

Article

Environmental Effects on the Spatiotemporal Variability of Fish Larvae in the Western Guangdong Waters, China

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Abstract: Spawning grounds occupy an important position in the survival and reproduction of aquatic life, which plays an important role in the replenishment of fishery resources, especially in the China coasts where fishery resources are depleting. This study investigated environmental effects on the spatiotemporal variability of fish larvae in the western Guangdong waters (WGWs), on the basis of generalized additive models (GAMs) and center of gravity (CoG). Satellite data including sea surface salinity (SSS), sea surface temperature (SST), and in situ observations for fish larvae from April to June in 2014–2015 were used. Results showed that 40.3% of the total variation in fish larvae density was explained. SST, SSS, and depth showed positive effects in 23–24 °C and 27–30 °C, 24–32 PSU, and 0–60 m, and showed negative effects in 24–27 °C, 32–34.2 PSU, 60–80 m. Based on the stepwise GAMs, the most important factor was month, with a contribution of 10.6%, followed by longitude, offshore distance, depth, and latitude, with contributions of 7.0%, 7.0%, 6.3%, 4.2%, 3.9%, and 1.3%, respectively. Fish larvae CoG shifted northward by 0.6° N and eastwards by 0.13° E from April to June. The distribution of fish larvae in the WGWs was affected by complex submarine topography in the Qiongzhou Strait, coastal upwelling in the WGWs, and runoff from the Pearl River.

Keywords: fish larvae; environmental effects; spatiotemporal variability; generalized additive model; western Guangdong waters



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1. Introduction

The western Guangdong waters (WGWs), extending from the west of Pearl River Estuary (PRE) to the northeast of Hainan Island, is rich in fish resources and critical to the spawning, feeding, breeding, and migration of many commercial fishes [1]. As an important place to the survival and reproduction of aquatic lives, the WGWs plays an important role in the replenishment of fish resources [2]. The early life history of fish is mainly divided into three stages: the embryonic stage, the larval stage, and the juvenile stage. The strength of this generation and the abundance of fish resources depend on the early replenishment quantity and survival rate [3,4]. The larval stage, which is the most vulnerable yet shortest period in the life history of fish, is a transitional period during which the larvae undergo prominent changes in morphology, physiology, and ecology. The survival and quantity of larvae are the basis for the replenishment of fish stocks and their sustainable utilization [5,6]. In the marine ecosystem, larvae are the major prey and important consumer of secondary productivity [7]. Research on larvae is essential and fundamental to the study of fish population dynamics and marine ecology. Studies have shown that there is a strong link between the natural and predatory mortality of larvae

and the marine environment [8–10]. The successful recruitment of larvae require the sense acuity of temperate fish larvae and their behavioral response to the estuarine cues present in coastal areas [11], and it might control their dispersion in coastal areas according to their larval stage [12]. The relative numerical values of fish classes exhibit great fluctuations from year to year, and there are three prominent features that attract chief consideration: birth rate, age distribution, and migration [13].

The relationship between fish resources and marine environment is complex, characterized by nonlinearity and nonadditivity [14]. Moreover, the results differ greatly under different observation scales [15,16]. The generalized additive models (GAMs), which is an additive model proposed by Hastie et al. [17], can deal with the nonlinear relationship between dependent variables and multiple independent variables [18]. As it can be used to evaluate the influence and importance of spatiotemporal and environmental factors on fish resources, it is widely used in the relationship between fish resources and environmental factors [19,20]. In this study, we assumed that the spatiotemporal distribution of fish larvae in the WGWs was affected by local habitat (sea surface temperature (SST), sea surface salinity (SSS), depth, and distance). Based on satellite and in situ observations, the quantitative relationship between fish larvae and marine environments were analyzed. The specific aims of this work were to (1) characterize the spatiotemporal distribution characteristics of fish larvae in the WGWs and (2) determine the quantitative relationship between fish larvae and marine environments. These can enhance our understanding of the early replenishment mechanism and the habitat requirements of the fish population in the WGWs, and can provide a reference for the restoration and protection of the spawning grounds in the South China Sea.

2. Materials and Methods

2.1. Fish Larvae Data

The fish larvae data in the WGWs came from the survey of spawning grounds in 2014–2015 (April to June). The study area was located within 19.78°–21.73° N, 110.43°–112.73° E (Figure 1). Fish larvae were sampled by macroplankton nets with hauling speed 1.5 n mile/h and preserved in 5% formaldehyde solution. The fish larvae were identified by their morphological characteristics [21]. In this study, the number of survey data was 289. Major species of fish larvae identified were *Sardinella aurita*, *Nemipterus virgatus*, *Anchoviella commersonii*, *Upeneus bensasi*, and Carangidae (Table 1). The proportion of major larvae density to total density was 53.2%, 10.4%, 8.5%, 8.0%, and 6.0%, respectively. Fish larvae were grouped by $0.25^\circ \times 0.25^\circ$ grid cells. The unit of fish larvae density was $10^{-3} \text{ ind m}^{-3}$. The statistics covered fishing trips, survey hours, longitude, latitude, and fish larvae density. The collection and analysis of fish larvae were based on the specifications for oceanographic survey [22].

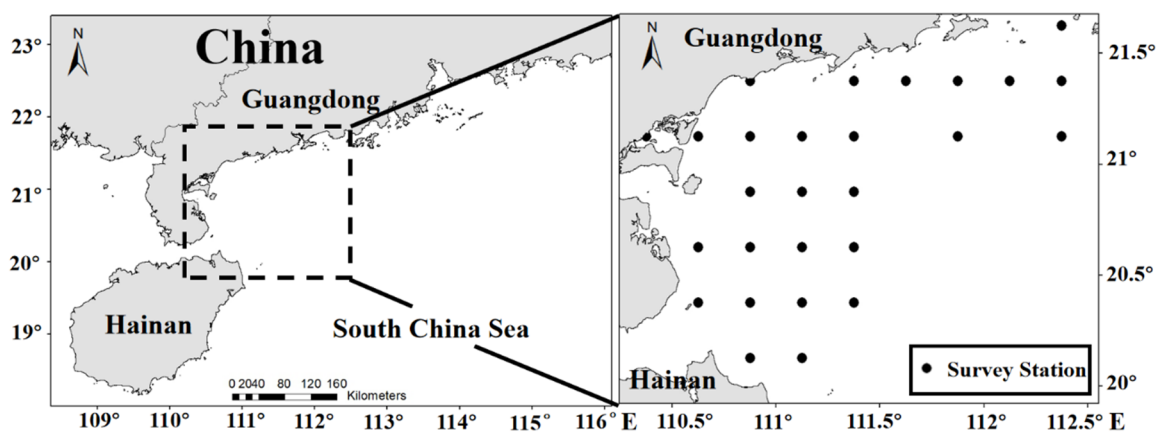


Figure 1. Research area and survey stations. Dotted box shows the extraction range of satellite data.

Table 1. Major catch species and their proportion.

Species/Families	Survey Month	Proportion
<i>Sardinella aurita</i>	Apr/May/Jun	53.2%
<i>Nemipterus virgatus</i>	Apr/May/Jun	10.4%
<i>Anchoviella commersonii</i>	Apr/May/Jun	8.5%
<i>Upeneus bensasi</i>	Apr/May/Jun	8.0%
Carangidae	Apr/May/Jun	6.0%

2.2. Environmental and Geographic Data

Satellite remote sensing data included sea surface temperature (SST), sea surface salinity (SSS), sea surface chlorophyll-a concentration (Chl-a), and digital elevation model (DEM) of the submarine topography. Among them, SST and Chl-a data were from MODIS Aqua satellite data products of NASA (<https://ocancolor.gsfc.nasa.gov/> (accessed on 11 March 2021)), with a temporal resolution of eight days and a spatial resolution of four kilometers. SSS data came from the Global Ocean Physical Reanalysis Product data of the Copernicus Marine Environment Management Service (CMEMS; <http://marine.copernicus.eu> (accessed on 11 March 2021)), with a temporal resolution in months and a spatial resolution of $1/12^\circ \times 1/12^\circ$. The DEM data were from Google Earth elevation data, with the elevation in 18 levels and a spatial resolution of 8.85 m.

MATLAB software was used to extract the remote sensing data of SST, Chl-a, and SSS in the study area. The total number of SST, Chl-a, and SSS data was 289. Invalid values were discarded and the data were monthly averaged. The remote sensing data were interpolated by ordinary kriging using ArcGIS 10.3 software [23,24] to plot the remote sensing map. ArcGIS10.3 software was used to draw the bathymetry (elevation) and submarine topography slope map [25]. The total number of depth, slope, and distance data was 91.

2.3. GAMs Fitting Procedures

In this study, GAMs was used to analyze fish larvae density and selected factors. The general expression of GAMs was as follows [17]:

$$Y = \alpha + \sum_{j=1}^n f_i(x_j) + \varepsilon \quad (1)$$

where Y is the fish larvae density (10^{-3} ind m^{-3}); x_j , the explanatory variable, that is, the spatiotemporal and environmental factors of each station; α , the intercept that fits for the function; ε , the residual error; $f_i(x_j)$, a one-variable function of the independent variable, which is a spline smoothing function. In this study, the mgcv package in software R was used to construct and test the model [26,27]. To determine the expression form of GAM, the stepwise method was used to select variables that have significant influence on the model.

2.4. Model Test

The stepwise method of Akaike information criterion (AIC) was used to test the fitting degree of the model. The smaller the value, the better the fitting effect of the model [28]. Generalized cross-validation (GCV) was used to evaluate predictor variables of the model. The smaller the value, the better the modeling ability [29,30]. F-test and chi-square test were used to evaluate the significance of each factor and the nonlinear contribution of nonparametric effects [29]. The calculation of AIC follows [28]:

$$AIC = \theta + 2df\varphi \quad (2)$$

where θ is the deviation; df is the effective degree of freedom, controlling the smoothness of the curve [31]; and φ is the variance.

2.5. Center of Gravity of Fish Larvae Density

The center of gravity (CoG) method was used to analyze the spatiotemporal variability of fish larvae [32]. The formula for calculating the CoG of fish larvae density follows:

$$X = \frac{\sum_{i=1}^K (C_i \times X_i)}{\sum_{i=1}^K C_i}$$

$$Y = \frac{\sum_{i=1}^K (C_i \times Y_i)}{\sum_{i=1}^K C_i} \quad (3)$$

where X and Y are the longitude and latitude of the CoG; C_i is the yield of the fishing area i ; X_i and Y_i are the central longitude and latitude of the fishing area i ; and K is the total number of fishing areas.

3. Results

3.1. GAMs Analysis

Variables that impose significant influence on the model were selected based on AIC value and significance (p -value) by the stepwise method [33]. F-test and chi-square test were used to evaluate the influence of predictor variables on the interpretation of the model [34]. According to variation inflation factor (VIF) analysis, impact factors (month, longitude, SSS, depth, latitude, distance, and SST) showed no strong collinearity ($VIF < 10$) [35] (Table 2). Therefore, the spatiotemporal and environmental variables selected by the model included month (Month), longitude (Lon), sea surface salinity (SSS), water depth (Depth), latitude (Lat), offshore distance (Distance) and sea surface temperature (SST). The expression of GAM obtained follows:

$$\log(Y + 1) = s(\text{Month}) + s(\text{Lon}) + s(\text{SSS}) + s(\text{Depth}) + s(\text{Lat}) + s(\text{Distance}) + s(\text{SST}) \quad (4)$$

GAM was used to fit the cumulative explanatory bias of spatiotemporal and environmental factors on fish larvae density (Table 2). The cumulative explanatory bias of GAM on fish larvae density was 40.3% with an R^2 of 0.343.

Table 2. Variation inflation factor (VIF) analysis.

Factors	VIF
Month	7.611
SSS	3.092
SST	7.664
Lon	2.996
Distance	1.449
Depth	2.579
Lat	4.379

In GAMs, the contribution of selected factors represents the influence degree of each factor on fish larvae density (Table 3). Among them, Month was the most important factor affecting fish larvae density, with a contribution of 10.6%, followed by SSS, SST, Lon, Distance, and Depth, with contributions of 7.0%, 7.0%, 6.3%, 4.2%, and 3.9%, respectively; Lat had the least impact on fish larvae density, with a contribution of 1.3%. F-test showed that Month, Lon, SSS, Depth, SST, and Distance were significantly correlated with fish larvae density ($p < 0.05$), while Lat was insignificantly correlated with fish larvae density ($p > 0.05$). Chi-square test showed the nonparametric smoothing effect of predictive variables. According to chi-square test, Month, Lon, SSS, and SST had the best nonparametric smoothing effect, and the nonparametric smoothing effect of Distance and Lat was lower than that of other variables.

Table 3. Deviance analysis for the general additive models (GAMs) fitted to the fish larvae density.

Model Factors	Residual Deviance	Adjusted R ²	AIC	GCV	Deviance Explained (%)
Log(Y + 1) = NULL	1701.12	0.00	1336.43	5.93	0.0
Log(Y + 1) = s(Month)	1521.02	0.10	1307.99	5.37	10.6
Log(Y + 1) = s(Month) + s(Lon)	1414.34	0.16	1290.70	5.06	16.9
Log(Y + 1) = s(Month) + s(Lon) + s(SSS)	1294.96	0.22	1271.01	4.73	23.9
Log(Y + 1) = s(Month) + s(Lon) + s(SSS) + s(Depth)	1227.56	0.25	1260.75	4.57	27.8
Log(Y + 1) = s(Month) + s(Lon) + s(SSS) + s(Depth) + s(Lat)	1206.33	0.26	1260.38	4.56	28.9
Log(Y + 1) = s(Month) + s(Lon) + s(SSS) + s(Depth) + s(Lat) + s(Distance)	1135.03	0.29	1258.24	4.55	33.3
Log(Y + 1) = s(Month) + s(Lon) + s(SSS) + s(Depth) + s(Lat) + s(Distance) + s(SST)	1016.41	0.34	1239.84	4.28	40.3

Akaike information criterion (AIC) was applied to check the fitting degree of the model. The smaller the value, the better the model fit. Generalized cross-validation (GCV) was used to assess predictor variables of the model. The smaller the value, the better the generalization ability.

The contribution of time factor (Month) was the highest, which was 10.6% in GAMs (Table 4). From April to June, as the month increased, fish larvae density first increased and then decreased (Figure 2a). Fish larvae density increased gradually from April to May and reached a peak in May, and then decreased sharply from May to June.

Table 4. Contributions of the selected variables in GAMs.

Variables	d.f.	Contribution (%)	Pr(F)	Pr(chisq)
Month	1.57	10.6	1.116×10^{-7} ***	4.401×10^{-8} ***
SSS	2.88	7.0	1.654×10^{-5} ***	9.811×10^{-6} ***
SST	6.14	7.0	0.0001469 ***	8.203×10^{-5} ***
Lon	1.95	6.3	3.16×10^{-5} ***	2.148×10^{-5} ***
Distance	2.95	4.2	0.0325 *	0.02894 *
Depth	2.64	3.9	0.001677 **	0.001399 **
Lat	2.64	1.3	0.2094	0.2122

***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. SSS, sea surface salinity; SST, sea surface temperature; Lon, Longitude; Lat, Latitude; d.f., degrees of freedom; Pr(F), p -value from an ANOVA F-ratio test; Pr(chisq), a type of score test to evaluate the nonlinear contribution of nonparametric effects.

The contribution of spatial factors (Lon, Lat, Depth, Distance) was 15.7%, of which the contribution of Lon is 6.3% in GAMs (Table 4). In the range of 110.5° to 112.0° E, fish larvae density remained at a high level. In the range of 112.0° to 113.75° E, fish larvae density decreased sharply with the increase of longitude (Figure 2b). The contribution of Lat was 1.3% in GAMs (Table 4). In the range of 19.8° to 21° N, fish larvae density remained at a high level, the confidence interval decreased and the confidence level increased. In the range of 21°–22° N, with the increase of latitude, fish larvae density decreased slowly, the confidence interval increased and the confidence level decreased (Figure 2e). The contribution of depth was 3.9% (Table 4). In the range of 40–70 m, fish larvae density decreased with the increase of depth. In the range of 0–40 m, fish larvae density was stable at a higher level, the confidence interval decreased and the confidence level increased (Figure 2d). The contribution of distance was 4.2% (Table 4). In the range of 0–30 km, fish larvae density increased with the increase of offshore distance, the confidence interval decreased and the confidence level increased. In the range of 30–60 km, fish larvae density decreased with the increase of offshore distance; the confidence interval increased and the confidence level decreased (Figure 2f).

Environmental factors (SST, SSS) contributed 14% of which SST contributed 7% in GAMs (Table 4). In the range of 23–24 °C and 27–30 °C, fish larvae density increased with the increase of SST. In the range of 24–26 °C and 30–32.5 °C, fish larvae density

decreased with the increase of SST. As SST increased, the confidence interval increased and the confidence level decreased (Figure 2g). The contribution of SSS was 7% (Table 4). In the range of 24–32 PSU, fish larvae density increased with the increase of SSS, the confidence interval decreased and the confidence level increased; and in the range of 32–34 PSU, fish larvae density decreased with the increase of SSS, the confidence interval decreased and the confidence level increased (Figure 2c). The fish larvae were mainly distributed in the waters of 110.5–112.0° E and 19.8–21° N.

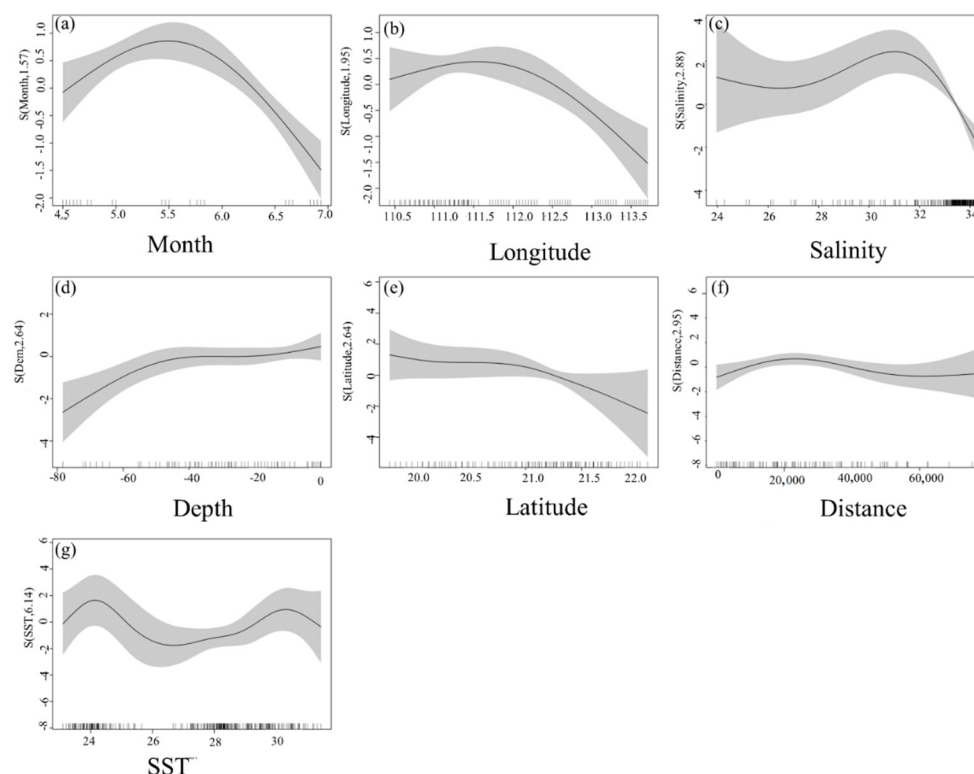


Figure 2. GAMs analysis on the impact of spatiotemporal and environmental factors on fish larvae density: (a) month, (b) longitude, (c) sea surface salinity, (d) water depth, (e) latitude, (f) offshore distance, (g) sea surface temperature. Shaded area shows the 95% confidence interval. Dotted line on the x-axis indicates the density of data point

3.2. Relationship between Spatiotemporal Variability of Fish Larvae, SST, and SSS

Spatiotemporal distribution of fish larvae and SST in the WGWs (Figure 3) showed that from April to June, with the increase of SST, fish larvae density first increased and then decreased, and the maximum density appeared in May. SST was 22–24 °C in April, 24–27 °C in May, and 27–30 °C in June. High fish larvae density was mainly distributed in the area with SST being 23–24 °C (Figure 3a) in April, in the sea area with SST being 26–27 °C (Figure 3b) in May, and in the area with SST being 28–30 °C (Figure 3c) in June. Fish larvae density in June was lower than that in April and May, and was mainly distributed in the sea area with SST higher than 28 °C (Figure 3c).

From April to June, SSS in the WGWs increased gradually, and waters with high SSS moved to the northwest (Figure 3d–f). High fish larvae density was concentrated in waters with SSS of 33.2–33.5 PSU (Figure 3d), in the area with SSS of 33.7–33.8 PSU (Figure 3e) in May, and in the area with SSS of 33.9–34.2 PSU (Figure 3f) in June.

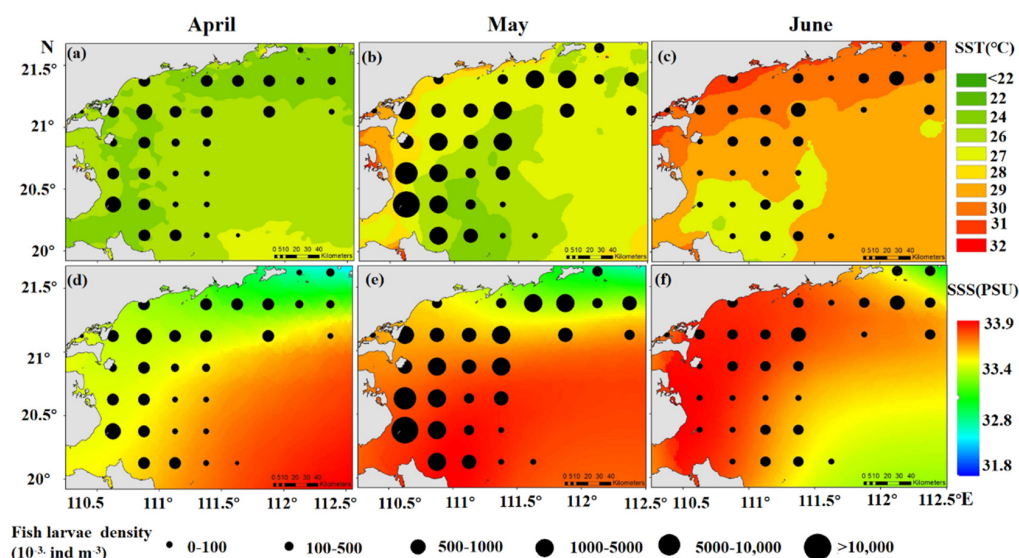


Figure 3. Relationship between spatiotemporal variability of fish larvae, SST, and SSS: (a) fish larvae density and SST in April, (b) fish larvae density and SST in May, (c) fish larvae density and SST in June, (d) fish larvae density and SSS in April, (e) fish larvae density and SSS in May, (f) fish larvae density and SSS in June.

3.3. Relationship between Spatiotemporal Variability of Fish Larvae, Depth and Slope

Spatiotemporal distribution of fish larvae density, water depth, and slope in the WGWs (Figure 4) showed that in general, fish larvae density in coastal waters was higher than that in offshore waters (Figure 4a). Fish larvae density was high in shallow waters (5–40 m) and low in deep waters (40–80 m, Figure 4a). It reached the peak at a depth of about 40 m ($7462.73 \times 10^{-3} \text{ ind m}^{-3}$); (Figure 4a). Qiongzhou Strait and the area east of Hainan Island have large depth and slope (submarine topography slope $> 1^\circ$), due to which fish larvae density in this area is generally higher than that in other areas (Figure 4b).

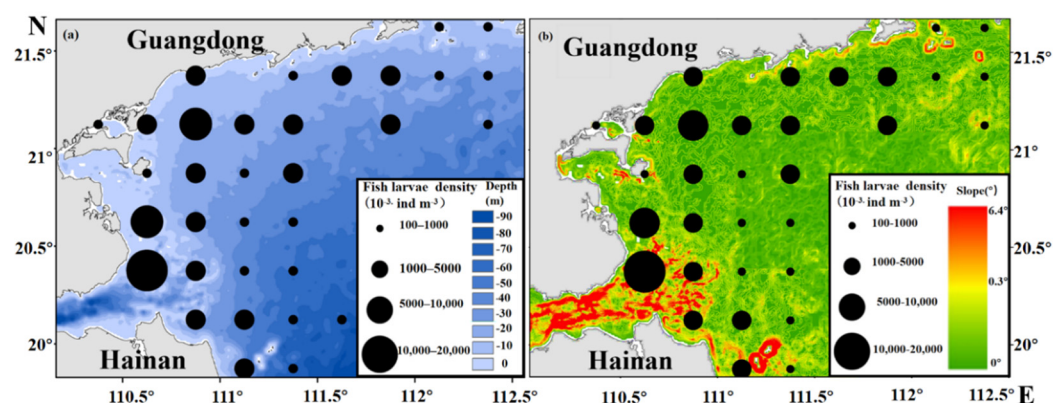


Figure 4. Relationship between the fish larvae density and spatial factors in the western Guangdong waters (WGWs): (a) distribution of fish larvae density and depth, (b) distribution of fish larvae density and slope.

3.4. Spatiotemporal Variability of Center of Gravity (CoG) of Fish Larvae Density

From April to June, the CoG of fish larvae density in the WGWs first moved to the southwest, then to the northeast (Figure 5). The CoG of fish larvae density was near the PRE (111.30° E , 21.03° N) in April, moved to the southwest (111.15° E , 20.76° N) in May, and to the eastern Guangdong waters (111.90° E , 21.16° N) in June. From April to May, the CoG of fish larvae density moved 0.15° N to the south and 0.27° E to the west. From May to June, the CoG of fish larvae density moved 0.75° N to the north and 0.4° E to the East.

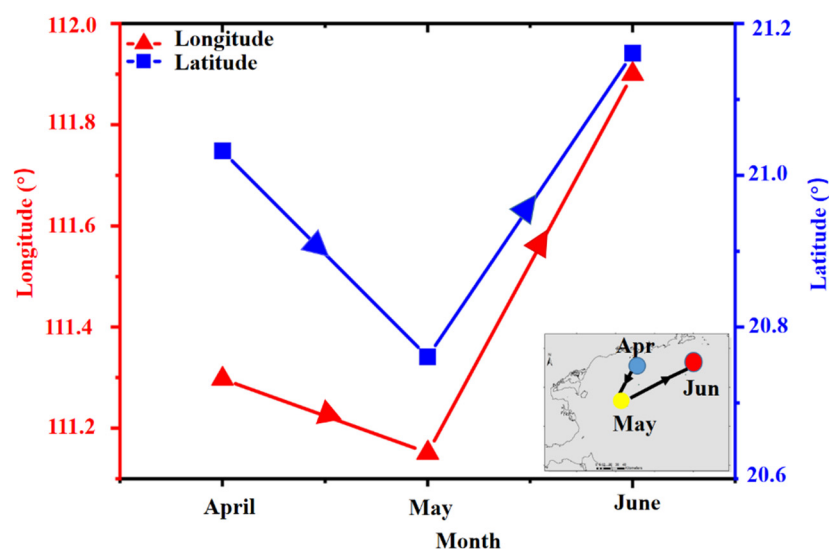


Figure 5. Variation of center of gravity (CoG) of fish larvae density in the WGWs.

4. Discussion

The habitat of fish larvae in the WGWs was connected with local marine ecosystem including SST, SSS, Chl-a, depth, slope, etc. In addition, macrogeographical attributes, seasonal upwelling, and runoff from the Pearl River influenced the habitat.

4.1. Effects of SST and SSS on Fish Larvae

GAM is an effective tool for analyzing the quantitative relationship between response variables and predictive factors, and can intuitively evaluate the effect and importance of habitat factors on organisms. In the WGWs, the spatiotemporal distribution of fish eggs was subject to coastal current, cyclonic circulation, and South China Sea warm current, and was related to salinity, water temperature, water depth, and other factors [36]. In the East China Sea, fish larvae were determined by water temperature, as the larvae mainly live in the warm side of the temperature front [37]. The distribution of *Gadus macrocephalus* larvae in the Yellow Sea was closely related to bottom water temperature, bottom sediment, and bottom salinity [38]. The present study showed that SST in GAM also played a great role on fish larvae density (with a contribution of 7%, Table 4). Major commercial fishes in the WGWs are *Trichiurus haumela*, Carangidae, and *Nemipteras virgatus* [39,40]. Among them, *Trichiurus haumela* had a relatively concentrated spawning ground in the WGWs, and its fish larvae were mainly distributed in the waters with SST being 25–28 °C [41]. In the WGWs, fish larvae were mainly distributed in the waters with SST being 22–32 °C, and the most suitable SST for fish larvae was 24–30 °C. There were two peaks at 24 °C and 30 °C, which might be attributed to the characteristics of the multispecies fishery in the WGWs [42]. Water temperature was one of the key factors affecting embryonic development and larval growth. Studies showed that temperature affected larva metabolism [43], movement [44], gene expression [45], and embryo survival rate and deformity rate [46], and further affected the growth, feeding, quantity, and distribution of larvae [47]. The larvae density decreased gradually in June in the WGWs. On the one hand, the average water temperature in June was high (>28 °C), which lead to the mortality of some eggs that could not survive higher temperature [48], resulting in the decrease of larvae quantity. On the other hand, high water temperature in June was a stress factor for the growth of some larvae [47], as high water temperature accelerated their metabolism expenditure [49], and insufficient endogenous nutrition plus the poor ability to obtain exogenous nutrition seriously affected larvae growth and development, which caused the low survival rate of larva. In the East China Sea, the number of larvae in summer (June) was lower than that in spring, which was different from the results of this study. This might be related to the higher water temperature in the East China Sea. The water temperature in the WGWs in June

(28–32 °C) was higher than that in the East China Sea (20.73–27.13 °C) [37]. A previous study showed that larvae density decreased when the temperature was too low or too high [50]. The larvae had their suitable temperature range. Due to their poor adaptability to the environment and stress response, irregular change of temperature would cause the death of larvae [51].

SSS explained 7% of the variation in fish larvae density (Table 4). Salinity was one of the important environmental factors affecting the larvae. A survey on the spawning grounds in the Yangtze Estuary [52,53] showed that salinity was an important factor deciding larvae distribution. It affected not only the distribution of larvae, but also their metamorphosis process [9,44]. If the salinity exceeded the tolerance range of larvae, the deformity rate of larvae would increase and the vitality of fry would decrease [54]. The fish larvae were mainly distributed in the waters with SSS being 31.5–34.5 PSU in the WGWs, and the most suitable salinity range for fish larvae was 33.0–33.8 PSU (Figure 2c). This may be due to the strong swimming ability and salt tolerance of fish larvae during the preflexion period. In addition, with the development of individuals and the improvement of organs, the salt tolerance of individuals will be stronger [55]. In the WGWs, the suitable salinity for the spawning ground of *Trichiurus haumelais* was 33.0–34.5 PSU [41], and the suitable salinity was 33.94–34.92 PSU for *Nemipterus virgatus* [56], which was consistent with this study. Previous study showed that when the salinity was too high, larvae density decreased sharply; when the salinity was low, larvae density tended to increase [57]. On the one hand, a low salinity level was in line with the osmotic pressure of body fluids of some fish, which was conducive to the growth and development of larvae, and as a result, the survival rate of larvae was high [58,59]. On the other hand, large quantities of fish larvae in the postflexion period appeared in the waters with lower salinity [60]. In contrast, a high salinity level would accelerate the metabolism velocity of larvae, which was unfavorable for the survival of larvae [61]. Salinity could affect the metamorphosis of larvae, also. When the salinity increased, the metamorphosis of larvae was accelerated, causing the reduction in larvae quantity. In addition, the salinity gradient also affected larvae density to a certain degree. Northeast of the WGWs, the salinity gradient was high due to dilution by the Pearl River. In this study, the salinity played a great role on fish larvae density (Table 4). On the contrary, in Laizhou Bay of Bohai Sea, the salinity gradient of the water body was low, because of which the salinity had little effect on larvae density [62].

4.2. Effects of Depth, Slope, and Offshore Distance on Fish Larvae

GAM analysis showed that depth explained 3.9% of the variation in fish larvae density (Table 4). In the WGWs, fish larvae density decreased with the increase of depth. Different fish required different spawning depth [63], and the depth affected the spatial distribution of spawning grounds [64]. The spawning grounds of *Trichiurus haumela* are mainly distributed in the waters with a depth of 40–100 m, especially 40–70 m [41]. In spring and summer, the catch of Carangidae was high in waters with a depth ≤ 60 m [65], while most *Nemipterus virgatus* inhabited at the sediment bottom of 60–80 m [54]. The deep-water *Nemipterus virgatus* in the northern shelf area of the South China Sea is located in the coastal area of Guangdong with a water depth of 60–150 m [66]. The fish larvae of *Anchoviella commersonii* were mainly distributed in the waters less than 20 m in the Yangtze River Estuary [67]. The fish larvae of *Sardinella aurita* were mainly distributed around 10 m near the Yangjiang Nuclear Plant [68]. Studies showed that the spawning grounds in the coastal waters of the North Sea are mainly distributed in the middle and shallow waters (<40 m) [64,69], which is similar to the distribution of fish larvae (≤ 40 m) in the WGWs (Figure 2d). This may be connected with shallow water and local topography, which are favorable for the existence of warm but chlorophyll-rich water, providing a favorable environment for the development of larvae [70]. In addition, changes in the fish behavior at different stages of early development also play an important role in influencing the abundance of fish larvae in the nearshore waters [71]. In the postflexion of fish larvae and juvenile stage, the fins are formed and the swimming ability of the fish larvae is gradually

strengthened, and a surprising capacity for swimming endurance [72], which would lead to higher recruitment [73]. Therefore, they could choose the habitat and gradually move to the shallow waters with abundant food [74]. Slope reflects the macrogeographical attribute of the habitat environment [75,76]. Qiongzhou Strait has a deep slope and large current velocity [77], because of which the fish larvae density is high in this area. On the one hand, the complex topography of Qiongzhou Strait reduced the velocity of flow, which is favorable for larvae to gather in the area [78]. On the other hand, the complex submarine topography provides an ideal environment for spawning [79]. The results showed that fish larvae density was the highest when the depth was less than 40 m and the slope is $>0.3^\circ$, indicating that the fish population tended to spawn in shallow waters with a small slope.

The offshore distance explained 4.2% of the variation in fish larvae density (Table 4). In this study, survey stations were distributed 0–60 km offshore, and the fish larvae density first increased and then decreased with the increase of the offshore distance (Figure 2f). The larvae density in offshore waters was lower than that in coastal waters, partly because some fish in the WGWs migrated to the coastal area for breeding migration, forming spawning grounds in the coastal area [37].

4.3. Effects of Seasonal Upwelling on Fish Larvae

There is a local cyclonic circulation in the eastern waters of Leizhou Peninsula ($20^\circ20'N$ – $21^\circ10'N$, $110^\circ50'E$ – $112^\circ00'E$) [80–82]. The cyclonic circulation exists all year, and is strong in summer and weak in winter. In summer, the bottom water rises and forms an upwelling (cold eddy). There is a Qiongdong upwelling in the shallow coastal waters in the west of the WGWs ($18^\circ30'N$ – $20^\circ00'N$, $111^\circ30'E$) at a depth of 30 m from the shore of Qiongdong [83]. The upwelling appears during April and September each year, and is the strongest from June to July [84]. High fish larvae density appeared in these two upwelling areas (Figure 3). The upwelling brought high nutrients to the surface, replenishing nutritive salts in the seawater near the spawning grounds. As larvae could move on a small scale, their apparent vertical movement day and night and active feeding behavior enabled them to stay in the area with food organisms [85]. In addition, the larvae moving along the current tended to gather in the waters near the eddy area [86]. Hence, they tended to gather where there was an upwelling. From April to May, the CoG of fish larvae density shifted to the southwest of the WGWs and showed a tendency for gathering in the upwelling area (Figure 5), which might be related to the southwestern Qiongdong upwelling. In June, the CoG of fish larvae density shifted to the northeast and the fish larvae density in the upwelling region decreased. This might be related with fish larvae drifting northeasterly with the west coast current of Guangdong Province, leading to the decrease of fish larvae density in the upwelling region in June [81].

5. Conclusions

This study analyzed for the first time the response of fish larvae to marine environments in the WGWs, using satellite and survey data. The most important factor affecting fish larvae density was the month, followed by SST, SSS, longitude, distance, depth, and latitude. The fish larvae in WGWs were mainly distributed in areas where SST is 24 – 30°C , SSS is 33.2 – 34.2 PSU, and depth is 5 – 50 m. This was caused by the submarine topography, the current field in the WGWs, and the Pearl River runoff. In this study, only SST, SSS, Chl-a, and other environmental factors for which data could be obtained by satellite remote sensing were selected. In the follow-up study, climatic anomaly, catching intensity, and other parameters will be considered to improve the accuracy of the model and provide reference for more accurate prediction of spawning grounds.

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