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The Factors Driving the Spatial Variation in the Selection of Spawning Grounds for *Sepiella japonica* in Offshore Zhejiang Province, China

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Abstract: Due to overfishing and marine pollution, the status of fishery resources and the ecological environment in the sea areas have considerably changed. The proliferation and release of fishery resources have become the main means of human intervention to maintain and conserve the resource populations. The annual output of *Sepiella japonica* (*S. japonica*), once one of the four major seafood species in the East China Sea, has now recovered to a level of 4000 t. However, do the traditional spawning grounds of *S. japonica* still exist? Have the spawning grounds shifted? These scientific questions are worthy of attention. Based on the survey data of fishery resources and environment at 120 stations in coastal Zhejiang waters from 2015 to 2022, the spatial and temporal distribution and resource center of gravity of *S. japonica* in springtime were analyzed. Random forest (RF) was used to explain the importance of six environmental variables, including water depth, sea surface temperature, sea surface salinity, chlorophyll a, pH, and dissolved oxygen. The generalized additive model (GAM) nonparametric smoothing function was used to analyze the relationship between environmental factors and the distribution of *S. japonica* inhabiting the offshore areas of Zhejiang province, and the effects of environmental factors on spawning habitat selection of *S. japonica* were revealed. This study found that there was a significant interannual variation in *S. japonica* resources, with an overall increasing trend in the resource. The spawning grounds were mainly distributed in the Jiushan Islands Marine Reserve, the Dachen Islands Marine Reserve, and their nearby sea areas. The resource peaked at latitude 28.3° N. Additionally, the most important variables affecting the distribution of *S. japonica* were depth of water, followed by sea surface salinity, pH, dissolved oxygen, sea surface temperature, and chlorophyll a. *S. japonica* mainly inhabited sea areas with a depth of 15~25 m and a sea surface salinity of 26~32. When the pH ranged from 7.6 to 8.3, dissolved oxygen ranged from 6 to 9 mg/L, sea surface temperature ranged from 14 to 17 °C, and chlorophyll a ranged from 2.5 to 5 μg/L, *S. japonica* was more likely to be present. This study provides insights into the spatial distribution of *S. japonica* in offshore Zhejiang province, offering a reference for the rational utilization and scientific protection of this resource.

Keywords: *Sepiella japonica*; spatiotemporal distribution characteristics; resource center; marine environment; random forest; generalized additive model

Key Contribution: This study analyzed the spatial and temporal distributions and center changes of *Sepiella japonica* and the effects of environmental factors on its distribution based on the 2015 to 2022 spring (April) fishery resources survey data in offshore Zhejiang province, China. The findings of this study offer significant insights for the protection and restoration of *Sepiella japonica* spawning grounds, resource conservation, and management.

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1. Introduction

Due to factors such as high-intensity fishing activities and poor fishery management, global catch species have gradually shifted from long-lived, high-trophic, bottom-feeding fish species to short-lived, low-trophic pelagic, invertebrate species [1]. Cephalopods are among the most promising fisheries species globally due to their short lifecycles, rapid growth, and adaptability to climate change, leading to a continuous increase in their production over the past 60 years. Future research on cephalopod and related industries is expected to remain a long-term topic of interest. Currently, China is one of the leading countries in cuttlefish fishing. In recent years, changes in marine habitats and fishery structures resulting from human activities and climate change have led to a decline in the cuttlefish species resources and changes in their spatial distribution, which have affected the structure and function of marine ecosystems [2–4].

Sepiella japonica (*S. japonica*) is the main economic species of cuttlefish in China, Japan, and South Korea. It is distributed along the coast of Russia in the northwestern Pacific Ocean, from the Kanto area of Honshu Island in Japan to South Korea, the East China Sea and the South China Sea, mainly in the offshore area of Zhejiang, the sea area in eastern Fujian and Guangdong in China, and the sea area west of Japan [5,6]. *S. japonica* is the most populous and productive cuttlefish along the coast of China, and it was once named one of the four major seafoods in the East China Sea, together with *Larimichthys crocea*, *Larimichthys polyactis*, and *Trichiurus japonicus* [7]. In 1959, the highest annual production of *S. japonica* in the East China Sea District exceeded 70,000 t. The main distribution areas were in the Zhejiang's offshore area, the seas of eastern Fujian, and the Zhejiang's offshore area, the latter of which had the largest production, accounting for about 80% of the total production of this species of cuttlefish in the offshore areas of China [5,6,8]. From the mid-1970s to the early 1980s, with the diversification of operating tools and methods (cuttlefish cages, trawls, paired nets, custom-made tension nets, etc., with motor-sailed fishing vessel trawling gradually becoming the main operation method for catching cuttlefish), the number of fishing vessels increased sharply, and the fishing effort continuously increased, with a total fishing effort that was more than double that of the 1960s. In 1993, the development of single-trawler operation in Zhejiang province caused significant changes in the resource status of cuttlefish. These changes affected not only the quantity and spatial distribution of resources but also the replacement of catch species. Among them, the dominant species of cuttlefishes have undergone wide changes compared with those before the 1990s. *Sepia esculenta* and *Sepia kobiensis* have replaced *S. japonica* as the most abundant species, while it has been difficult for *S. japonica* to form a fishing season [5,9].

All organisms living in specific marine environmental conditions are closely tied to their living environment, and the importance of different environmental factors on biological effects significantly differ. Changes in fish resources and the distribution of fishing grounds are often related to multiple factors, such as time, space, and the marine environment [10]. *S. japonica* is an offshore migratory species, with parents that reproduce in groups near the coast from April to May. The reproductive period is a crucial stage in the life cycle of *S. japonica*; recruitment is primarily determined by the number of fertilized eggs and the survival rate of offspring [11]. *S. japonica* makes some choices regarding the spawning grounds; therefore, this resource is susceptible to the influence of the natural environment and human factors [5]. This study analyzed the spatiotemporal distribution characteristics and resource centers of *S. japonica* during the reproductive period using resource survey data from the Zhejiang's offshore area between 2015 and 2022. This study investigated the effect of environmental elements on their distribution using random forest (RF) and a generalized additive model (GAM), combined with environmental data. This study aims to establish a scientific foundation for the conservation and management of *S. japonica* resources, serving as a reference for the sustainable use of offshore cephalopod resources.

2. Materials and Methods

2.1. Data Source

The data were collected during the spring (April) of 2015–2022 from the bottom-trawl survey of fishery resources in the Zhejiang's offshore area (surveyed sea aea was 27°00′ N–31°00′ N, 120°50′ E–123°75′ E). Along the protected coastline and *S. japonica* spawning grounds (Notice of the Zhejiang Provincial Oceanic and Fishery Administration on the Establishment of the Spawning Ground Protection Areas of the Major Economic Fishes in Zhejiang Offshore, Zhehai Yuzheng (2017] No. 16, https://www.zj.gov.cn, accessed on 1 December 2023), a site was set up every 0.5°, for a total of 120 sites, and the site survey method was used for sampling in the different years (Figure 1).

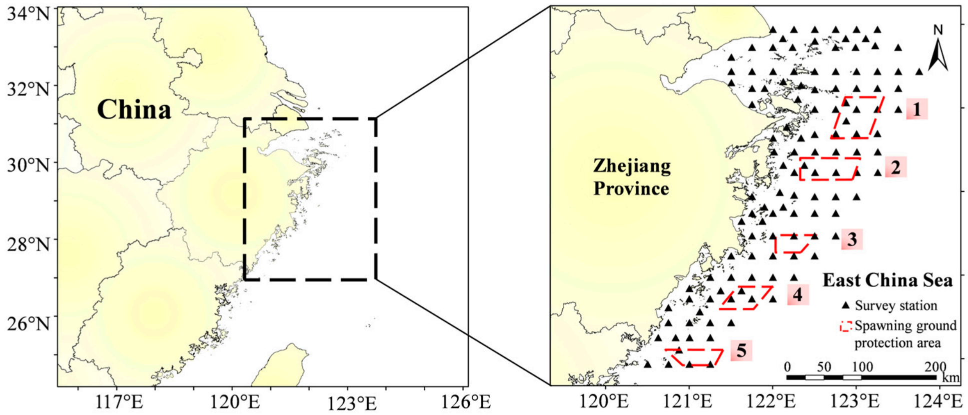

Figure 1. Map of bottom trawl survey areas in Zhejiang province, China, and adjacent waters. 1: Zhoushan fishing ground spawning ground protected area, 2: Jiushan Islands spawning ground protection area, 3: Dachen Islands spawning ground protection area, 4: Wen-tai fishing ground spawning ground protected area, and 5: Qixing Islands spawning ground protected area.

The type of fishing boat used was a single-bottom trawler, with a main engine power of 220 kw. The surveys were conducted at 3 knots for about 30 min on average. The mesh size of the capsule net was 25 mm, and the perimeter of the net port was 50 m. A catch was landed at each survey station, and the weight of the catch was converted into the catch per unit net. The relative resource abundance of *S. japonica* (unit g/h) was obtained via standardization with a trawling speed of 2.0 kn and trawling duration of 1.0 h. The environmental data were measured using an offshore synchronous conductivity, temperature, depth (CTD) instrument, which measured water depth, seawater surface temperature, seawater surface salinity, chlorophyll a, pH, and dissolved oxygen. The collection, processing, and analysis of the samples were performed in accordance with the regulations of the "Specifications for oceanographic survey-Part 6: Marine biological survey, GB/T 12763.6-2007" [12].

2.2. Data Processing

The ln(y+1) obtained from the natural logarithmic transformation of the relative resource abundance y was used to analyze the habitat distribution characteristics of *S. japonica*: the relative resource abundance y was processed as a binary variable (presence/absence) for use in RF and GAM analyses, where y was used as a response variable, while six environmental factors (Depth, SST, SSS, Chl-a, pH, and DO) were used as explanatory variables (Table 1).

Table 1. Statistical summary of explanatory variables.

Variable	Description	Range (Mean)							
		2015	2016	2017	2018	2019	2020	2021	2022
Depth	Water depth (m)	3.57–71.22 (32.79)	4.07–69.45 (33.17)	3.80–71.01 (32.67)	4.83–75.78 (32.34)	3.57–71.22 (32.52)	6.60–70.33 (32.84)	4.22–68.89 (32.6)	5.82–72.51 (32.45)
SST	Sea surface temperature (°C)	12.83–16.85 (14.74)	13.05–18.01 (15.12)	12.92–19.62 (15.82)	12.41–19.49 (15.86)	13.43–19.90 (16.44)	13.53–19.86 (15.60)	12.66–19.82 (15.64)	13.97–18.87 (16.15)
SSS	Sea surface salinity	8.23–32.87 (27.20)	12.01–33.53 (27.27)	10.61–33.73 (27.18)	6.81–34.16 (28.61)	8.82–34.23 (27.63)	12.90–34.24 (27.31)	12.28–33.21 (27.52)	12.22–33.66 (27.79)
Chl-a	Chlorophyll a (µg/L)	0.52–18.87 (3.69)	0.15–9.73 (3.54)	0.42–27.26 (5.32)	0.04–29.87 (4.38)	0.02–10.57 (2.47)	0.42–29.70 (4.75)	0.07–23.70 (3.13)	0.10–29.72 (2.71)
pH	Potential of hydrogen	7.34–8.56 (8.22)	7.85–8.87 (8.37)	7.40–8.80 (8.18)	6.34–8.92 (8.35)	7.34–8.83 (7.94)	7.34–8.90 (8.16)	7.34–8.87 (8.36)	7.37–9.06 (8.39)
DO	Dissolved oxygen (mg/L)	5.22–9.06 (7.58)	4.97–9.15 (7.69)	5.22–9.02 (7.46)	4.76–9.28 (7.23)	4.90–9.67 (7.39)	5.05–9.66 (7.71)	5.95–9.99 (7.78)	5.39–9.84 (7.83)

2.3. Research Methods

2.3.1. Fishery Resource Center

The formulas for calculating the longitude and latitude of the center of gravity of the relative resource abundance of *S. japonica* are as follows:

$$\boldsymbol{X} = \frac{\sum_{i=1}^{n}(\boldsymbol{C_i} \times \boldsymbol{X_i})}{\sum_{i=1}^{n}\boldsymbol{C_i}},\ \boldsymbol{Y} = \frac{\sum_{i=1}^{n}(\boldsymbol{C_i} \times \boldsymbol{Y_i})}{\sum_{i=1}^{n}\boldsymbol{C_i}}$$

The center of gravity of the relative resource abundance volume in a certain year is represented by $\boldsymbol{X}$ and $\boldsymbol{Y}$, which correspond to longitude and latitude, respectively. $\boldsymbol{C_i}$ represents the relative resource abundance of *S. japonica* at the $\boldsymbol{i}$-th station, where $\boldsymbol{X_i}$ and $\boldsymbol{Y_i}$ are the longitude and latitude of the $\boldsymbol{i}$-th station. There were 120 stations in this study.

2.3.2. Random Forest

Random forest (RF) is a machine learning algorithm that combines classification and regression trees (CART). It uses self-lifting sampling and randomly selects variables from the sample as decision tree nodes. Each decision tree acts as a classifier and determines the final classification result through voting [13–15]. The parameters mtry and Ntree settings were optimized through cross-validation and hyperparameter grid search. The RF model was used to calculate the importance of explanatory variables in the training process. The average decline rate of the Gini coefficient was selected as the index of variable importance [16]. To comprehensively evaluate the model's performance, all years were used as both training and test data. The dataset was divided into training and test sets in chronological order, ensuring that each test set contained data from different years. To evaluate the performance of the model, metrics such as accuracy, precision, recall, and F1 score were used. The RF model was created using the "randomForest" and "caret" packages in R.

2.3.3. Generalized Additive Model

Generalized additive models (GAMs) are particularly suitable for capturing the nonlinear relationships between a response variable and explanatory variables, and nonparametric methods can be used to detect the data structure and find patterns [17,18]. In this study, based on a GAM, a nonlinear correlation between the distribution of *S. japonica* and important explanatory variables was established. The GAM was constructed using the "mgcv" function library in R, "logistic" was chosen as the link function to construct the GAM equation. The chi-square test and p value were used to test the importance of the explanation variables. The smoothed curve was fitted using the natural spline function, and the 95% confidence interval was defined as the optimal habitat environmental range for *S. japonica*.

3. Results and Analysis

3.1. Distribution Characteristics of S. japonica

3.1.1. The Interannual Distribution Characteristics of *S. japonica*

The annual variation in *S. japonica* resources was obvious, and the overall resources fluctuated and increased. Among them, the relative resource abundance fluctuated greatly from 2015 to 2019, and the resources were relatively stable from 2020 to 2022. From 2015 to 2022, the spatial distribution pattern of *S. japonica* was roughly the same, which was concentrated in the central and south-central islands and reefs in the study area (Figure 2).

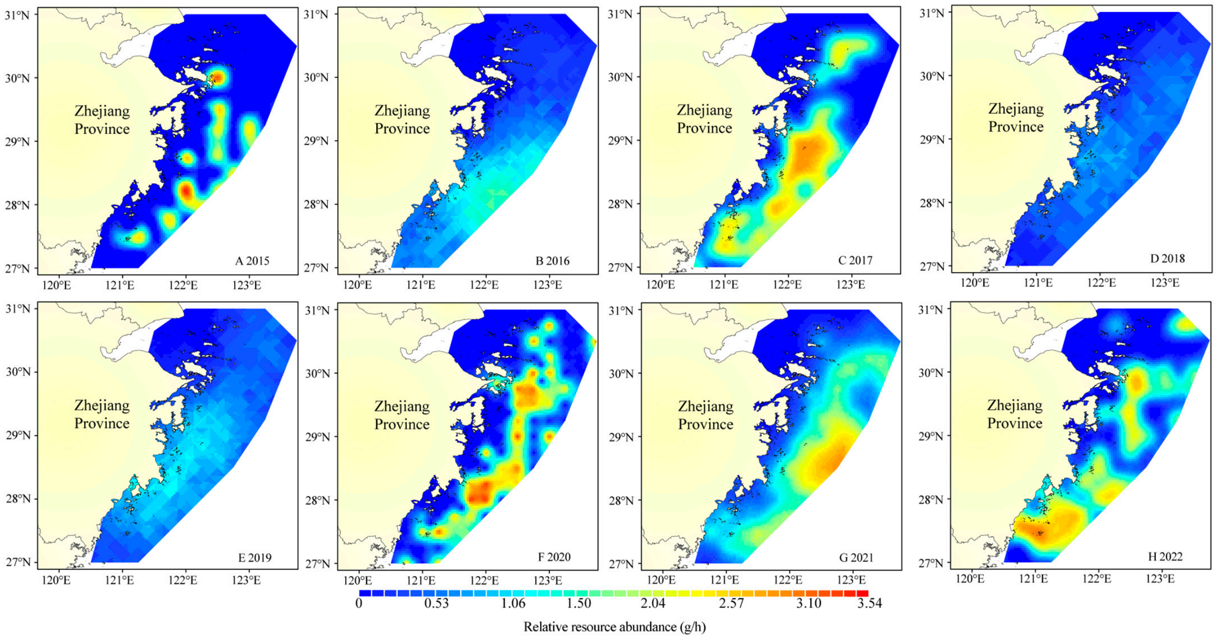

Figure 2. Spatial distribution of *S. japonica* from 2015 to 2022. ((**A**): 2015; (**B**): 2016; (**C**): 2017; (**D**): 2018; (**E**): 2019; (**F**): 2020; (**G**): 2021; (**H**): 2022).

3.1.2. Resource Center of *S. japonica*

From 2015 to 2022, the distribution range of the resource center of *S. japonica* was 122°00′ E–122°30′ E and 28°20′ N–29°00′ N, mainly located near the waters of the Jiushan Islands protected spawning ground area and Dachen Islands protected spawning ground area in the central part of the Zhejiang's offshore area. From the perspective of the spatial change trajectory of the resource center: in 2015–2016, the resource center of *S. japonica* shifted to the southwest; in 2017–2018, the resource center shifted to the northeast; the change pattern in 2019 was consistent with that in 2016; and in 2020–2022, the resource center shifted in the southwest offshore direction (Figure 3).

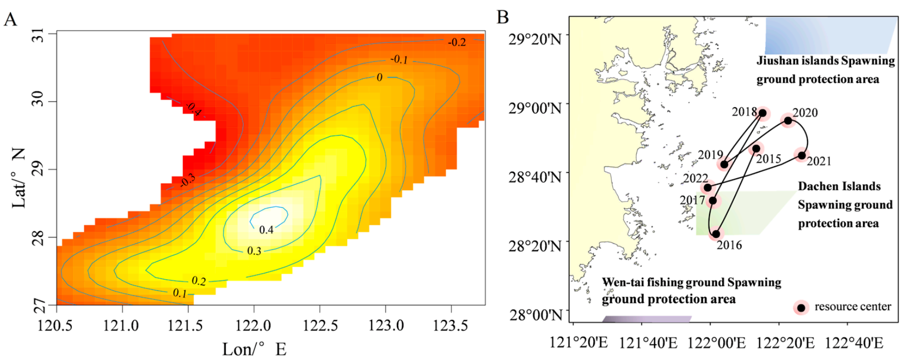

Figure 3. Distribution of *S. japonica* resource center: (**A**): 2015–2021 spatial distribution of *S. japonica* resource center; (**B**): distribution and change trajectory of resource center of gravity each year.

3.2. FR Analysis

3.2.1. Multicollinearity Test

The variance inflation factor (VIF) is used to measure the correlation between explanatory variables. A higher VIF value indicates a stronger correlation, and collinearity becomes more severe. A VIF value greater than 10 generally indicates a strong collinearity problem. After conducting tests, it was found that the VIF values of each explanatory variable in this study were less than 10 (Table 2), indicating the absence of any serious collinearity problem. Therefore, the model could be expanded without any concern.

Table 2. Multicollinearity test of explanatory variables.

Parameter	Explanatory Variable					
	Depth	SST	SSS	Chl-a	pH	DO
VIF	2.664	1.258	1.806	1.148	1.102	2.776

3.2.2. Importance of Explanatory Variables

The importance of the environmental factors regarding the distribution of *S. japonica* was ranked using the RF output (Figure 4). MDG represents the heterogeneous effects of the observed values of the nodes on the classification trees and environmental factors. Its value represents and is proportional to the importance of the explanatory variables. It is therefore an important indicator for determining the importance of each factor. The environmental factors affecting the distribution of *S. japonica* distribution were ranked as Depth, SSS, pH, DO, SST, and Chl-a from first to last. The model's accuracy, precision, recall, and F1 score were calculated using the data from the confusion matrix (Table 3). The mean accuracy value of 0.74 indicated a high proportion of correct model tests, and the mean precision value of 0.78 was also noteworthy. The mean recall of 0.90 showed that the model could correctly identify most positive samples. The results indicated that the model's accuracy improved when testing for the presence of *S. japonica*. The mean F1 score of 0.83 indicated that the model achieved a good balance between accuracy and recall (Table 3). The random forest model performed well in this test.

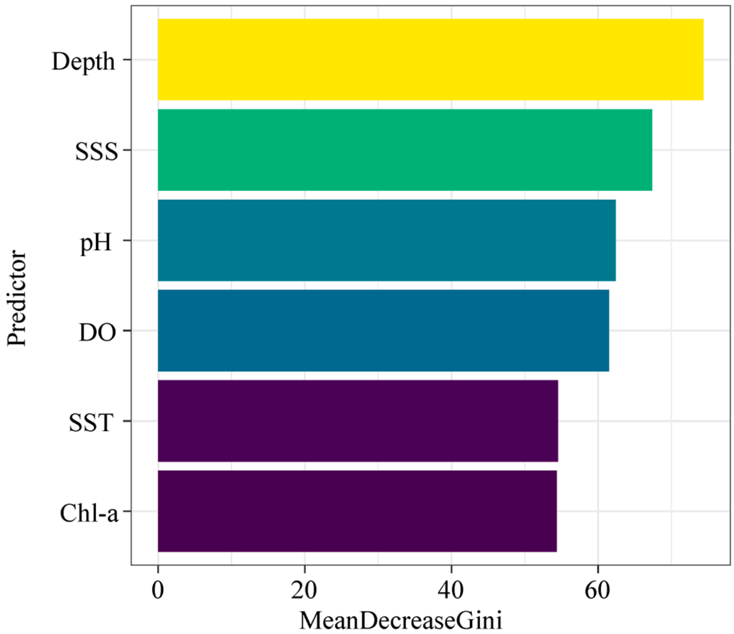

Figure 4. Environmental factor importance sorting results of RF model.

Table 3. RF model's performance parameters.

	Accuracy (95% CI)	Precision	Recall	F1 Score
RF 1 (2015)	0.88 (0.80, 0.93)	0.91	0.95	0.93
RF 2 (2016)	0.79 (0.71, 0.86)	0.79	0.99	0.88
RF 3 (2017)	0.76 (0.67, 0.83)	0.79	0.86	0.82
RF 4 (2018)	0.85 (0.77, 0.91)	0.88	0.95	0.92
RF 5 (2019)	0.63 (0.54, 0.72)	0.78	0.70	0.74
RF 6 (2020)	0.73 (0.64, 0.80)	0.74	0.95	0.83
RF 7 (2021)	0.65 (0.56, 0.73)	0.65	0.96	0.78
RF 8 (2022)	0.65 (0.56, 0.73)	0.67	0.87	0.76

3.3. GAM Analysis

Figure 5 displays the results of the GAM analysis of six explanatory variables: Depth, SSS, pH, DO, SST, and Chl-a. The species were mainly found at water depths ranging from 15 to 60 m, being concentrated at depths of 15~25 m. The optimal sea surface salinity ranged from 26 to 32, while the optimal pH range was 7.6–8.3. The optimal DO range was 6~9 mg/L, and the optimal sea surface temperature range was 14~17 °C. The optimal range of Chl-a was 2.5~5 µg/L. The results of the test on *S. japonica* and environmental variables (Table 4) indicate that Depth, SST, DO, and pH were significantly correlated with the distribution of *S. japonica* ($p < 0.05$). Specifically, the chi-squared values of pH and DO for *S. japonica* were 18.325 and 23.665, respectively ($p < 0.01$). The chi-squared value of the depth of the distribution of *S. japonica* was 39.384 ($p < 0.001$). SSS and Chl-a were not significantly correlated with the distribution of *S. japonica* ($p > 0.05$).

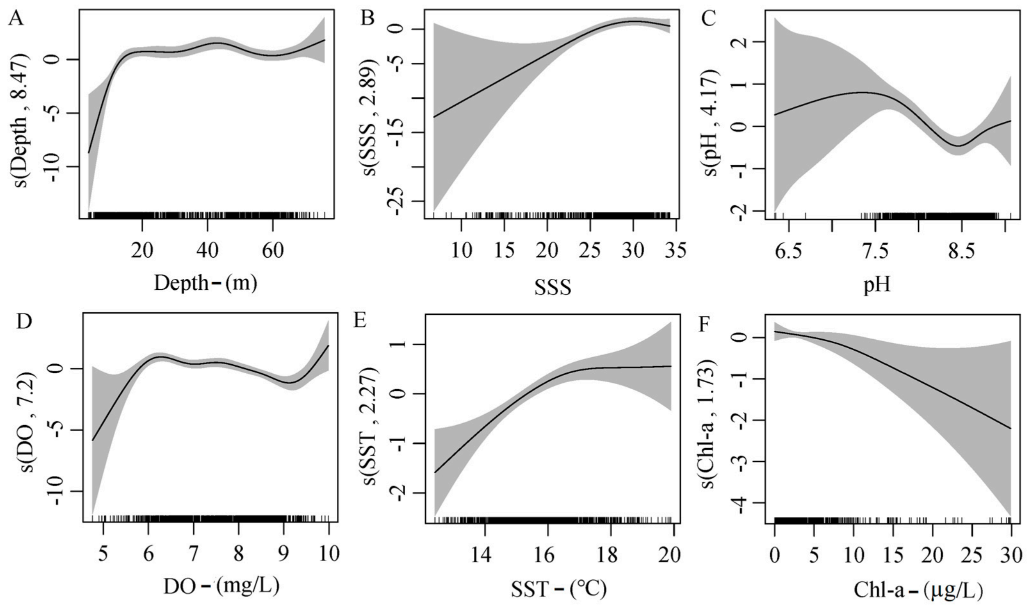

Figure 5. GAM-derived Effects of environmental factors on the *S. japonica*, based on the model constructed using: (**A**) Depth, (**B**) SSS, (**C**) pH, (**D**) DO, (**E**) SST, and (**F**) Chl-a. The plot includes a spline function (s) and the corresponding edf value. The shaded area represents the point-by-point standard deviation of the fit function, which indicates the upper and lower bounds of the 95% confidence interval.

Table 4. GAM verification results.

Variable	edf	Ref.df	Chi.sq	*p*-Value
Depth	8.764	8.969	39.384	<0.001 ***
SSS	3.457	4.273	10.586	0.05691
pH	3.020	3.764	18.325	0.00139 **
DO	5.584	6.732	23.665	0.00117 **
SST	1.001	1.002	17.239	<0.001 ***
Chl-a	1.730	2.170	2.065	0.42100

*** significant correlation at the 0.001 level; ** significant correlation at the 0.01 level.

4. Discussion

4.1. Spatial–Temporal Distribution Characteristics of S. japonica

The characteristics of the habitat and distribution of *S. japonica* are complex and influenced by various factors. In spring, the northeasterly wind strengthens and the offshore water temperature rises. *S. japonica* migrates from the open sea to the offshore area for reproduction, showing a northwestward trend [5]. The distribution of *S. japonica* in the offshore area of Zhejiang from 2015 to 2022 followed the same trend as the water depth contour and sea surface salinity contour, mainly in the northeast–southwest direction. It was primarily distributed in sea area with water depth contours of 14~56 m and salinity of 26~34, and the fish resources showed an overall increasing trend (Figure 2; Figure 6). Since 2013, Zhejiang province has taken fishery restoration and revitalization actions. The implementation of the summer fishing moratorium system, the ecological restoration measures and the release tens of billions of aquatic species seedlings have had a decided effect on the replenishment of the *S. japonica* resources in the offshore area of Zhejiang.

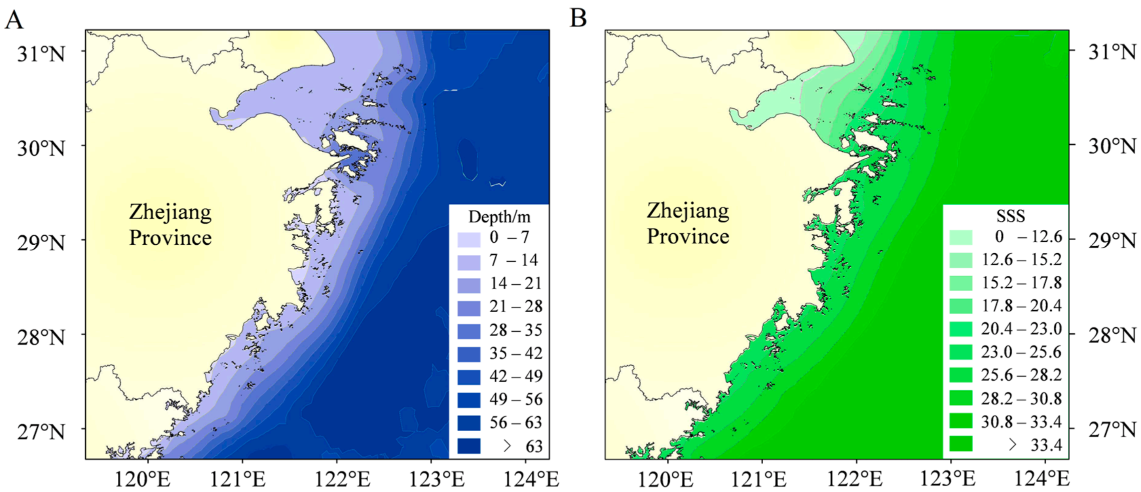

Figure 6. Sea depth and sea surface salinity contours in Zhejiang. (**A**): Mean bathymetry contours from 2015 to 2022; (**B**): mean surface salinity of seawater contour from 2015 to 2022.

For marine life, global climate change is mainly reflected in changes in sea surface temperatures. The results showed that the mean sea surface temperature in the spring of 2015 to 2022 was increasing. According to the results of the analysis of the trend, the relative resource abundance of *S. japonica* increased with slight increases in sea surface temperature. As the surface water temperature continued to rise, the amount of the resource showed a downward trend (Figure 7). A small increase in temperature was found to have some stimulating effect on the resources of *Octopus ocellatus* by Cui et al. [19]. However, if the temperature rises too high, it can have an adverse effect on *O. ocellatus* resources, indicating that cephalopods are sensitive to environmental changes. The ocean warming model driven by climate in China is parallel to and is exceeding the trend of the rising global average temperature. Different species or different life stages of a species have different heat tolerance limits. Although warmer water temperatures may be beneficial to the growth and reproduction of some species, cephalopod responses to climate change can be extremely complex [20]. Changes in ocean temperature may lead to earlier life cycle events such as cephalopod migration, maturation, and reproduction. At the same time, changes in ocean temperature may affect population flow and abundance by changing the type and amount of the food eaten by cephalopods and the characteristics of their spawning habitats [21–23]. As an annual cephalopod, climate change may have profound effects on the species' biological, physiological, and behavioral changes, which can further impact its distribution.

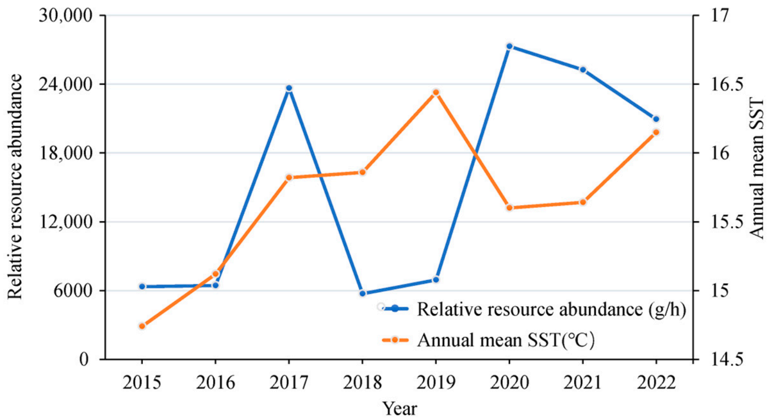

Figure 7. Resources of *S japonica* and sea surface temperature in Zhejiang's offshore area.

4.2. Trends of the Change in the Resource Center of S. japonica

Human activities and climate change may alter the distribution of a population and the changes in the location where a species is abundant [23]. Since the late 1970s, due to the trapping of spawning groups outside the spawning grounds, the mass fishing of overwintering cuttlefish, and the destruction of the spawning grounds, the *S. japonica* resources have decreased and their group composition and fishing status have changed (e.g., small central fishing ground, gorgonians, seaweed, and other spawning substrates are insufficient) [5,24,25]. Additionally, climate change is causing the geographic range of species to expand toward the poles [26]. Based on an analysis of the resource status of *S. japonica* from south to north (Nanji, Beiji, Pishan, Yushan, Jiushan, Zhongjieshan, and Shengsi Sea areas) in Zhejiang's offshore area from 1964 to 1984, Tang et al. [25] found that the fishing season in the spawning grounds of *S. japonica* in the offshore area of Zhejiang gradually disappeared in the late 1970s due to the decline of *S. japonica* stocks. Despite being a traditional spawning ground for *S. japonica*, the *S. japonica* fishing has not been prosperous in the Zhongjieshan fishing area, but the *S. japonica* production in Shengsi and the North Sea area has improved. The central fishery has tended to move northward from the small Zhoushan fishery [27]. Ni et al. [28] evaluated the *S. japonica* resources in Zhejiang's offshore area, and the results showed that the maximum sustainable yield in northern Zhejiang was 3.48 times that in southern Zhejiang, and the populations in southern Zhejiang and eastern Fujian could not form a fishing season. Chen et al. [29] showed that the density of cephalopod resources was high near 30.5°N in the coastal waters of Zhoushan and 28.5°N in the coastal waters of Taizhou, followed by the sea area off the Nanji Islands (121° E, 27°–27.5° N). In the large coastal area of Zhejiang province, the resource center of *S. japonica* shifted from the north to the central part, but this does not mean that the resource center of *S. japonica* shifted southward. Compared with the historical studies of 1964–1986, the resource center showed a northward trend. In general, the ecological environment of traditional spawning grounds has been deterioration, and the natural substrates used for attachment, such as gorgonian and *Sargassum fusiforme*, have been severely damaged, no longer meeting the reproduction and habitat needs of *S. japonica*, which has thus shifted its resource center in search of more suitable spawning grounds [24,30]. At the end of 1980s, the growth rate of cuttlefish accelerated, the sexual maturity advanced, and the fishing season gradually advanced. The accelerated individual growth and early sexual maturity, on the one hand, showed that the population was in a recession stage; on the other hand, it also showed that the time when cuttlefish enter the spawning ground also advanced. Under the influence of factors such as sea and meteorological conditions, the spawning ground of *S. japonica* has migrated. For example, in April every year, the surface water of the East China Sea enters the coastal waters of Zhejiang and converges with the runoff coastal waters of the Yangtze River and Qiantang River under the action of mixing. The water temperature is high in the south and low in the north, and high in the outside and low in the inside. After the *S. japonica* enters the spawning ground from the wintering ground, it quickly enters the breeding state under suitable water temperature and salinity conditions. At the same time, changes in habitat and the marine food web caused by global warming and extreme weather (El Niño and La Niña events) further affect the selection of spawning sites and changes in resource centers of *S. japonica* [31,32].

4.3. Effects of Environmental Factors on the Habitat and Distribution of S. japonica

Changes in the marine environment have a major impact on the habitat and reproduction of species, affecting their distribution and abundance [33]. Guerra et al. [34], regarding the spawning habitat of cuttlefish in northwestern Spain, showed that substrate type, depth, temperature, season, and spatial orientation (latitude and longitude) have significant effects on the distribution of cuttlefish eggs. Most of the exploited cephalopod species have short life cycles, typically only 1–2 years, and their short life cycles, high metabolic rates, and high growth rates are associated with a high degree of plasticity in life history traits and sensitivity to environmental change [35,36].

S. japonica is an offshore warm-water benthic animal. In spring, it migrates from the coastal deep-water overwintering ground (60~80 m) to the spawning ground in shallow coastal water, and where they spawn in the surface-to-50 m water layer [5]. Water depth, as an important factor affecting the distribution of the cuttlefish, has an important effect on its habitat, reproduction, and migration. Li et al. [24] showed that the water depth suitable for egg attachment in the Jungshan Islands was 10~20 m. The concentration of *S. japonica* in this study was at water depths of 15-25 m, which is consistent with the results of historical studies. Compared with deep water, the natural adhesion base in the shallow sea and near the islands and reefs is rich in resources, enabling easy spawning and attachment. In addition, shallow seas usually provide more biological food resources. For example, small fish and shrimp are mainly distributed in shallow waters and near islands and reefs. At the same time, *S. japonica* tends to be weak light, and afraid of strong light (preferring weak light), so it generally lives in the sea areas near coastal islands around rocks and seaweed during the breeding period [37].

The habitat of *S. japonica* is limited by salinity. In spring, the overwintering adults perform reproductive migration from the deep high-salt and low-temperature waters of the open sea to the shallow seas in coastal areas with higher temperature and lower salinity. In late autumn and early winter, the juvenile cuttlefish hatch after spawning and scatter in the high-temperature and low-salt waters along the coast to grow into overwintering adults. Then, they gradually swim toward high-salt sea areas [5] as they mature and forage. Salinity is an important ecological factor in marine ecosystems, and its fluctuation affects the behavior, immunity, and other physiological responses of marine organisms [38]. For cephalopods, salinity changes cause a series of physiological stress responses, including abnormalities in osmotic regulation, immunity, and hormone secretion [39]. *S. japonica* has a wide salt tolerance range and has a good low-salt tolerance. If the salinity exceeds the appropriate values, abnormal behavioral changes such as severe ink-jet phenomena occur, which result in energy consumption and serious damage to the tissues and organs that affect reproduction.

Studies have shown that ocean acidification has negative effects on larval development and calcification in mollusks [40]. For cephalopods, the binding of oxygen to the cephalopod respiratory protein, hemocyanin, is highly dependent on pH, and the increase in seawater

CO_2 concentration may further negatively affect cephalopod respiratory metabolism [41,42]. The pH tolerance range of *S. japonica* is narrow, between 7.6 and 8.3, and the oxygen consumption rate of *S. japonica* increases in more acidic environment, which is also not conducive to bivalve growth. In addition, gorgonian is an important substrate for *S. japonica* spawning, accounting for about 60% of *S. japonica* spawning attachment in natural waters. Corals are very sensitive to changes in the marine environment [43]. The negative effects of ocean acidification on corals are multifaceted, affecting not only the growth and survival of the corals but also causing significant damage to the entire marine ecosystem.

Due to their fast growth, cephalopods have a high demand for oxygen [36]. All activities of cephalopods require oxygen consumption, and the oxygen consumption rate of *S. japonica* is positively proportional to the water temperature. In areas with low dissolved oxygen levels, the growth of *S. japonica* slows, which reduces its metabolic rate and affects individual activities [44–48]. As the seasons change, the water temperature gradually increases, which is beneficial for the growth and development of *S. japonica* in the areas of the sea with higher dissolved oxygen concentrations. In the short life of most cephalopods (except Nautilus), they lay eggs later in their lives, die soon after the end of parental reproduction, and the spawning grounds turn into nurseries for the offspring. Sea areas with a higher dissolved oxygen concentration not only provide a more suitable ecological environment for the cuttlefish parents but also sustain the hatchlings of a large number of cuttlefish eggs and ensure the survival of the larvae.

Wang et al. found that sea surface temperature had a significant effect on cuttlefish fishing [49]. As an important marine environmental factor, sea water temperature directly affects the time when cuttlefish enters the spawning ground and the rate of reproduction, thus affecting the distribution of this resource. There is a certain correlation between the concentration of chlorophyll a and the distribution of cephalopods in the water. For example, the distributions of *Loligo edulis*, *Sepia kobiensis*, *Sepia esculenta*, and *Octopus variabilis* fishing grounds are influenced by the concentration of chlorophyll a. Fish and shrimp (which feed on algae and other organic matter) are important food for cephalopods. Chlorophyll a, as an important indicator of phytoplankton abundance, can provide favorable growth conditions for planktonic organisms [50]. During the reproductive period, *S. japonica* shows decreased feeding intensity but still requires a large amount of food to promote gonad development and ensure sufficient energy for reproduction.

5. Conclusions

Cephalopods actively respond to changes in the marine environment, allowing for both active migration and passive utilization. As one of the most promising species for fisheries, as increasingly emphasized by fishery managers around the world, and the increase in global warming, fishery productivity and the distribution of fishery resources will change [36]. In this study, we investigated the interannual variation in and spatial distribution characteristics of the abundance of *S. japonica* and its response to environmental factors in the offshore waters of Zhejiang province. The results showed that *S. japonica* concentrated in the Dachen Sea area, and the spawning ground had shifted compared with the historical locations. The environmental factors affecting the distribution of *S. japonica* were water depth, salinity, pH, dissolved oxygen, water temperature, and Chl-a in descending order of importance. Among these factors, water depth, water temperature, dissolved oxygen, and pH were significantly correlated. The results of this study can be used to characterize the resource quantity and spawning area locations of *S. japonica* to a certain extent, providing theoretical guidance for resource conservation, spawning habitat protection and restoration, and the scientific management of *S. japonica* resources within the context of global climate change. There are many factors influencing changes in species distribution, and the factors included in this study may not be comprehensive. Therefore, in future work, we will continue to identify more influencing factors and comprehensively consider the effects of these additional factors on the spatial and temporal distribution of *S. japonica*. This will further improve the prediction accuracy and provide theoretical support for the scientific conservation, propagation, and release of *S. japonica*.

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