

# Modelling the Spatial Distribution of Habitats of Main Cephalopod Taxa in Inshore Waters of Zhejiang Province at Spring and Autumn

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## Research Article

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# Abstract

Due to the declining catch of the ground fish, cephalopod as a short-lived invertebrate with commercially important value has become the main fishery target species of East China Sea (ECS) in recent decades. Therefore, it is necessary to explore its habitat for the sustainable utilization. In this study, with the individual density of cephalopod derived from the fishery survey data in the coast of Zhejiang Province from 2014 to 2019 and remote sensing data, the habitat suitability index (HSI) model of typical cephalopod (Loliginidae, Octopodidae, Sepiidae, and Sepiolidae) in spring and autumn was obtained. The habitat isolines of core zone, common zone and marginal zone were also established and then compared among different typical cephalopod taxa based on arithmetic mean model (AMM). The distribution ranges of SST and chlorophyll-a of cephalopod were respectively 12.95~21.91 °C and 0.52~5.57 mg/m<sup>3</sup> in spring and 17.02~22.94°C and 0.26~6.02 mg/m<sup>3</sup> in autumn. The prediction results of the HSI model suggested that the cephalopod distribution areas were concentrated in the range of 122°~124°E, 29.5°~31°N, displaying the distribution direction from coastal area to the northeast. The accumulative density of the four cephalopod taxa in the area with HSI>0.6 accounted for 73.9%. The overlap between the prediction results of HSI model and the actual density in 2019 also proved the good predictability of HSI model based on AMM. Four cephalopod taxa showed distribution differences. Sepiolidae had the widest distribution area, whereas Octopodidae had the narrowest distribution area.

# Introduction

Cephalopod is a kind of invertebrate marine animals distributed in every corner of the world's ocean (Jereb and Roper, 2005, 2010; Jereb et al., 2014). It also plays an important role in marine ecosystems (Navarro et al., 2013). As some of the species tend to gather as an assemblage, the different cephalopod species assemblage known as cephalopod community showed significant spatial distribution variations in the global ocean (Rosa et al., 2008a; Pissarra, 2017). The diversity of cephalopod community is more abundant in neritic waters than that in oceanic waters due to the difference in oceanographic conditions (Rosa et al., 2008b, 2019). Northwest Pacific Ocean, especially the East China Sea (ECS), has the most abundant cephalopod species in the world (Pissarra, 2017; Rosa et al., 2019). With the high fishing intensity and climate variability in recent three decades, the Chinese coastal cephalopods have undergone overexploitation and the catch and species composition have significantly fluctuated (Pang et al., 2018; Kang et al., 2021).

The oceanographic environment is one of the fundamental factors in the survival of cephalopods and each marine animal has its own specific habitat condition (Leporati et al., 2007; Aceves-Medina et al., 2017). Abiotic environments affect the distribution of cephalopod individuals or population (Pierce et al., 2008; Robin et al., 2014). Fishery scientists endeavor to explore the relationship between the distribution of cephalopods and the environment by establishing suitable models (Xavier et al., 2016; Yu et al., 2016; Alabia et al., 2020). Currently, the habitat suitability index (HSI) model proposed by United States Fish and Wildlife Service (USFWS) in early 1980s is the most widely used evaluation model of wildlife habitats (Brooks, 1997). As an evaluation system integrating animal abundance with environment features, HSI

model has been widely used in fishing forecast, ecological ecosystem restoration and the conservation and management of aquatic animals as a popular evaluation model (Agnew et al., 2002; Brambilla et al., 2009; Tian et al., 2009; Guerra et al., 2016).

Cephalopod is a typical short-lived marine organism with approximately one-year lifetime (Lipiński, 1998). This characteristic enables it to passively experience different kinds of environment and makes it sensitive to the environment change during its life history (Robin et al., 2014). The cephalopod habitat distribution can be changed by some exceptional environment events (Puerta et al., 2015; Keller et al., 2016). In the early life stage, cephalopod has limited movement ability and usually stay on the surface (Rodhouse et al., 1992). Thus, the sea surface temperature (SST) is one of most important oceanographic factors that influence the early life stage of cephalopod and play a vital role in the spatial distribution (Rosa et al., 2011; Yu et al., 2016, 2018). Meanwhile, cephalopod distributions are also related to the food availability, which can be also reflected by chlorophyll-a (Chl-a) in the corresponding area (Puerta et al., 2014; Mohamed et al., 2018). In addition, sea surface height anomaly (SSHA) may also affect the distribution of some cephalopod species due to their diel vertical migration (Alabia et al., 2016; Yu et al., 2019; Jin et al., 2020; Jereb and Roper, 2006, 2010).

The habitat distribution and related environment characteristics of oceanic cephalopod species in most open waters have been already investigated (Xu et al., 2016; Igarashi et al., 2018; Yu et al., 2016, 2019; Wang et al., 2020; Mohamed et al., 2018; Xavier et al., 2016). The distribution of abundant neritic cephalopod species is also influenced by different kinds of oceanographic environments (Jin et al., 2020). Sanchez et al. (2008) analyzed the habitat distribution of *Loligo vulgaris* in Northwest Mediterranean Sea based on SST, Chl-a, SSHA and photosynthetically active radiation (PAR). Moreno et al. (2014) suggested that there was a close relationship between bottom salinity, river runoff and habitat distribution of *Octopus vulgaris* in the coast of Portugal. Puerta et al. (2015) indicated that Chl-a concentration had the positive relationship with the habitat distribution of *Eledone cirrhosa* and *Illex coindetii*. Chl-a concentration is also the key factor that influences the cephalopod distribution in Yellow Sea (Jin et al., 2020).

In general, the cephalopod habitat distribution in the neritic area of China was seldom explored (Jin et al., 2020). The most abundant taxa of cephalopod are Loliginidae, which habit in the pelagic area, and Octopodidae, Sepiidae, Sepiolida, which prefer to live in the benthic water (Jin et al., 2020). Previous studies mainly discussed the species composition, the number of individuals, and characteristics of spatial agglomeration (Yu et al., 2009; Qin et al., 2011; Zhu et al., 2014; Song et al., 1999; Li et al., 2006; Xu et al., 2008). These studies only focused on the importance of each environmental factor, but the relationship between habitat distribution and environment characteristics was rarely explored. Therefore, the cephalopod habitat in the ECS is not obscure. In addition, most of the current studies focused on the area of offshore ECS and ignored the inshore area, the main spawning ground of neritic cephalopod (Zheng et al., 1999). In order to develop a suitable conservation and restoration approach of cephalopod habitat, it is urgently necessary to explore the cephalopod habitat change and oceanographic environment response (Kang et al., 2021).

In this study, the integrated HSI model was used to simulate the potential habitat distribution pattern of neritic cephalopod taxa (Loliginidae, Octopodidae, Sepiidae, Sepiolidae) based on important environmental factors in the coast of Zhejiang Province. In addition, the different types of the habitat distributions were evaluated so as to explain the variations of cephalopod habitats with seasons and taxa. The study provides the scientific evidence for the sustainable development and coastal ecological protection of neritic cephalopods.

## Materials And Methods

### Survey data

Scientific survey data were obtained in the bottom trawl survey conducted by the Marine Fisheries Research Institute of Zhejiang Province (MFRI-ZJ) in spring (April to May) and autumn (November) from 2014 to 2019. Most of the sampling stations were arranged according to the spatial resolution of  $0.15^{\circ} \times 0.15^{\circ}$  along the coast of Zhejiang Province (Fig. 1). The survey was conducted by the R/V “Zhepuyu 43019” with the same gear and protocol to keep the survey consistency. The trawl net had a cod-end mesh size of 2.5 cm, a headline height of 6.5–9.0 m, and a span of 28 m between its wings (Chen et al., 2020). The trawl survey started in the daytime with average speed was 3.0 knots and the duration of each trawl survey for each species at each station was standardized as 1 h (Jin et al., 2020). Thus, the location (latitude and longitude) and the number of individual cephalopods were included in this independent survey.

In this study, the individuals' number of each cephalopod taxa is calculated as the CPUE (catch-per-unit-effort) (Can et al., 2004):

$$CPUE_{ijk} = \frac{d_{ijk}}{(1-E) a_{ijk}},$$

where  $CPUE_{ijk}$  is the standardized CPUE of the  $i$ -th taxa at the  $j$ -th station in the  $k$ -th year (ind./km<sup>2</sup>);  $d_{ijk}$  is the sum number of individuals of the  $i$ -th taxa at the  $j$ -th station in the  $k$ -th year,  $a_{ijk}$  is the swept area of the  $j$ -th station in the  $k$ -th year (km<sup>2</sup>);  $E$  is escapement rate and set as 0.5 in this study.

More than 10 cephalopod species were determined (Jereb and Roper, 2005, 2010; Jereb et al., 2014) in the survey of 5 consecutive years. Considering the difficulty of species separation and similar habitat characteristics within sibling species, we classified all the cephalopod species into four main taxa at the family level (Loliginidae, Octopodidae, Sepiidae, and Sepiolidae (Table 1)) as representatives to analyze the dynamics of cephalopod habitat and related oceanographic environment.

### Environmental data

Two key oceanographic environmental factors, sea surface temperature (SST) and chlorophyll-a concentration (CHLA), were selected for the subsequent analysis due to their important influences on the

cephalopod distribution and abundance (Keller et al., 2016; Yu et al., 2016; Jin et al., 2020). Remote sensing data of monthly SST (0.04 × 0.04 resolution) and CHLA (0.04 × 0.04 resolution) were downloaded from National Oceanic and Atmospheric Administration (NOAA) (<https://oceanwatch.pifsc.noaa.gov/>). The oceanographic environmental factors in the whole survey area were acquired. All the environmental data were gridded to 0.15° × 0.15° for each season to match the spatial resolution of survey data.

### HSI model development and validation

Habitat suitability Index (HSI) model has been widely used to evaluate the cephalopod distribution pattern in recent studies (Yu et al., 2018, 2019; Wang et al., 2020). Generally, this model should include all the environmental factors and the suitability index (SI) can be estimated based on the relationship between fishing/survey data and each environmental factor. Thus, the SI is calculated by dividing CPUE in the interval of each environmental factor by the maximum CPUE in each interval (Li et al., 2014):

$$SI = \frac{CPUE_i}{Max(CPUE_i)},$$

where SI is the suitability index in each interval of each environmental factor;  $CPUE_i$  is the accumulative CPUE in a given environmental factor interval;  $Max(CPUE_i)$  is the maximum value of the accumulative CPUE in a certain interval. The intervals of SST and CHLA were respectively chosen as 1 °C and 0.5 mg/m<sup>3</sup> and were with several classes.

The observed SI values were combined with the interval value of each environmental factor (SST and CHLA) first and then converted into SI curve based on the exponential function between them (Yu et al., 2016). For each environmental factor, the SI curve function is expressed as:

$$SI = \exp[a \times (X_{SST} - b)^2],$$

$$SI = \exp[a \times (X_{CHLA} - b)^2],$$

where  $a$  and  $b$  are the parameters in the model and the solutions of the two parameters were obtained from least squares estimation so as to minimize the residuals between the observed and predicted SI values;  $X_{SST}$  and  $X_{CHLA}$  are the interval values of each factor. The SI value of each environmental factor ranged from 0 to 1.

Then, the fitted SI models of all environmental factors were integrated into an integrated HSI model. Some commonly used models were applied in the model evaluation (Gong et al., 2011) and the Arithmetic Mean Model (AMM) performed best and could accurately predict the suitable habitat of cephalopod (Yu et al., 2016, 2019). The weighted AMM method, which fully considered the difference in

the influences of various environmental factors on the habitat, was ultimately employed as the empirical HSI model to predict the habitat suitability of different cephalopod taxa along the coast of Zhejiang Province (Xue et al., 2017). The weighted model for each season (spring and autumn) is expressed as (Xue et al., 2017):

$$HSI = \frac{1}{n} \sum_{i=1}^n (SI_{SST} + SI_{CHLA}),$$

where  $SI_{SST}$  and  $SI_{CHLA}$  correspond to the SI curve for each environmental factor;  $n$  is the number of environmental factors in the HSI.

In this study, we adopted AMM-based HSI model developed with survey and environmental data for each taxon in 2014–2018, the same type of data in 2019 were used to evaluate the HSI performance. The survey data of the cephalopod distribution of different taxa in each season in 2019 was then overlaid on the predicted AMM-based HSI maps of the same year for visualization and comparison (Yu et al., 2019; Jin et al., 2020). Meanwhile, the accumulative individual density in highly suitable habitat ( $HSI > 0.6$ ) was also used in the validation of HSI model accuracy (Yu et al., 2019).

### Habitat isoline of different cephalopod taxa

The values of HSI were obtained from the above calculation. The range of HSI was from 0 to 1. We determined the areas with different HIS values ( $HSI < 0.2$ ,  $0.2 \leq HSI \leq 0.6$  and  $HSI > 0.6$ ) respectively as poor, normal and suitable habitats for each cephalopod taxa in spring and autumn of each year (Yu et al., 2019). In order to better understand the spatial distribution edge and the overlap area of typical cephalopod taxa in inshore areas of Zhejiang Province, the isolines of  $HSI < 0.2$ ,  $0.2 \leq HSI \leq 0.6$  and  $HSI > 0.6$  were respectively regarded as core zone, common zone and marginal zone to describe the distribution patterns of each cephalopod taxa.

## Results

### SI curves for each environmental factor in different seasons

According to CPUE in relation to the environmental factor (SST and CHLA), SI curves in spring and autumn were established (Fig. 2). All the SI models were well fitted ( $P < 0.01$ ) with high correlation coefficients ( $R^2 > 0.9$ ) and low Root Mean Square Errors (RMSEs  $< 0.2$ ) (Table 2).

SST preference was different in different taxa and seasons (Fig. 2). In spring, all the cephalopods were distributed in the range of SST from 12.95 to 21.91°C in the whole survey period (Fig. 2A). The inferred suitable ranges determined from the suitable SI values ( $SI > 0.6$ ) for four taxa of Loliginidae, Octopodidae, Sepiidae and Sepiolidae were 14.21~16.02°C, 13.69~15.52°C, 15.10~16.50°C and 14.28~17.76°C, respectively (Fig. 2A). The highest SI values for the above four cephalopod taxa were respectively 15.12°C, 14.61°C, 15.80°C and 16.02°C (Fig. 2A). In autumn, cephalopod individuals were distributed in

the range of SST from 17.02 to 22.94°C (Fig. 2B). The suitable ranges ( $SI>0.6$ ) for Loliginidae, Octopodidae, Sepiidae and Sepiolidae were respectively 20.56~21.93°C, 20.62~21.66°C, 21.07~22.34°C and 21.21~22.34°C (Fig. 2B). The highest SI values for the mentioned four cephalopod taxa were respectively 21.24°C, 21.14°C, 21.71°C and 21.78°C (Fig. 2B). Cephalopod preferred to concentrate in narrower SST ranges in autumn than those in spring.

In terms of CHLA preference, the CHLA range also differed among various taxa and seasons (Fig. 3). All the cephalopods were distributed in the range of CHLA from 0.52 to 5.57 mg/m<sup>3</sup> during the whole survey in spring (Fig. 3A). The inferred suitable ranges ( $SI>0.6$ ) of four taxa of Loliginidae, Octopodidae, Sepiidae and Sepiolidae were respectively 1.72~3.20 mg/m<sup>3</sup>, 1.79~2.41 mg/m<sup>3</sup>, 1.89~3.96 mg/m<sup>3</sup> and 1.44~2.55 mg/m<sup>3</sup> (Fig. 3A). The highest SI values of the above four cephalopod taxa were respectively 2.46 mg/m<sup>3</sup>, 2.10 mg/m<sup>3</sup>, 2.92 mg/m<sup>3</sup> and 1.99 mg/m<sup>3</sup> (Fig. 3A). In autumn, cephalopod individuals were distributed in the range of CHLA from 0.26 to 6.02 mg/m<sup>3</sup> (Fig. 3B). The suitable ranges ( $SI>0.6$ ) for Loliginidae, Octopodidae, Sepiidae and Sepiolidae were respectively 0.80~1.28 mg/m<sup>3</sup>, 1.78~2.17 mg/m<sup>3</sup>, 0.80~1.30 mg/m<sup>3</sup> and 0.75~1.41 mg/m<sup>3</sup> (Fig. 3B). The highest SI values for the mentioned four cephalopod taxa were respectively 1.04 mg/m<sup>3</sup>, 1.97 mg/m<sup>3</sup>, 1.05 mg/m<sup>3</sup> and 1.07 mg/m<sup>3</sup> (Fig. 3B). Cephalopod also preferred to concentrate in narrower CHLA ranges in autumn than those in spring.

## HSI model analysis and validation

According to the HSI maps of different cephalopods (Fig. 4), they had the similar distribution pattern with highly suitable habitat in the area of 122°~124°E, 29.5°~31°N in spring (Fig. 4A). The HSI value of the habitat of Octopodidae was smaller than that of other taxa (Fig. 4A). The highly suitable habitats for the four cephalopod taxa in autumn were concentrated in the same area to that in spring (Fig. 4B).

Octopodidae still presented weaker suitability with a smaller HSI value than other taxa (Fig. 4B). The area of suitable habitats for the four cephalopod taxa in autumn was obviously smaller than that in spring (Fig. 4). However, the abundance of cephalopod in autumn was much more than that in spring (Fig. 4). Meanwhile, the suitable habitats for the four cephalopod taxa in two seasons showed an identical distribution pattern from coast to northeast (Fig. 4). The high-density areas were highly overlapped with the suitable habitat ( $HSI>0.6$ ) for each taxon in both spring and autumn (Fig. 4).

Furthermore, the accumulative individual density proportions of different taxa in highly suitable habitat ( $HSI>0.6$ ) respectively ranged from 76.84–97.39% in spring and from 73.88–92.23% in autumn (Fig. 5A). Additionally, the predicted HSI distribution map also largely overlapped the individual density data obtained in the survey in 2019 (Fig. 6). The AMM-based HSI models for four cephalopod taxa had a good prediction effect with the accuracy above 70% and could be used to predict the cephalopod distribution and abundance.

## Different types of habitats for cephalopod taxa

The isoline distributions of different types of habitats were different among four taxa (Fig. 7). Habitat isoline of Sepiolidae showed the widest coverage with the outmost edge (black line) (Fig. 7), followed by

Sepiidae (yellow line), Loliginidae (red line) and Octopodidae (blue line). All the above isoline distributions existed in each type of habitat and season (Fig. 7). The isolines in the marginal zone were similar among taxa in both spring and autumn and mainly concentrated in the area of 28°N northward and 121°E eastward (Fig. 7). Compared with the marginal zone, the common zone approached the inshore zone and had a smaller area in spring and the common zone for each taxon overlapped the marginal zone for other taxa (Fig. 7). In autumn, the isolines of common and marginal zones had nearly the same distribution pattern (Fig. 7). Octopodidae had the smallest core zone compared with other three taxa, displaying the similar distribution pattern in spring (Fig. 7). The core zone showed the shrinking trend in autumn (Fig. 7).

## Discussion

Key environmental factors significantly influence the habitat distribution of cephalopods and SST is an important environmental factor in the life history of individuals (Pecl et al., 2008; Sanchez et al., 2008; Xu et al., 2016; Jin et al., 2020). Each cephalopod taxa presented the similar environmental preference as well as little difference for the HSI models based on SST and Chl-a (Figs. 2 and 3). The cephalopod species composition in the coast of Zhejiang Province (western coast of ECS) was mainly composed of neritic species (Song et al., 2009). This kind of cephalopod species or group has the characteristics of seasonal migration behavior. They live at the offshore wintering ground in winter, migrate westward to the coast for feeding and reproductive activity at feeding ground and spawning ground in spring and summer, move to the offshore of wintering ground and finally complete their life cycle (Chen et al., 2019). Their preference SST and Chl-a were consistent with the previous results (Song et al., 2008, 2009; Ho, 2016). Cephalopods in the east coast of ECS share a similar oceanographic environment with shallow water zone (10-40 m), although different kinds of cephalopods prefer to inhabit in different layers of water. Cuttlefish, octopus and bobtail squid spend their most lifetime in bottom water, whereas loligo squid moves between surface at daytime and bottom at night (Jin et al., 2020). Thus, it is reasonable to analyze their habitat distribution based on surface environmental factors.

In the ECS, the northward Taiwan current converges with freshwater from Yangtze River to form the complicated current front in Yangtze estuary. Highly nutritional water easily becomes the fishing ground attracting a large number of fishery species and the physical oceanography also drives the migration of marine animals (Song et al., 2018). In addition, all the habitat data highly depended on the sampling stations during the survey. This may explain the similar habitat distribution pattern among different cephalopods in this study. However, according to the prediction results based on HSI model, the habitat distribution pattern varied with cephalopod taxon (Fig. 4). As the dominant species of Loliginidae in this study, *Uroteuthis edulis* is mainly distributed in the south of 30°N in the edge of the continental shelf (Song et al., 2018) with the migration pattern from southwestern inshore to the northeastern offshore (Li et al., 2021). The other two main species, *Uroteuthis duvauceli* and *Loliolus beka*, were mainly concentrated in the area of southward of 29°N along the coast (Song et al., 2018). Octopus (family Octopodidae), including *Octopus minor* and *Octopus sinensis*, is typical benthic species with the weaker movement ability compared with other cephalopod species. Additionally, the bottom sediment is also an important factor that influences the octopus habitat (Hermosilla et al., 2011). Therefore, the suitable

habitat of octopus was concentrated in the north part (around 30°N) in spring in this study, but the suitable habitat (HSI>0.6) did not exist in autumn (Fig. 4). The species in Sepiidae, especially *Sepiella maindroni*, had the moderate movement ability and preyed on crustacea as benthic habitant (Wu et al., 2010). The suitable habitat of cuttlefish had obvious seasonal changes from the southwest (121°E -122°E, 28°N-29°N) in spring to the offshore zone in the north (123°E -125°E, 30°N) (Fig. 4). This seasonal change was also in accordance with the migration characteristics of cuttlefish in ECS (Pang et al., 2018). As a cephalopod taxon with a small size and a large abundance, bobtail squid (Sepiolidae) is widely distributed in the Yellow Sea (YS) and ECS (Jin et al., 2020). Bobtail squid also plays an important role in coast water (Rodrigues et al., 2011). Thus, the habitat distribution areas of between Sepiidae and Sepiolidae were highly overlapped in autumn (Fig. 4B) due to their potential predator and prey relationship (Cheng and Zhu, 1997).

The habitat with a high individual density accounted for a large proportion (>70%) of suitable habitats (HSI>0.6) for the four cephalopod taxa in both seasons (Fig. 5). However, the abundance of cephalopod varied with taxon and season (Fig. 4). Among the four taxa, Sepiolidae species had the most dominant individual abundance and Sepiidae species had the least individual abundance in this study (Fig. 4). Bobtail squid has a relatively large abundance and exists as prey in the marine ecosystems of the YS and ECS (Yu et al., 2009; Jin et al., 2020). The other three cephalopod taxa (Loliginidae, Octopodidae and Sepiidae) are mainly commercial species with a large size. In the previous surveys, the main taxa of the swimming animal community are fish and crustacean (crab and shrimp), which account for more than 80 % of the total individuals in spring (Chang et al., 2012). Therefore, the cephalopods had only less than 10% of the total individuals in each tow in spring, which did not have enough space to accommodate cephalopods with a large size. This situation would change during season shift. In later autumn, the fish migrates to the offshore area for wintering and leave enough space and food for the cephalopod's living (Yoneda et al., 2002; Kawazu et al., 2015). Therefore, the proportion of cephalopod individuals increased during the survey. Importantly, cephalopod migrated eastward and still inhabited shallow water, thus presenting a long and band-shaped habitat distribution with poor habitat (HSI<0.2) in the coastal area in autumn (Fig. 4B) compared with that in spring (Fig. 4A).

According to the comparison analysis results of the three types of spatial distribution zones of cephalopods in neritic water of east coastal areas of ECS, we can understand the distribution difference among different cephalopod taxa. Sepiidae had the largest distribution area among cephalopods (Fig. 5). The above phenomenon also existed in three types of isoline HSI in both seasons (Fig. 5). Sepiidae may have stronger adaptation and be less conquered by the environmental change. Octopodidae had a small range among cephalopods in three types of habitats (Fig. 5). The heavily oceanographic change might change the suitable habitat. The change was strongly correlated with its habitation characteristics, including inhabiting the seabed and short-distance migration from deep subtidal zone to the shoal for spawning (Song et al., 2009). In terms of the suitable habitat (HSI>0.6), the isoline extended to the southeast coast of Zhejiang Province (26°N) in spring, but shrank to 26°N in the north without any coastal distribution in autumn (Fig. 5). Temperature and food abundance are the main reasons that control the suitable isoline shift (Yu et al., 2016, 2019). The differentiation of habitat isolines among

different cephalopod taxa is a kind of self-adaptation and can avoid species competition in the limited space (Passarella and Hopkins, 1991).

## Conclusions

The habitat suitability index (HSI) model was used to describe the distribution pattern of four main cephalopod taxa (Loliginidae, Octopodidae, Sepiidae, and Sepiolidae) based on the survey in the coast of Zhejiang Province. The similar distribution pattern was observed among different cephalopod taxa. The isoline of habitat suitability also indicated the different distribution areas among various cephalopod taxa. Temperature and food availability were the two main factors influencing the spatial distribution of cephalopods. As multiple species inhabit in the coast of Zhejiang Province, the influence of species competition on the habitat distribution of cephalopods will be considered in the future.

## Declarations

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**Author contribution:** FC contributed to the conception, data analyses and manuscript writing; GW contributed to the conception and figure drawing; NL contributed significantly to data analyses and modelling; ZF contributed to the manuscript conception, writing and revising, especially some constructive discussions, also supported the finance; HZ helped perform the analysis and manuscript revising; YZ provided some important literatures and revised the manuscript; RJ helped the modelling process and manuscript revising. All authors read and approved the final manuscript.

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## Tables

**Table 1.** Proportions of total catch and occurrence proportion of each cephalopod species in the coast of Zhejiang Province during the survey from 2014 to 2019.

Families	Genera	Species	Proportions of the total catch	Occurrence proportion in all stations
Loliginidae	<i>Uroteuthis</i>	<i>Uroteuthis edulis</i>	88.0%	95%
		<i>Uroteuthis duvauceli</i>	10.0%	20%
		<i>Uroteuthis chinensis</i>	1.0%	2%
		others	1.0%	28%
Octopodidae	<i>Amphioctopus</i>	<i>Amphioctopus fangsiao</i>	10.0%	30%
		<i>Amphioctopus ovulum</i>	15.0%	38%
	<i>Octopus</i>	<i>Octopus sinensis</i>	4.0%	27%
		<i>Octopus minor</i>	70.0%	97%
	others	1.0%	14%	
Sepiidae	<i>Sepia</i>	<i>Sepia esculenta</i>	30.0%	64%
		<i>Sepiella maindroni</i>	65.0%	78%
		<i>Sepia kobeensis</i>	2.0%	8%
		others	3.0%	37%
Sepiolidae	<i>Sepiola</i>	<i>Sepiola birostrata</i>	97.0%	99%
		<i>Euprymna morsei</i>	1.5%	5%
	<i>Euprymna berryi</i>	1.5%	5%	

**Table.2** Suitability index (SI) models of cephalopods in the inshore area in Zhejiang Province.

Seasons	Environmental variable	Taxa	Suitability	R <sup>2</sup>	P	RMSE
Spring	SST	Loliginidae		0.926	<0.01	0.091
		Octopodidae		0.933	<0.01	0.108
		Sepiidae		0.994	<0.01	0.027
		Sepiolidae		0.910	<0.01	0.188
	CHLA	Loliginidae		0.908	<0.01	0.117
		Octopodidae		0.976	<0.01	0.110
		Sepiidae		0.932	<0.01	0.159
		Sepiolidae		0.915	<0.01	0.120
Autumn	SST	Loliginidae		0.993	<0.01	0.036
		Octopodidae		0.995	<0.01	0.028
		Sepiidae		0.959	<0.01	0.085
		Sepiolidae		0.977	<0.01	0.062
	CHLA	Loliginidae		0.924	<0.01	0.085
		Octopodidae		0.941	<0.01	0.077
		Sepiidae		0.924	<0.01	0.122
		Sepiolidae		0.905	<0.01	0.103

## Figures

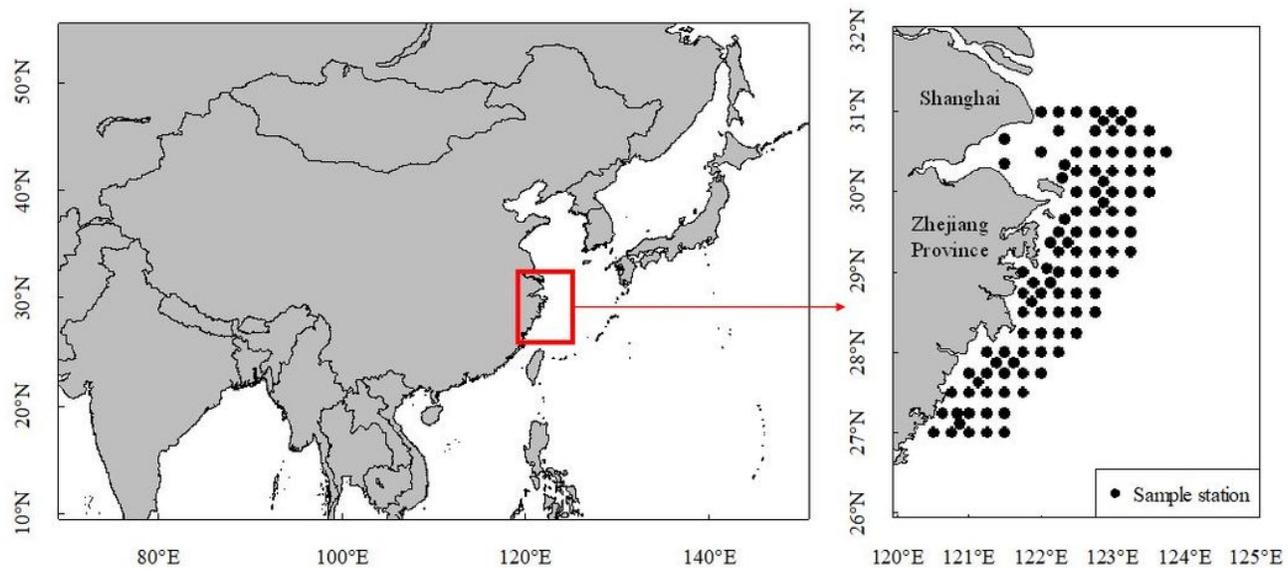
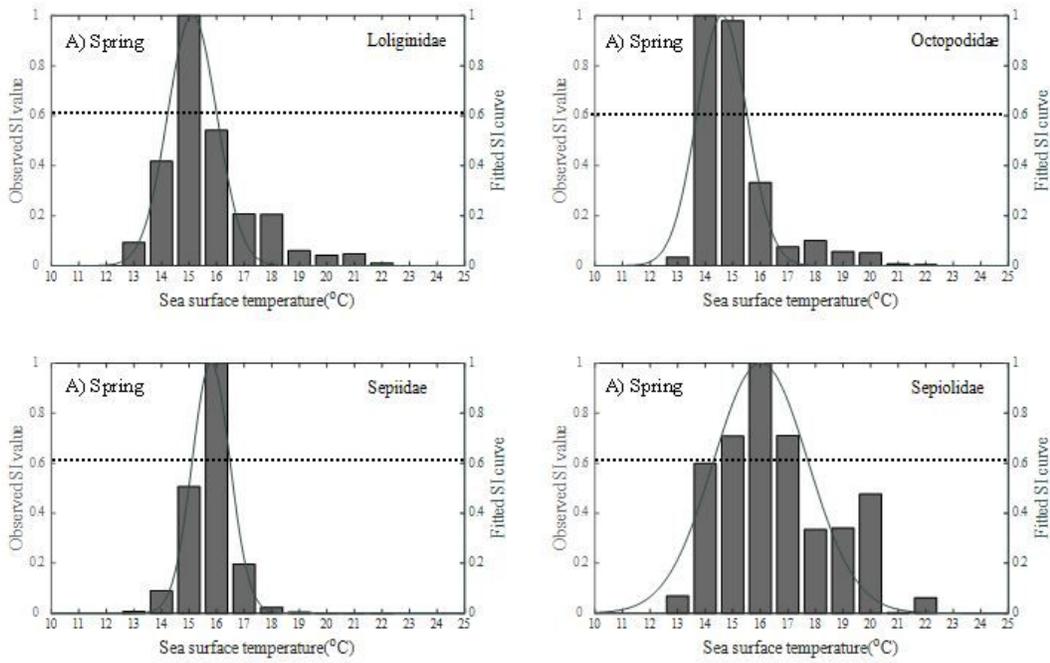


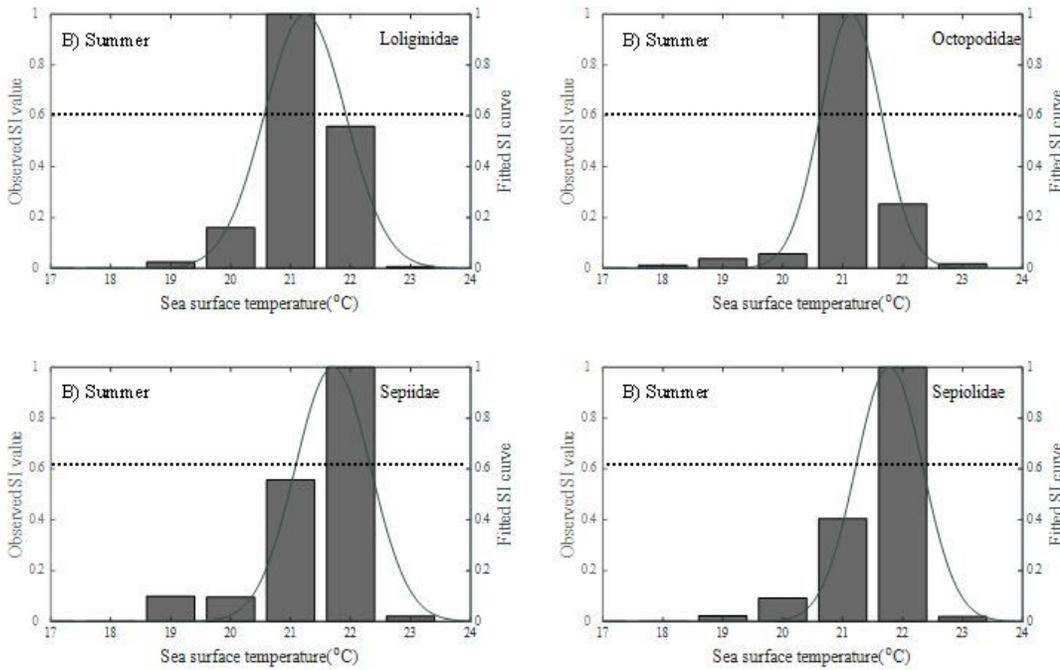
Fig. 1

**Figure 1**

Survey area and station in the inshore area of Zhejiang Province in this study.



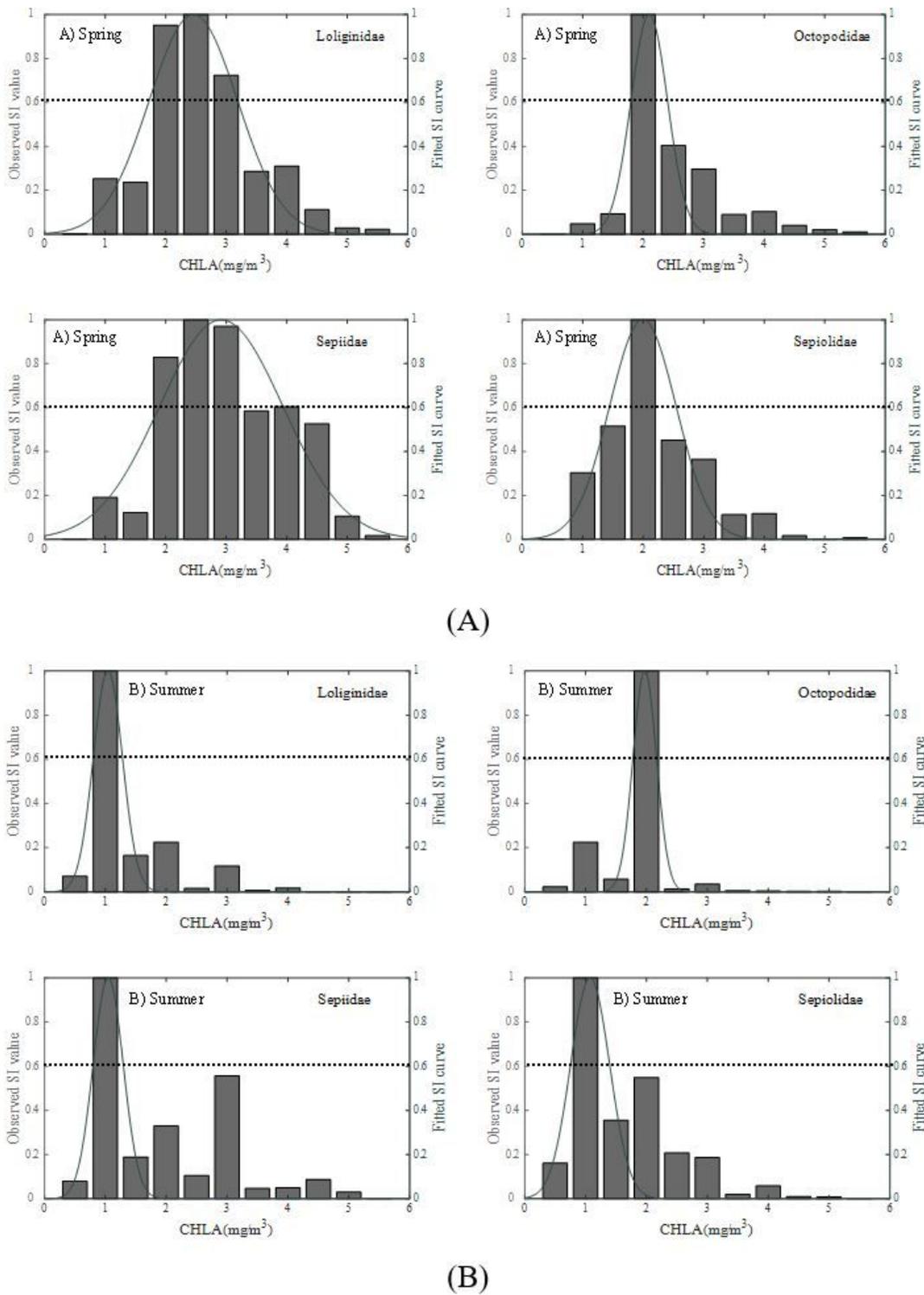
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(B)

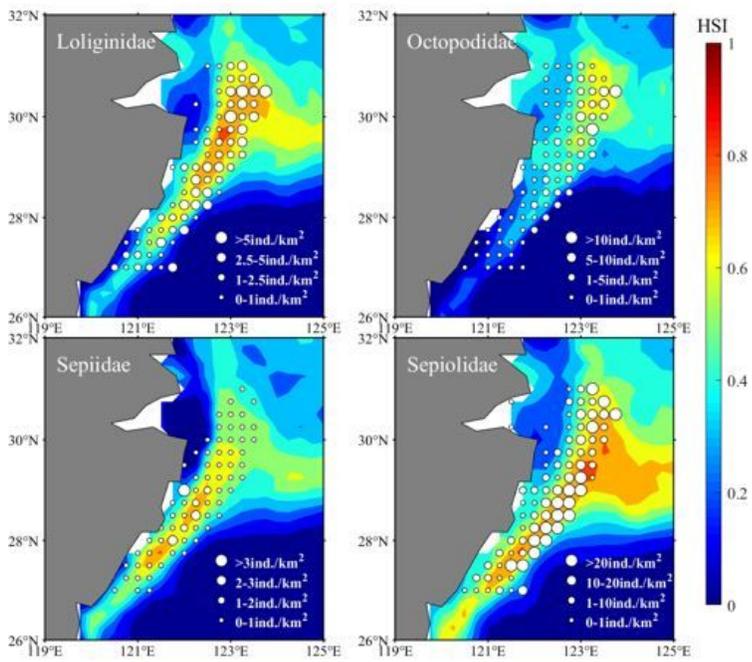
**Figure 2**

Suitability index (SI) curves inferred from the relationship between individual density of cephalopods in the inshore area of Zhejiang Province and sea surface temperature (SST) in spring (A) and autumn (B).

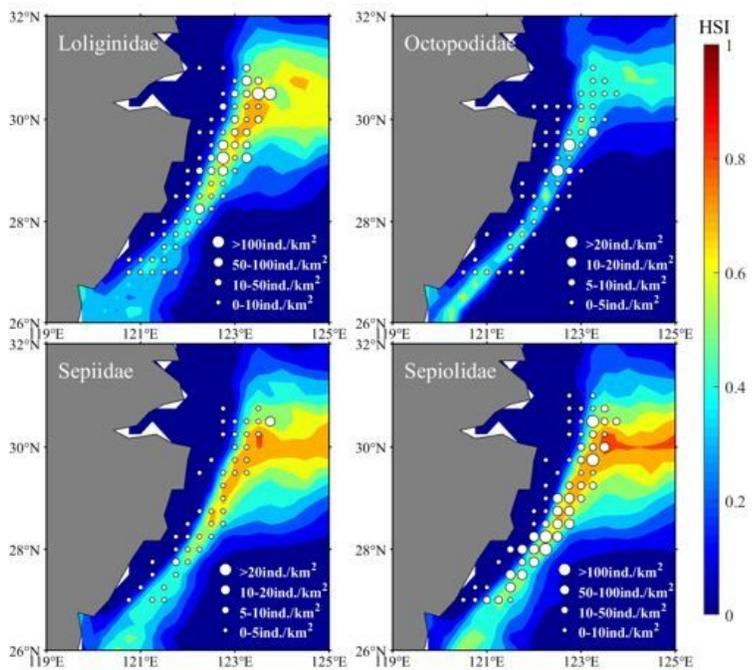


**Figure 3**

Suitability index (SI) curves inferred from the relationship between individual density of cephalopods in the inshore area of Zhejiang Province and chlorophyll-a concentration (CHLA) in spring (A) and autumn (B).



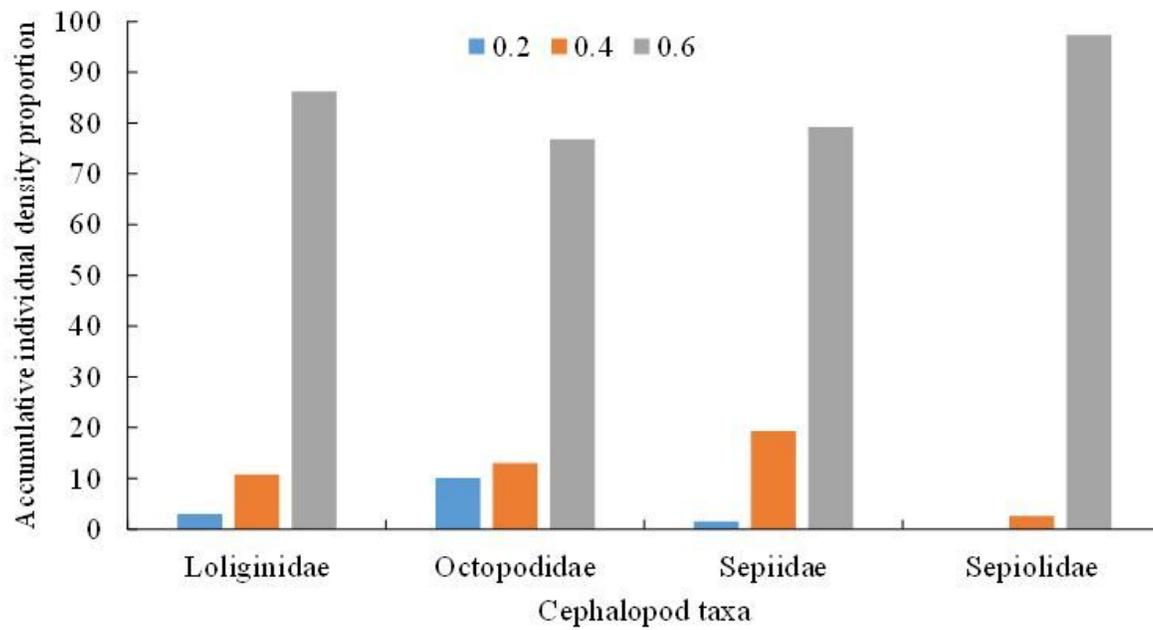
(A)



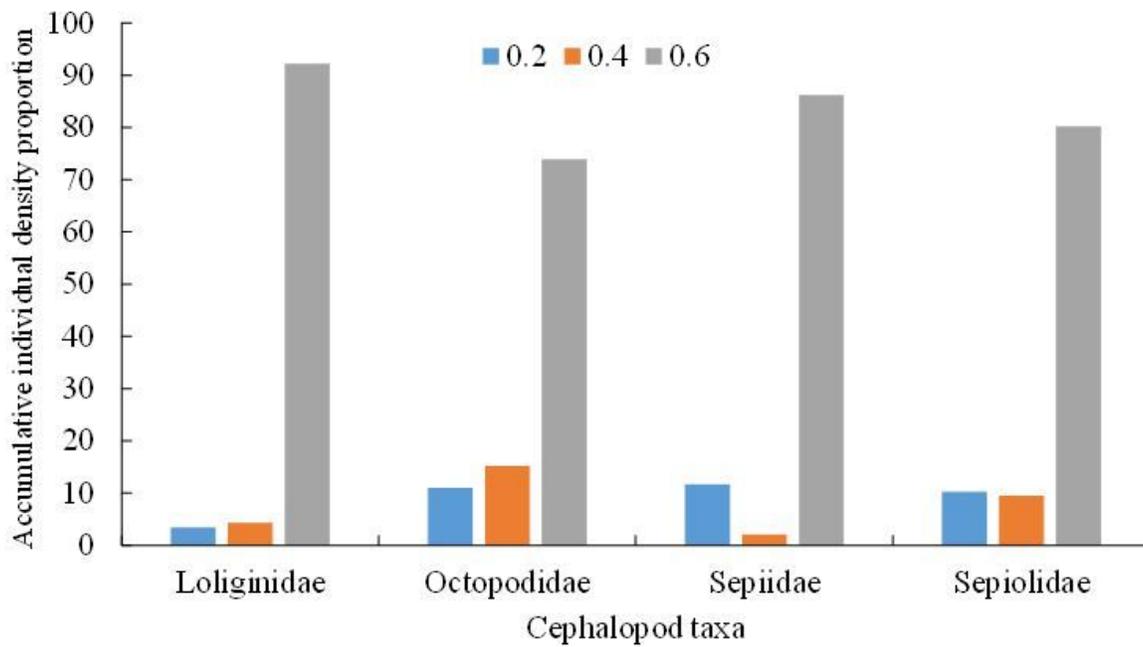
(B)

**Figure 4**

Distribution of HSI and individual density of cephalopods in the inshore area of Zhejiang Province in spring (A) and autumn (B) from 2014 to 2018.



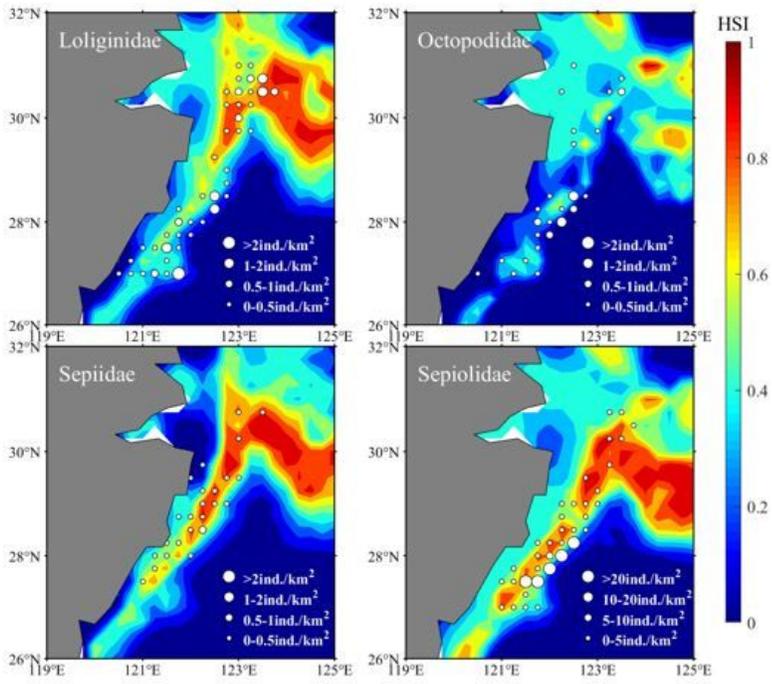
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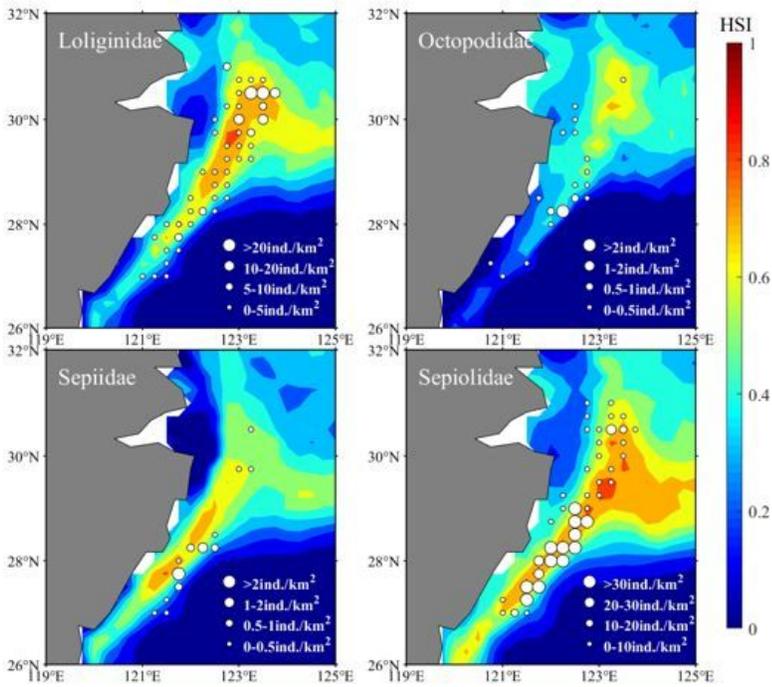
(B)

**Figure 5**

Relationship between HSI and individual density of cephalopods in the offshore area of Zhejiang Province in spring (A) and autumn (B) from 2014 to 2018.



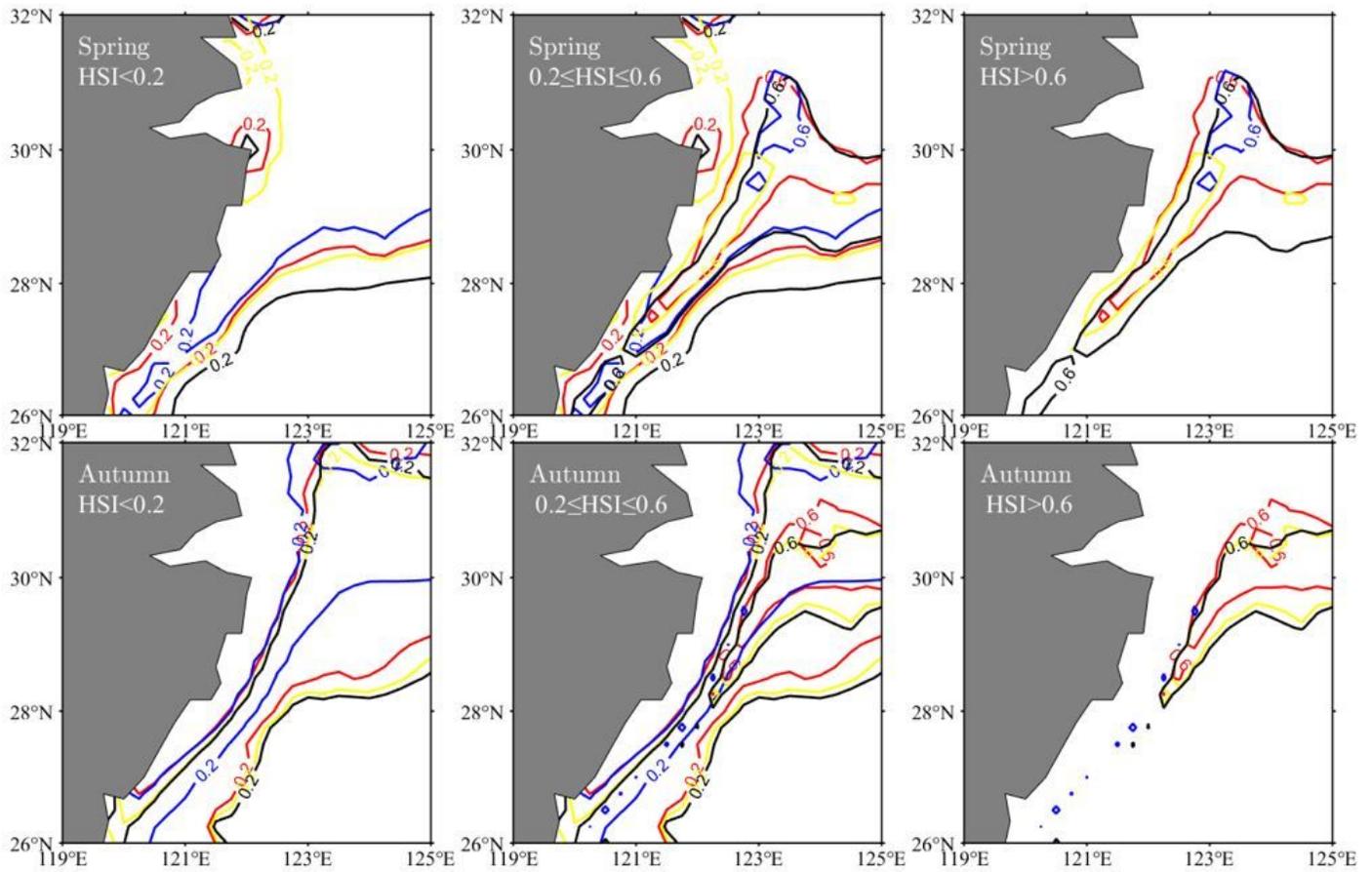
(A)



(B)

**Figure 6**

Distribution of HSI and individual density of cephalopods in the offshore area of Zhejiang Province in spring (A) and autumn (B) in 2019.



**Figure 7**

Isolines and comparison of cephalopods the inshore area of Zhejiang Province in spring and autumn.  
 Note: The red line is the contours of Loliginidae HSI; the blue line is the contours of Octopodidae HSI; the yellow line is the contours of Sepiidae HSI; the black line is the contours of Sepiolidae HSI.