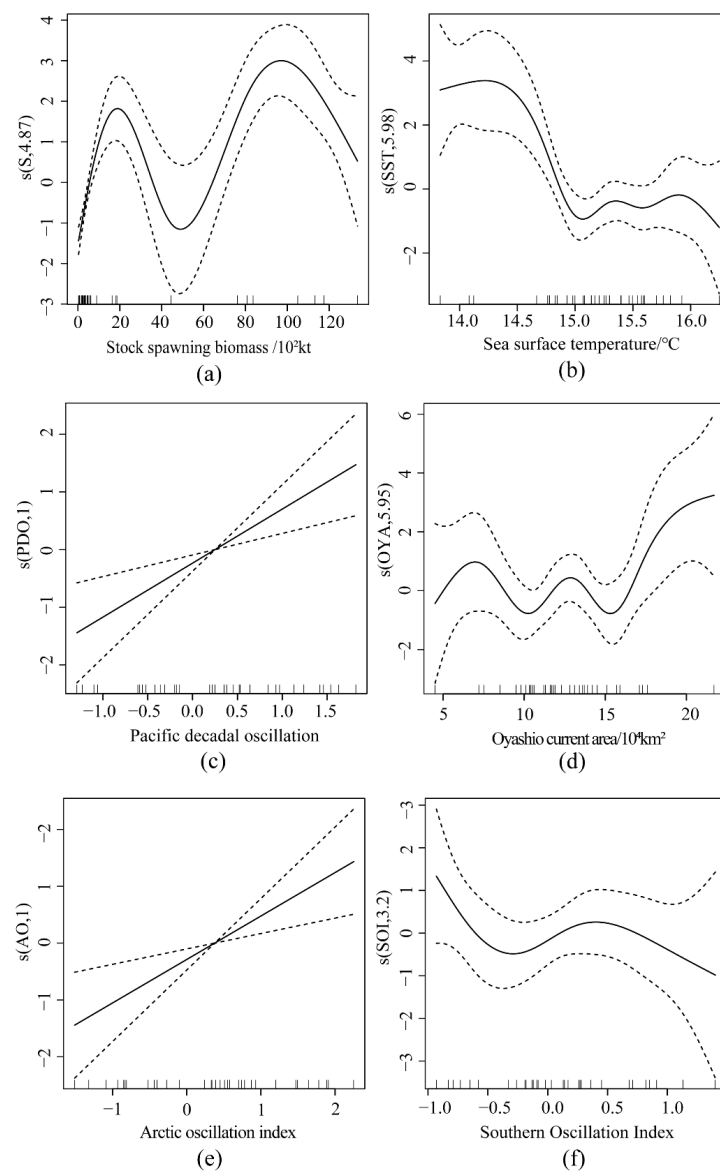
Table 4 shows that *S* had the largest explained deviation and *Rsq.(adj)*, followed by *SST* with 76.40% and 61.70%, and 0.724 and 0.503, respectively. The results of the single factor analysis of the GAM showed that each environmental factor was statistically significant and had a significant effect ( $p < 0.05$ ). In addition, the estimated degrees of freedom (edf) of *PDO* and *AO* were 1, indicating that *PDO* and *AO* had a linear relationship effect on  $\ln(R/S)$  in the single factor model. Another factor, edf, was greater than 1, indicating nonlinear effects.

**Table 4.** Results of the GAM single factor fit of *S. melanostictus*.

B.Smooth Terms	edf	Ref. df	F Value	p Value	GCV	Deviance Explained	Rsq.(adj)	AIC
s( <i>S</i> )	4.87	4.99	18.9	$<2 \times 10^{-16}$ ***	0.848	76.4%	0.724	94
s( <i>SST</i> )	5.98	6.67	6.32	$<2 \times 10^{-16}$ ***	1.484	61.7%	0.536	114
s( <i>PDO</i> )	1	1	11.16	$<2 \times 10^{-16}$ ***	2.094	25.20%	0.229	127
s( <i>OYA</i> )	5.95	6.62	2.16	$<2 \times 10^{-16}$ ***	2.487	35.8%	0.221	132
s( <i>AO</i> )	1	1	9.60	$<2 \times 10^{-16}$ ***	2.167	22.5%	0.202	128
s( <i>SOI</i> )	3.2	3.83	0.88	$<2 \times 10^{-16}$ ***	2.705	15.80%	0.070	136

Note: Signif. codes: '\*\*\*' means  $p$  value  $\in [0, 0.001]$ .

The trend in Figure 6a shows two peak values at  $20 \times 10^2$  kt and  $95 \times 10^2$  kt. Before  $20 \times 10^2$  kt and between  $48 \times 10^2$  kt and  $95 \times 10^2$  kt, the  $\ln(R/S)$  showed an increasing trend. Meanwhile, the periods of  $20 \times 10^2$  kt– $48 \times 10^2$  kt and  $95 \times 10^2$  kt– $130 \times 10^2$  kt showed a decreasing trend. Figure 6b shows that at  $14.0$  °C, the  $\ln(R/S)$  was the highest, whereas, between  $14$  °C and  $15$  °C, the  $\ln(R/S)$  rapidly decreased; between  $15$  °C and  $16$  °C *SST*, the  $\ln(R/S)$  fluctuated after experiencing a reduction. Furthermore, the  $\ln(R/S)$  decreased when temperatures surpassed  $16$  °C. Figure 6c,e show that the effects of *PDO* and *AO* on  $\ln(R/S)$  exhibited an increasing linear trend; with an increase in the *PDO* and *AO* indices, while  $\ln(R/S)$  also increased. Figure 6d shows the  $\ln(R/S)$  fluctuating variation of *OYA* between  $5 \times 10^4$  km<sup>2</sup> and  $15 \times 10^4$  km<sup>2</sup>. The *OYA* significantly increases in  $\ln(R/S)$  after  $15 \times 10^4$  km<sup>2</sup> –  $20 \times 10^4$  km<sup>2</sup>. Figure 6f shows a decreasing trend of  $\ln(R/S)$  at the *SOI* of  $-0.6$ , with a change at  $-0.5$ . At less than  $-0.5$ , the  $\ln(R/S)$  decreased with an increasing *SOI*; at an *SOI* greater than  $-0.5$ , there was a gradual positive correlation, with  $\ln(R/S)$  increasing with *SOI*.



**Figure 6.** GAM single factor fitting residual diagram (dashed parts are confidence intervals). (a) Residuals of stock spawning biomass; (b) Residuals of sea surface temperature; (c) Residuals of Pacific decadal oscillation; (d) Residuals of Oyashio Current; (e) Residuals of Arctic Oscillation Index; (f) Residuals of Southern Oscillation Index.

### 3.4.2. Multifactor Analysis

Table 5 indicates that the best model for a single environmental factor was GAM2. Compared to GAM1, the *AIC* decreased from 94.4 to 70.6, while the *R*-sq. (adj) increased from 0.72 to 0.88, indicating a significantly improved fit with the addition of the environmental factor. After adding the remaining environmental factors to GAM2, the best model was GAM3, with a decrease in the *AIC* to 67.2 and an increase in *R*-sq. (adj). We found that, after adding four factors to GAM4 and then adding the environmental factors *OYA* and *SOI*, the *AIC* increased to 58.20 and 60.00, respectively. The *R*-sq. (adj) values did not increase significantly. Therefore, we determined that the model with the addition of four factors (GAM4) was the best. The GAM expression was as follows.

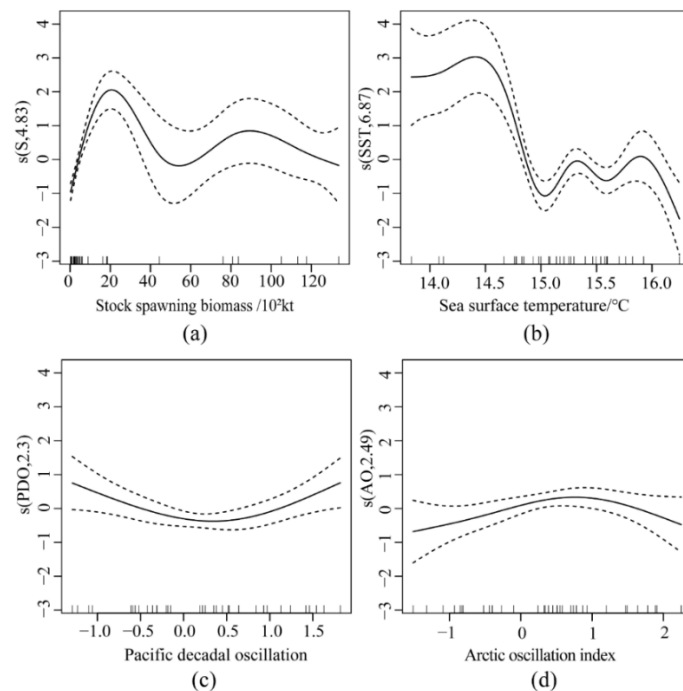
$$\ln(R/S) = s(S) + s(SST) + s(PDO) + s(AO). \quad (8)$$

**Table 5.** Comparison of the best models with different numbers of factors in the GAM.

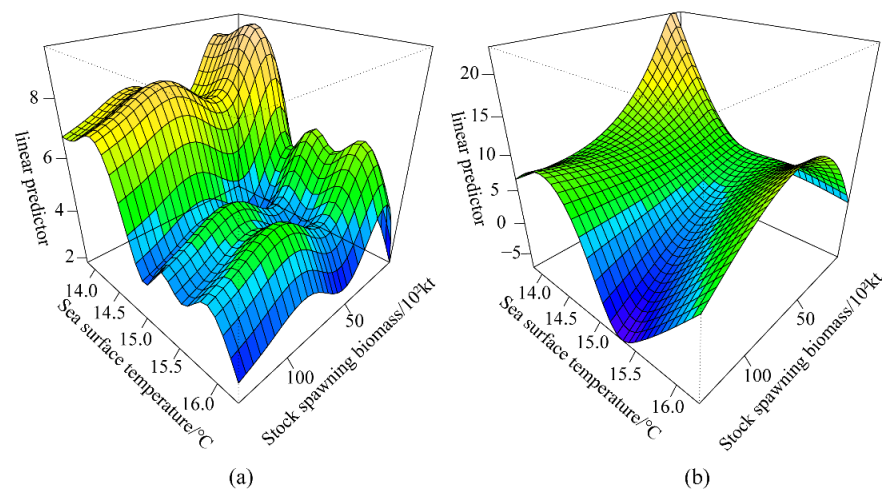
Model	Formula	edf	t Value	p	adjR <sup>2</sup>	Explained	AIC	BIC
GAM1	$\ln(R/S) \sim s(S)$	4.87	32.2	***	0.72	76.40%	94.4	105.0
GAM2	$\ln(R/S) \sim s(S) + s(SST)$	4.91 6.75	48.1	*** ***	0.88	91.90%	70.6	91.8
GAM3	$\ln(R/S) \sim s(S) + s(SST) + s(PDO)$	4.9 6.72 1.83	50.9	*** ***	0.89	93.40%	67.2	91.3
GAM4	$\ln(R/S) \sim s(S) + s(SST) + s(PDO) + s(AO)$	4.83 6.87 2.30 2.49	58.6	*** *** * .	0.91	95.70%	57.9	86.7

Note: Signif. codes: '\*\*\*' means  $p$  value  $\in [0, 0.001]$ , '\*\*' means  $p$  value  $\in (0.001, 0.01]$ , '\*' means  $p$  value  $\in (0.01, 0.05]$ , '.' means  $p$  value  $\in (0.05, 0.1]$ , no cod means  $p$  value  $\in (0.1, 1)$ .

Figure 7b indicates the highest values at 14.4 °C, corresponding to the highest  $\ln(R/S)$ . The  $\ln(R/S)$  decreased significantly between 14.4 °C and 15 °C. It fluctuated between 15 °C and 16 °C, with two relatively small peaks at 15.3 °C and 15.9 °C. Figure 7c,d show that  $PDO$  and  $AO$  had opposite effects on  $\ln(R/S)$ . With a negative  $PDO$  index,  $\ln(R/S)$  decreased, whereas, with a positive  $PDO$  index,  $\ln(R/S)$  increases;  $AO$  was precisely the opposite of  $PDO$ . The visual analysis of Figure 7 revealed a possible interaction between the environmental factor  $SST$  and spawning (Figure 8a). Figure 8b shows a significant interaction between  $SST$  and spawning ( $p < 0.001$ ), with either a too high or too low  $SST$  interacting with spawning, thus affecting the recruitment.



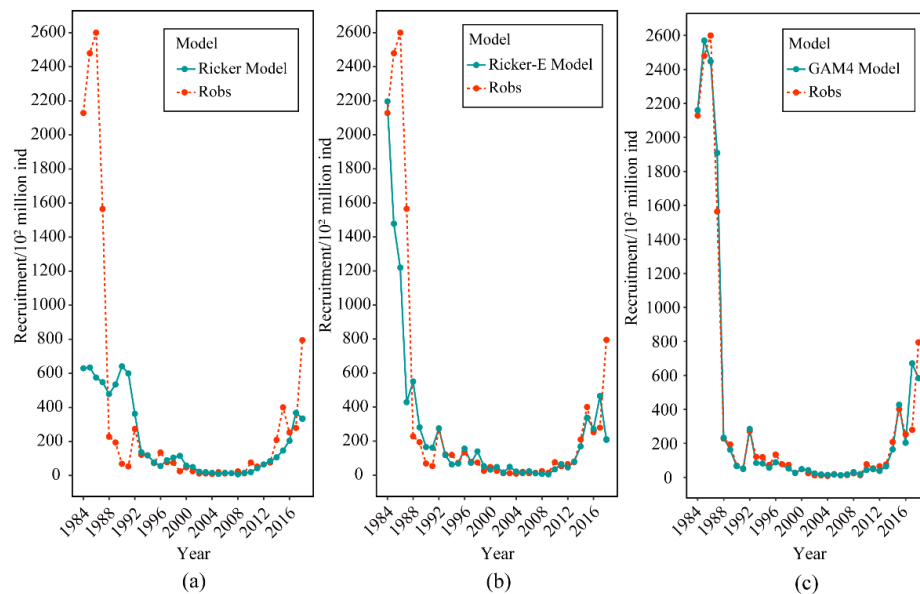
**Figure 7.** GAM multifactor fitting residual diagram (dashed parts are confidence intervals). (a) Residuals of stock spawning biomass; (b) Residuals of sea surface temperature; (c) Residuals of Pacific decadal oscillation; (d) Residuals of Arctic Oscillation Index.



**Figure 8.** Interaction effects of the optimal GAM. (a) Possible interaction between environmental factors SST and spawning (b) Significant interaction between SST and spawning.

3.5. Fitting Verification of the Optimal Model

According to GAM single factor and multivariate analysis, GAM4 was the best model. A fitting test of the model was carried out to confirm the accuracy of the results. Figure 9 indicates the fit of the predicted values of the three models to the observed values, as well as the degree of fit of the three models to the recruitment varies. All three models were fitted well by the predictor variables after 1992. However, for the prediction of recruitment during 1984–1992, the fitted line of the traditional Ricker model (Figure 9a) was compared with the fitted line of the Ricker model, with the addition of environmental factors (Figure 9b). We found that the latter was less variable. As a result, the difference between the predicted and observed values was smaller, and the fitting effect was better. However, the fit of the GAM to recruitment (Figure 9c) showed a significantly better model fit with less variation than the previous two. This may be because environmental factors strongly influenced it before 1992, and the GAM had a better fit and better explained the effects of the environment on recruitment.



**Figure 9.** Comparing the optimal model predicted value to the observed value fit. The Robs represents the observed value of the recruitment (red line), and the (a) Ricker model, (b) Ricker-E model, and (c) GAM4 represent the predicted value of each optimal model (green line), respectively.

## 4. Discussion

### 4.1. S-R Model

The Ricker model is widely used to describe S-R relationships in stock assessment, but it is more inclined toward the influence of biological factors such as SSB on recruitment [50]. However, the influence of abiotic factors in the ecosystem, including the environment, food, and other factors on recruitment, cannot be ignored [51,52]. The GLM and GAM are widely used for studying environmental impacts on fisheries [53–55]. Langley et al. [56] developed a GLM to study changes in the recruitment of yellowfin tuna (*Thunnus albacares*) under changing marine environmental factors. In our study, a linear model (Ricker-E) and nonlinear model (GAM) were used to study the S-R relationship between the environment and *S. melanostictus*. The Ricker-E model fit better than the traditional Ricker model, which indicates that a model incorporating environmental variables better describes the S-R relationship [57]. The GAM had the smallest AIC (57.9), proving that the nonlinear model was better than the linear model. Deyle et al. [58] found that nonlinear (state-dependent) models produced better predictions than linear models, after studying environmental effects on sardine ichthyoplankton. Cardinale and Arrhenius [59] noted that the GAM was better than the Ricker-E model in describing the number of environmental strengths in the recruitment of cod. Megrey et al. [60] concluded that the GAM, a nonparametric approach, is better than parametric methods in predicting parameter estimates in recruitment intensity. Shih et al. [61] found that GAM could fit the data better than the linear model in their study of environmental effects on recruitment for North Pacific Albacore tuna (*Thunnus alalunga*). The fitting results (Figure 9) indicate that the nonlinear GAM had a smaller prediction error relative to the Ricker-E model and was the best model to describe the environment of the S-R relationship of *S. melanostictus* [62].

In addition, the interaction between environmental SST and *S* was determined through visualization of the optimal model (Figure 8). The highest value of SST in Figure 8 was approximately 14 °C. Therefore, SST was the main environmental factor influencing the S-R relationship in this study.

### 4.2. The Effect of the Environment on Recruitment

Small pelagic fish are susceptible to environmental changes, and warm and cold changes in seawater alter stratification, habitat, and biological rates, thereby affecting population changes in marine fish. Large-scale climate indices such as AO, PDO, and SOI have been widely demonstrated to affect population fluctuations of small pelagic fish, including sardines [34,63–66]. Yastu et al. [34] reported that a wide range of environmental indices, such as PDO and AO, may be helpful in understanding and predicting the effects of the environment on the productivity and recruitment of sardines.

#### 4.2.1. Kuroshio Oyashio Regional

Jacobson and MacCall [67] showed that SST affects changes in the recruitment of Pacific sardines. As sardines spawn in winter or early spring near the Kuroshio in southern Japan, their juvenile and adult fish pass through the Kuroshio and Kuroshio extension, to feed in the Oyashio area [68,69]. Therefore, the SST in this study area is important for sardine recruitment. Takasuka [70] suggested that a cooler SST in winter spawning grounds improves the success rate of sardine recruitment. Water temperature and zooplankton abundance affect sardine survival during early growth stages (up to 1 year old) [71]. Typically, warm events are associated with low productivity, where the release of larval predators during warm periods outweighs the scarcity of food, thereby affecting the survival of eggs and larvae. Typically, the low productivity associated with warmth affects the survival rate of eggs and larvae [29,72]. Noto and Yasuda [73] indicated that winter–spring SST in the Kuroshio extension and its southern recirculation zone was positively correlated with the effect of natural mortality of *S. melanostictus* larvae from late stages to age 1. This study showed that SST was significantly correlated with *S. melanostictus* recruitment ( $p < 0.05$ ), and that SST was the dominant environmental influence. Furthermore, the

GAM results showed that  $\ln(R/S)$  increased with increasing temperature and achieved a maximum of 14.4 °C. However, after a rapid decrease after reaching 14.4 °C, the rate of decline slowed down and fluctuated. We speculate that this elevated temperature may promote the growth of fish cells until a critical point is reached, but exceeding the critical point affects the metabolic rate of sardines, leading to a decrease in growth [74]. Takasuka et al. [21] stated that the optimal growth temperature for sardine larvae is 16.2 °C, while the maximum  $\ln(R/S)$  achieved at 14.4 °C in this study may be the result of multifactorial climatic effects.

The dynamics of the OYA affect the migration and abundance of pelagic fish, through changes in primary productivity and mesopelagic biomass [75]. The results of the GAM single factor fit showed that the effect of the OYA on *S. melanostictus* recruitment was significant, with an explanation of variance of 35.8% (Table 4). This study found that the effect on recruitment was small and irregular when the OYA was small. However, with an area of  $15 \times 10^4$  km<sup>2</sup>, recruitment tended to increase with increasing OYA (Figure 5d). The positive correlation between OYA and *S. melanostictus* recruitment at this point may be due to the low water temperature, low salinity, and rich nutrient characteristics of the Oyashio, which ensure sardine feeding.

#### 4.2.2. Large-Scale Climatic Patterns

SST anomalies (cooling or warming) caused by alternating cold and warm PDO periods impact the temperature and location of fish spawning grounds. During positive PDO indices, cooler seas in the western North Pacific are favorable for sardine populations to flourish in Kuroshio systems [70]. Parrish [76] showed that the main positive PDO periods were associated with the accumulation of larger sardine biomass. However, the PDO was negative, and the SST gradually warmed, consistent with the rapid decline in sardine biomass [77]. Similarly, Figure 7c confirms this view. When the PDO index was  $-1.5$  to  $0$ , the  $\ln(R/S)$  showed a decreasing trend. In contrast, when the PDO index was positive, the  $\ln(R/S)$  started to show an increasing trend. This indicates that the positive and negative PDO indices affected *S. melanostictus* population changes, with a positive direction favoring recruitment growth, and a negative direction inhibiting recruitment growth. Sardines are suited to living in cooler environments and grow more slowly in warmer environments [21]. During the negative PDO period, the population decline was due to low reproductive success, resulting in a total mortality exceeding recruitment. Pitcher and Hart [78] indicated that the highest correlation was between sardine recruitment during the spawning season and the PDO index, which may be related to the cumulative effect of the before-spawning environment on adult sardines. Interestingly, Sakuramoto [66] showed that the partial regression coefficients associated with PDO were not statistically significant in the S-R prediction model of *S. melanostictus* populations in the Pacific.

Table 2 shows that the AO was significantly correlated with the Ricker-E model fit ( $p < 0.015$ ). In the GAM single factor fit, AO showed a positive linear correlation with  $\ln(R/S)$  (Figure 6e). Meanwhile, the multifactor fit showed a nonlinear relationship and the opposite trend to the PDO variation. Positive PDO abnormalities imply low levels of recruitment, while negative abnormalities are associated with high levels. The AO tends to be in a positive phase when the stratospheric vortex is strong in winter [79]. A positive AO affects snow melting, resulting in a large runoff into the ocean and causing sea surface salinity, density, and temperature changes [80]. Negative AO affected recruitment by changing the food supply of sardines through cold air temperatures [81]. Many reports have shown that the AO affects different regional populations. Báez et al. [63] found that AO influenced the relative abundance of sardines in West Africa. Castro-Gutiérrez et al. [82] concluded that the extreme values (positive and negative) in the AO seemed to have a negative impact on the landings of European sardines in the same year.

Positive and negative changes in the SOI can lead to climate anomaly events, such as El Niño and La Niña, which manifest as large-scale persistent seawater anomalies. Large-scale ocean fluctuations such as ENSO events have been identified as possible causes of sardine

population fluctuations in the Pacific Ocean [83,84]. The *SOI* had a significant effect on recruitment in the GAM single factor analysis ( $p < 0.05$ ), but was not included in the final model in the multifactor analysis. The reason for this may be that its effect could not be highlighted under the combined influence of multiple factors or was replaced by other relevant strong environmental factors. There was an inflection point in the GAM single factor analysis when the *SOI* was positive or negative, where recruitment decreased and increased during El Niño, with the opposite trend during La Niña. El Niño events cause a weakening of cold currents and a decrease in upwelling, a decrease in the nutrient level of seawater, and an increase in the likelihood of extreme weather typhoons and storms. All of these factors have adverse effects on fish populations. Sogawa et al. [85] reported that the bottom-up effects of Kuroshio and Kuroshio extension areas supported the high productivity of sardines. The decrease in sea surface winter temperature caused by La Niña provides a suitable living environment for sardines. Consequently, there is an increase in recruitment. However, successive La Niña events caused sea surface temperatures to continue to decrease, at which point the temperature was no longer suitable for sardine survival and growth. In contrast with our conclusion, Deyle et al. [58] identified the *SOI* as one of the three variables least important for sardine dynamics, with a strong negative impact on prediction.

The influence of the marine environment on the population dynamics of *S. melanostictus* is complex. Uncertainties in fishery stock assessment and management cannot be ignored [86]. Sun et al. [87] developed harvest control rules based on management objectives, to control the impact of uncertainty. Environmentally induced changes in recruitment are one source of uncertainty in fishery stock assessment and management. Therefore, it is necessary to incorporate uncertain factors such as the environment into the evaluation management framework [88,89]. Tanaka et al. [90] used a bioclimate envelope model to confirm that climate change drove changes in habitat suitability, which favored increased recruitment of lobsters. This suggests that incorporating environmental variables into stock assessments and fisheries management can provide a more accurate picture of stock status. Siple et al. [91] also demonstrated that the inclusion of uncertainties, such as the environment in the management framework for assessing pelagic fish, can improve the accuracy of assessments. We can then include other issues that may create uncertainty in the fishery (species distribution, predator models, etc.) into the integrated management target system. There may be a delay in the current year's environmental influences on recruitment, especially with regard to the large-scale climate. In this study, we did not consider lags in environmental impacts. Therefore, we will consider the delay of environmental factors in future studies, to ensure that more accurate prediction models are developed to explore the environmental effects on the S-R relationship of *S. melanostictus*.

## 5. Conclusions

This paper used estimates of stock/recruitment density for *S. melanostictus*, as well as matching environmental data collected from 1980 to 2018. We fitted the Ricker-E, GAM, and traditional Ricker models to fit models to these data. The results showed that the nonlinear GAM was the most suitable model to describe changes in the recruitment of *S. melanostictus* under environmental influences. *SST*, *PDO*, and *AO* are environmental factors that influence the level of recruitment. Among them, *SST* is the most important environmental factor, with a negative impact on the level of recruitment. This has important implications for studying the recruitment changes of *S. melanostictus* under the influence of the marine environment.

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