



# Species Composition and Assemblages of Ichthyoplankton in Sansha Bay, Fujian Province, China

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Jiang Y, Lin B-a, He H-y, Ding G-m, Yan L-t, Zhang G, Liu M and Zheng L-m (2021) Species Composition and Assemblages of Ichthyoplankton in Sansha Bay, Fujian Province, China. Front. Mar. Sci. 8:758089. doi: 10.3389/fmars.2021.758089 Sansha Bay (26.40-27.00°N, 119.50-120.20°E) is a typical semi-enclosed bay, located in northern Fujian Province, China, and adjacent to the East China Sea. The ichthyoplankton species composition and assemblage structure were investigated based on monthly sampling at 25 stations in April-September 2019, covering the important spring and summer spawning seasons in the region. Sampling was conducted in the first 3-5 days of the full moon or new moon phases using a standard plankton net through horizontal and vertical tows during daytime. In total, 25,819 ichthyoplankton samples were collected, of which 25,449 samples (i.e., 24,757 eggs and 692 larvae) were from horizontal tows. For horizontal tow samples, the ichthyoplankton were classified into 58 taxa in 15 orders and 23 families with a combination of external morphology and DNA barcoding analyses, from pelagic to demersal and benthic species. The dominant order was the Gobiiformes, including 23 species (39.7% of all species). The dominant taxa, in terms of relative abundance and frequency of occurrence, consisted of commercially important fishes, such as Setipinna tenuifilis (Valenciennes, 1848) (Engraulidae), Epinephelus akaara (Temminck and Schlegel, 1842) (Serraenidae), Collichthys lucidus (Richardson, 1844), Nibea albiflora (Richardson, 1846) (Sciaenidae), Acanthopagrus schlegelii (Bleeker, 1854), and Pagrus major (Temminck and Schlegel, 1843) (Sparidae), accounting for 78.9% of the horizontal tow samples. Low-valued and small-sized fishes, such as Stolephorus commersonnii Lacepède, 1803 (Engraulidae), Solea ovata Richardson, 1846 (Soleidae), Nuchequula nuchalis (Temminck and Schlegel, 1845), and Photopectoralis bindus (Valenciennes, 1835) (Leiognathidae), were also dominant species, accounting for 11.4% of the horizontal tow samples. The ichthyoplankton assemblage was categorized into five different temporal assemblages based on the cluster and nonmetric multidimensional scaling analysis, namely, April, May, June, July, and August-September (ANOSIM, Global R = 0.656, p < 0.01) with the highest density and richness of ichthyoplankton occurred in May. The spatial distribution pattern showed that the high density (ind./m<sup>3</sup>) of ichthyoplankton occurred mainly in S12-S25 in Guanjingyang and along the Dongchong Peninsula coastline into Dongwuyang, while low density occurred mainly in S01-S11 in

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the northwest waters of Sandu Island (ANOVA, F = 8.270, p < 0.05). Temperature, salinity, and chlorophyll *a* were key factors structuring the ichthyoplankton assemblages in Sansha Bay. In addition, this study revealed the changes of the ichthyoplankton composition, density, and spatial distribution in Sansha Bay over the past three decades.

Keywords: abiotic and biotic factors, Chinese waters, DNA barcoding, fish eggs and larvae, spatial and temporal distribution

# INTRODUCTION

Fishes have various life stages, and different developmental stage requires different foods, habitats, and environmental factors (Rijnsdorp et al., 2009; Hamre et al., 2013; Petitgas et al., 2013; Madeira et al., 2020). For example, ripe fishes are sensitive to the hydrological conditions of the spawning grounds, such as current, tide, water temperature, salinity and dissolved oxygen, and prey availability and preference (MacKenzie et al., 1996; Costa et al., 2002). Ichthyoplankton include fish eggs and larvae, belonging to the early life stages. Due to their absence of or weakness on independent swimming capabilities, ichthyoplankton have a drifting nature with currents and tides (Lechner et al., 2016; Downie et al., 2020). Understanding the distribution patterns of different life stages and exploring the abiotic and biotic factors influencing the distribution patterns are crucial for assessing fish recruitment and stock restoration (Costa et al., 2002; Santos et al., 2017). Achieving the sustainability of fishery resources depends highly on the abundance and survival of fish eggs and larvae (Oeberst et al., 2009; Llopiz et al., 2014).

The identification of unambiguous species from fish eggs and larvae is challenging. It is mainly because of the high diversity of species of fishes and the limitation of morphological observation on different stages of eggs and larvae before metamorphosis (Li et al., 2014; Zhang et al., 2015; Hsieh et al., 2016). For example, eggs and larvae of Sciaenidae are difficult to identify to species level through morphological features (Zhang et al., 1985; Zhan et al., 2016), besides the challenges for identification of adult sciaenids (Chu et al., 1963). DNA barcode, which delimits species using a molecular marker (e.g., mitochondrial cytochrome c oxidase subunit I gene, COI), has been widely applied to facilitate the identification in all stages from egg to adult of fishes (Ward et al., 2005; Ko et al., 2013; Becker et al., 2015; Harada et al., 2015; Hou et al., 2021a). In recent studies, Kerr et al. (2020) successfully identified 564 fish eggs to 89 taxa collected from northwestern Cuba and across the Florida Straits using DNA barcode. Hou et al. (2021a) successfully identified 931 fish eggs and 229 larvae to 75 taxa collected from the Pearl River Estuary of China using a DNA barcode. However, identifying ichthyoplankton correctly through DNA barcoding relies highly on a powerful and accurate database. It is necessary, but still challenging, to build up a DNA barcoding library in a specific area.

The transitional region between the East China Sea and the South China Sea through the Taiwan Strait, Fujian Province, has a highly sinuated coastline forming many bays with some typically semi-closed by peninsulas (Yu et al., 1988). In terms of volumes of the marine capture fisheries, Fujian Province ranks third in China, contributing to approximately 15.6% of the national total marine capture volumes or 16.8% of the national total marine fish capture volumes in the past decade, 2010-2019 (MOA, 2010-2018; MARA, 2019). Sansha Bay (26.40-27.00°N, 119.50-120.20°E) is located in Fujian Province (Figure 1A) and connects with the East China Sea through the narrow Dongchong Channel of about 3 km in width (Figure 1B). This typical semi-enclosed bay is well-known because it was one of the 12 traditional spawning grounds along Chinese coastal waters for the large yellow croaker Larimichthys crocea (Richardson, 1846) (Sciaenidae) before the 1990s, a commercially important species that formed large spawning aggregations (Chu, 1985; Liu and Sadovy de Mitcheson, 2008). With the mariculture and industrial development since the 1990s, marine pollution has been exacerbated in Sansha Bay (Wang et al., 2019). The current status of Sansha Bay as L. crocea spawning ground function is unclear.

In Sansha Bay, species composition and assemblages of ichthyoplankton, which are essential for the estimation of spawning sites, reproductive seasons, and conservative strategies (Parrish et al., 1981; Bailey and Houde, 1989; Oliveira and Ferreira, 2008), remain insufficient attention. Species composition and temporal and spatial distribution of fish eggs and larvae were investigated only four times (i.e., 1990, 2007, 2008, and 2010) historically, mainly seasonally, and the samples were identified by external morphology only (Dai, 2006; Wang et al., 2010; Shen, 2011; Xu, 2018), which may lead to the missing of certain species and underestimate the diversity of the real species. The results of these previous studies showed that Sansha Bay was important for fish reproduction, and fish egg and larva density (ind./m<sup>3</sup>) were high in spring and summer. Moreover, the ichthyoplankton abundance of traditionally important fishery species showed dramatic declines over years. It merits further monthly and accurate studies with multiple identification methods and a high spatial coverage to evaluate the current status and long-term dynamics of ichthyoplankton assemblages in Sansha Bay.

In this study, we designed 25 stations throughout Sansha Bay for the ichthyoplankton collection. We conducted sampling monthly from April to September in 2019 covering the peak spawning seasons (i.e., spring and summer) mentioned earlier and applied DNA barcoding technique for species identification after external morphology examination, aiming to obtain a relative accurate species composition, to provide detailed characteristics of the ichthyoplankton assemblages, and to analyze the influence of abiotic and biotic variables on the distribution of ichthyoplankton in Sansha Bay. The results can be used to evaluate the current status of this traditional spawning ground and to compare the changes of



ichthyoplankton composition and spatial distribution over the past three decades in Sansha Bay.

# MATERIALS AND METHODS

#### Ichthyoplankton Collection

Ichthyoplankton samples were collected from 25 stations (S01–S25) (26.50–26.85°N, 119.52–120.09°E) in Sansha Bay, Fujian Province of China (**Figure 1B**). The sampling was conducted monthly from April to September 2019 within the first 3-5 days of the full moon or new moon phases during daytime.

The standard plankton net used for horizontal tows is 80 cm in net opening diameter (i.e., 0.5 m<sup>2</sup> net opening area) and 505  $\mu$ m in net mesh size (GB/T 12763.6, 2007). At each station, the net was towed horizontally right below the sea surface with the speed of approximately 2 km for 5–10 min.

The standard plankton net used for vertical tows is 50 cm in net opening diameter (i.e., 0.2 m<sup>2</sup> net opening area) and 505  $\mu$ m in net mesh size (GB/T 12763.6, 2007).

On board, ichthyoplankton samples collected were fixed with the formaldehyde concentration of 5%. The samples were further transferred to 95% ethanol solution within 12 h for the purpose of DNA barcoding.

## **Collection of Abiotic and Biotic Factors**

Sea surface temperature, salinity, dissolved oxygen, and pH were measured using YSI EXO2 Multiparameter Sonde during plankton sampling at each station.

Chlorophyll *a* (Chla) samples were collected and analyzed in the laboratory through fluorospectrophotometry within 24 h. For a sampling of vertical phytoplankton, the standard plankton net used is 37 cm in net opening diameter (i.e., 0.1 m<sup>2</sup> net opening area) and 77  $\mu$ m in net mesh size (GB/T 12763.6, 2007). On board, phytoplankton samples were fixed in Lugol's iodine solution with a concentration of 10%. For a sampling of vertical zooplankton, the standard plankton net used is the same as the vertical ichthyoplankton collection above. On board, zooplankton samples were fixed in the formaldehyde solution with a concentration of 5%.

# Ichthyoplankton and Plankton Identification

In the laboratory, all fish eggs and larvae collected were sorted and pooled under a dissecting microscope (Zeiss Stemi 2000-C, Germany) according to the external morphological features (Zhang et al., 1985; Shao et al., 2001; Wan and Zhang, 2016). For each egg or larva with a specific morphological feature, photo images were collected using the Leica M165FC Fluorescent Stereo Microscope and Canon EOS 600D Digital SLR Camera, and one or more samples were selected for DNA extraction and barcode COI fragment obtaining. Sizes of eggs and larvae were not measured because they were fixed and dehydrated in 95% ethanol solution for at least 2 months before sorting.

Genomic DNA was extracted using the Takara MiniBEST Universal Genomic DNA Extraction Kit Ver. 5.0 according to

manufacturer specifications and further used with no dilution for amplification and sequencing. A PCR was conducted, and the COI fragment was amplified using three universal COI gene primer pairs (i.e., LCO1490–HCO2198, FishF1–FishR1, and FishF2–FishR2) (Folmer et al., 1994; Ward et al., 2005) to obtain the target COI gene fragment (about 630 bp). For each PCR product, sequencing was performed using both corresponding forward and reverse primers that are used for PCR (Sangon Biotech, China).

Raw sequences were assembled using Bioedit 7.2. Assembled sequences of fish eggs and larvae were identified using reference sequences published in GenBank (NCBI)<sup>1</sup> or by the Barcode of Life Data System.<sup>2</sup> To assign a sequence to a species, genus, or family level, we required that the sequence matches with the database by at least 99.60, 91.29, or 85.48%, respectively (Hou et al., 2017). All sequences were further confirmed by ML and NJ phylogenetic trees with sequences from the GenBank and BOLD system using MEGA 6.06 with 1,000 bootstrap pseudo-replications. Categorization of species taxonomy was followed as suggested by Nelson et al. (2016).

Moreover, phytoplankton and zooplankton samples collected were identified based on the external morphology under a microscope (Liu et al., 2020a), following the taxonomic books in the region (Guo, 2003; Lin, 2009; Zhang et al., 2010; Ding, 2013; Slotwinski et al., 2014; Sun et al., 2015).

## **Plankton Calculations**

In the laboratory, the densities of ichthyoplankton (i.e., eggs and larvae) from horizontal tows were standardized:

$$A = N/V$$

where A is the density of ichthyoplankton (ind./m<sup>3</sup>), N is the number of ichthyoplankton (individuals) per plankton net, and V is the seawater volumes filtered into the plankton net (m<sup>3</sup>).

*V* was calculated by a flow meter (HYDRO-BIOS) attached to the center of the plankton net:

$$V = 0.3R \times S$$

where *R* is the number of revolution noted from HYDRO-BIOS, 0.3*R* means that when the flow meter rotates one number, the net moves 0.3 m based on HYDRO-BIOS product manual, and *S* is the net opening area ( $m^2$ ).

The dominant species of ichthyoplankton (i.e., eggs and larvae together) from horizontal tows were determined using the Index of Relative Importance (*IRI*) (Pinkas et al., 1971; Zhu et al., 2002):

$$IRI = N\% \times F\%$$

where *N*% and *F*% are relative abundance and frequency of occurrence of a specific species, respectively. Species with  $IRI \ge 0.02$  were considered to be a dominant species.

The three diversity indices, namely, the Shannon-Wiener diversity index (H'), Pielou's evenness index (J'), and

<sup>&</sup>lt;sup>1</sup>https://blast.ncbi.nlm.nih.gov/Blast.cgi

<sup>&</sup>lt;sup>2</sup>http://www.barcodinglife.org

Margalef's richness index (*d*), were calculated (Margalef, 1958; Shannon and Wiener, 1963; Pielou, 1966) to evaluate the current status of ichthyoplankton in Sansha Bay:

$$H' = -\sum_{i=1}^{s} P_i \ln P_i$$
$$J' = H' / \ln S$$
$$d = (S - 1) / \ln N$$

where *S* is the total number of ichthyoplankton species, *N* is the total number of individuals, and  $P_i$  is the proportion of the number of individuals for a specific ichthyoplankton species to the total number of individuals.

In addition, densities of phytoplankton and zooplankton from vertical tows were also calculated as for ichthyoplankton aforementioned:

$$A = N/V$$

where *A* is the density of phytoplankton (cells/m<sup>3</sup>) or zooplankton (ind./m<sup>3</sup>), *N* is the number of phytoplankton (cells) or zooplankton (individuals) per plankton net, and *V* is the seawater volumes filtered into the plankton net (m<sup>3</sup>).

## **Data Analysis**

We used only data from horizontal tows for further analyses for at least two reasons. First, the number of eggs and larvae and diversity of ichthyoplankton species from horizontal tows were much higher than those of vertical tows in sampling during every month. Second, the depths of sampling stations varied largely from as shallow as 1 m to about 40 m. Therefore, the seawater volumes filtered into the vertical tow nets varied largely that it subsequently influenced the number of eggs and larvae and the diversity of ichthyoplankton species collected. The vertical tow samples were only used for species diversity supplements.

For the data analysis below and specific calculation above (e.g., *IRI*), we combined the number of egg and larva samples together (Zhang et al., 2016; Huang et al., 2017; Hou et al., 2021a). A short hatchery period (i.e., hours to several days) and limited independent swimming capability of larvae were also the considerations for the combination of egg and larva data for analyses (Woynarovich and Horváth, 1984; Pauly and Pullin, 1988; Lechner et al., 2016; Downie et al., 2020).

The one-way ANOVA test was conducted with the IBM SPSS Statistics version 16.0 for revealing the significance of the monthly changes of environmental factors, the diversity indices, the spatial variation of average ichthyoplankton density, and the variation of average species richness among 25 stations; when necessary (ANOVA, p < 0.05, n > 2), a *post hoc* least significant difference (LSD) test was added. The cluster analysis and nonmetric multidimensional scaling (nMDS) based on the Bray-Curtis similarity and square root average density of ichthyoplankton were performed to clarify the temporal and spatial distribution patterns of the assemblages. After the cluster analysis, the tests for identifying the discrimination between

two observed sample clusters (SIMPEROF) and the similarities (ANOSIM) were performed using PRIMER version 6.0 to assess the significance and discrimination between sample clusters (Clarke and Gorley, 2006).

The detrended correspondence analysis (DCA) and canonical correlation analysis (CCA) or redundancy analysis (RDA) were performed using CANOCO version 5.0 to analyze the constrained relationships between environmental factors and ichthyoplankton communities. Before the analysis, DCA was performed to determine a suitable response according to the maximum gradient of length (>4, CCA; 3-4, CCA or RDA; <3, RDA) (Šmilauer and Lepš, 2014). Because the maximum gradient length of DCA was 6.34 (>4), CCA was subsequently selected in this study. Only species that occurred in >10% of the catches, based on all species density, were included in the analysis to reduce the effect of rare species. Data of species density were log (10,000x + 1) transformed to minimize the dominant effect of some species (Clarke et al., 2014). A Monte Carlo permutation test with 999 permutations was performed to confirm the key factors significantly affecting the assemblages ( $p \le 0.05$ ; Arora and Mehra, 2009; Hou et al., 2021a). The variance inflation factor (VIF) was conducted to examine the collinearity between independent environment variables. VIF < 10 indicated that the environmental variables were not collinear and were fit for CCA (Graham, 2003; Huang et al., 2017). The importance of the environmental variables was measured by interset correlation coefficients, when the value of interset correlation coefficients  $\geq$  $\pm 0.4$  variables were regarded conservatively as biologically important (Rakocinski et al., 1996; Ramos et al., 2017).

# RESULTS

## **Abiotic and Biotic Factors**

From April to September 2019, with the significant increase of sea surface temperature (F = 290.20, p < 0.05), salinity also showed an upward trend (F = 36.15, p < 0.05), while dissolved oxygen (F = 168.23, p < 0.05) and pH (F = 283.25, p < 0.05) illustrated a downward trend (**Table 1**).

Chla peaked in July, with significant intermonth variations (F = 22.91, p < 0.05), and the densities of phytoplankton (F = 17.47, p < 0.05) and zooplankton (F = 8.908, p < 0.05) peaked in May and April, respectively (**Table 1**).

## Ichthyoplankton Composition

A total of 25,449 ichthyoplankton samples, including 24,757 fish eggs and 692 larvae, were collected from horizontal tows. A total of 370 ichthyoplankton samples, including 315 eggs and 55 larvae, were collected from vertical tows. The numbers of eggs and larvae from horizontal tows were much higher than those of vertical tows.

According to different morphological features, 619 fish eggs and 192 larvae were selected for photography and further DNA extraction, from which high-quality COI fragments were obtained from 335 fish eggs (54.1%) and 117 larvae (60.9%). In total, 60 taxa were identified, 52 at species level, including 26 from eggs and 43 from larvae (**Supplementary Table 1**).

Factors	Unit	April	Мау	June	July	August	September
Temperature (T)	°C	$17.01 \pm 0.49^{a}$	$19.97 \pm 0.37^{\rm b}$	$23.18 \pm 0.35^{\circ}$	$25.95 \pm 0.45^{\rm d}$	$28.72 \pm 0.57^{\rm e}$	$29.44\pm0.45^{\rm f}$
Salinity (S)		$26.66 \pm 1.75^{a}$	$27.10 \pm 1.66^{a}$	$27.45 \pm 2.02^{a}$	$29.10 \pm 1.65^{b}$	$30.75 \pm 1.38^{\circ}$	$31.52 \pm 1.28^{\circ}$
Dissolved oxygen (DO)	mg/L	$7.68 \pm 0.18^{a}$	$7.27\pm0.25^{\text{b}}$	$6.79 \pm 0.31^{\circ}$	$5.83\pm0.36^{\rm d}$	$5.32 \pm 0.65^{\rm e}$	$5.27\pm0.46^{\rm e}$
рН		$8.11 \pm 0.06^{a}$	$8.13\pm0.05^{\text{a}}$	$7.98 \pm 0.04^{\circ}$	$7.95 \pm 0.06^{\circ}$	$8.05\pm0.10^{\text{b}}$	$7.55\pm0.05^{\rm d}$
Chlorophyll a (Chla)	μg/L	$0.64 \pm 0.63^{a}$	$0.28 \pm 0.12^{a}$	$0.53 \pm 0.39^{a}$	2.21 ± 1.27 <sup>c</sup>	$1.12 \pm 0.68^{b}$	$1.33 \pm 0.67^{b}$
Phytoplankton (Phy)	10 <sup>6</sup> cells/m <sup>3</sup>	$20.31 \pm 7.30^{a}$	$81.92 \pm 60.37^{\circ}$	$9.14 \pm 3.65^{a}$	$7.95 \pm 4.37^{a}$	$42.27 \pm 55.93^{b}$	$11.32 \pm 10.95^{a}$
Zooplankton (Zoo)	ind./m <sup>3</sup>	$80.54 \pm 89.52^{a}$	$45.44\pm34.02^{\rm b}$	$23.12 \pm 22.87^{\circ}$	$17.23 \pm 10.76^{\circ}$	$18.57 \pm 16.36^{\circ}$	$19.71 \pm 15.18^{\circ}$

TABLE 1 Temporal variation in abiotic and biotic factors (mean ± SD, n = 25 stations) from April to September 2019 in Sansha Bay of Fujian Province, China.

Values with different letters (a–f) indicate the significant difference at  $p \le 0.05$  among months, and values with the same letter indicate that the difference was not significant at p > 0.05.

From horizontal tows, 58 taxa were identified from 15 orders, 23 families with 51 taxa at species level; Gobiiformes was the most diverse order, representing 39.7% of all taxa (**Supplementary Table 1** and **Supplementary Figure 1**). Additionally, four larvae were identified at the genus level (i.e., *Pseudogobius* and *Rhinogobius* in Gobiiformes, *Hyporhamphus* in Beloniformes, and *Hippichthys* in Syngnathiformes), and three larvae at the family level (i.e., Gobiidae in Gobiiformes and Blenniidae in Blenniformes).

From vertical tows, 31 taxa were identified from 9 orders, 13 families with 27 at the species level, 3 at the genus level, and 1 at the family level (**Supplementary Table 2**). Among these, 29 taxa were also recorded in horizontal tow samples, and only two species [i.e., *Acentrogobius* sp. and *Lateolabrax japonicus* (Cuvier, 1828)] were only found in vertical tow samples. Eggs and larvae of two alien species, the red drum *Sciaenops ocellatus* (Linnaeus, 1766) (Sciaenidae) in Acanthuriformes and the gilthead seabream *Sparus aurata* (Linnaeus, 1758) (Sparidae) in Spariformes, were collected in horizontal tows, *S. ocellatus* eggs in August and September and *S. aurata* larvae in June (**Supplementary Table 1**). Eggs and larvae of *L. crocea*, a critically endangered species in the IUCN Red List, were collected in April–June in horizontal and vertical tows (**Supplementary Tables 1**, 2).

Ichthyoplankton from Engraulidae (two species), Soleidae (one species), Serranidae (one species), Leiognathidae (two species), Sciaenidae (two species), and Sparidae (two species) were dominant ( $IRI \ge 0.02$ ; **Table 2** and **Supplementary Table 1**), accounting for 90.3% of the horizontal tow samples. The yellow drum *Nibea albiflora* (Richardson, 1846) was dominant in May–September 2019 with a peak of *IRI* in September (IRI = 0.51).

The three diversity indices showed significant differences from April to September (H': F = 10.39, p < 0.05; J': F = 2.54, p < 0.05; d: F = 16.14, p < 0.05; **Figure 2**). The highest H' and d were found in May, while the lowest H' and d were found in September; J' in August was significantly higher than the other months.

# Temporal and Spatial Distribution Pattern of Ichthyoplankton

The ichthyoplankton richness ranged from 11 species (July) to 32 species (May) in horizontal tows (**Supplementary Table 1**). The average density of ichthyoplankton ranged from 0.18 ind./m<sup>3</sup> (August) to 2.10 ind./m<sup>3</sup> (May) (**Figure 3**).

The ichthyoplankton were classified into five representative assemblages in the Bray-Curtis similarity at 36.79% (p = 0.001), namely, April, May, June, July, and August–September (**Figure 4A**). The results of nMDS (**Figure 4B**) are consistent with those of the cluster analysis at the stress value < 0.2,

**TABLE 2** | Dominant ichthyoplankton species ( $IRI \ge 0.02$ ) from April to September2019 in Sansha Bay of Fujian Province, China.

Species	April	Мау	June	July	August	September
Setipinna tenuifilis			0.18	0.27	0.08	
Stolephorus commersonnii					0.05	
Solea ovata		0.14				
Epinephelus akaara			0.04			
Nuchequula nuchalis		0.07				
Photopectoralis bindus					0.27	0.03
Collichthys lucidus		0.03	0.05			
Nibea albiflora		0.48	0.43	0.32	0.04	0.51
Acanthopagrus schlegelii	0.26	0.04		0.02		
Pagrus major	0.38	0.06				



**FIGURE 2** Temporal variation of the three ichthyoplankton diversity indices (mean + standard deviation [SD], n = 25 stations) from April to September 2019 in Sansha Bay. H', Shannon-Wiener diversity index; J', Pielou's evenness index; d, Margalef's richness index. Values with different letters (a–c) indicate the significant difference at  $p \le 0.05$  among months, and values with the same letter indicate that the difference was not significant at p > 0.05.



illustrating the reliability of the results (Clarke et al., 2014). The R-statistic values by ANOSIM revealed the dissimilarity between the five assemblages over time (sample statistic: Global R = 0.656, p = 0.001; **Supplementary Table 3**). The ichthyoplankton assemblages of April, May, June, and July differed significantly from August and September, and no significant difference was found between August and September.

Although the cluster analysis of spatial assemblage was not significant (SIMPEROF, p > 0.05), ichthyoplankton density (total taxa) (**Figure 5**) and richness (**Figure 6**) varied by station and month. The highest density and species richness occurred in May, from May-S22 and May-S01, respectively. High density occurred mainly in S12–S25 in Guanjingyang and along the Dongchong Peninsula coastline (i.e., southeast Sansha Bay) into Dongwuyang (i.e., northeast Sansha Bay) in April–September, except for August, and low density occurred mainly in S01–S11 in northwest waters of Sandu Island in April–September (ANOVA, F = 8.270, p < 0.05). Although the spatial patterns for the species richness were not clear, it showed that around Sandu Island, especially S02, S03, S05, and S06, had a relatively high richness (ANOVA, F = 7.953, p < 0.05) during most of the sampling period.

# Relationship Between Ichthyoplankton Assemblages and Abiotic and Biotic Factors

The variance inflation factor (VIF) test and Monte Carlo permutation test indicated that abiotic factors (i.e., T, S, DO, and pH) and biotic factors (i.e., Chla, Phy, and Zoo) were not collinear (VIF < 10) and contributed significantly to explain ichthyoplankton assemblage structure (p < 0.05; **Table 3**).

The sum of all canonical eigenvalues occupied 18.12% of the sum of all eigenvalues. The cumulative percentage variance of species was 15.79%, and cumulative percentage variance of species environment was 87.12% (**Table 4**). The first two CCA axes (i.e., axes 1 and 2) explained 73.65% of the cumulative

percentage variance of species and 73.67% of the cumulative percentage variance of species environment.

Abiotic and biotic factors explained 18.1% variation in ichthyoplankton assemblages among months (Table 3). The main factors affecting ichthyoplankton assemblages were pH, DO, Phy, and Zoo, which were positively related with the first CCA axis in April and May, and were T, S, and Chla, which were negatively correlated with the first CCA axis while positively related with the second CCA axis in July, August, and September (Figure 7A and Table 3). Correlations between abiotic and biotic factors and the distribution of ichthyoplankton species were depicted in CCA (Figure 7B). Omobranchus punctatus (Opun) showed a close relationship with Chla; Nibea albiflora (Nalb), Boleophthalmus pectinirostris (Bpec), and Setipinna tenuifilis (Sten) were closely associated with S and Chla; and Aulopareia unicolor (Auni), Taenioides anguillaris (Tang), Gobiidae sp.-2 (Gibi2), and Stolephorus niphonius (Scom) showed a positive relationship with T but a negative relationship with pH. Acentrogobius caninus (Acan), Tridentiger barbatus (Tbar), Parachaeturichthys polynema (Ppol), Konosirus punctatus (Kpun) and Tridentiger bifasciatus (Tbif), Pagrus major (Pmaj) and Larimichthys crocea (Lcro) positively related with DO, pH, Phy and Zoo.

# DISCUSSION

# Ichthyoplankton Composition and Variation

We reported the first results combining the external morphology and DNA barcode technique to identify ichthyoplankton samples collected from April to September 2019 in Sansha Bay, which made the species richness increase significantly. In total, 60 taxa were identified from horizontal and vertical tows in this study, significantly higher than previous surveys (23–46 species in 1990–2010) from the same sampling area (**Table 5**). The high ichthyoplankton richness in this study was mainly from Gobiidae (21 species) and contributed to the application of COI gene fragment analysis with the high detection rate at the species level, rising from 39.1 to 74.2% (1990–2010) to more than 87.10% (2019) (**Table 5**).

The development of local or regional fish species COI barcodes library is highly recommended (Hou et al., 2021b). We demonstrated the importance of the accuracy and integrity of COI barcodes database in ichthyoplankton identification following the morphological feature collection. The development of a morphological database combining COI barcodes library of ichthyoplankton is needed for future investigation reference (Hubert et al., 2015; Hou et al., 2021a). In this study, we first preserved the ichthyoplankton samples in 5% neutral formalin and then transferred to 95% ethanol in less than 12 h. High-quality COI gene fragments obtained from eggs and larvae were 54.1 and 60.9%, respectively.

The 60 ichthyoplankton taxa identified in this study inferred the underestimation of the ichthyoplankton diversity in Sansha Bay because many fish larvae have a vertical distribution pattern on a diel basis (Ahlstrom, 1959; Rodríguez et al., 2006; Auth et al., 2007). Although we realized the importance of both day and night





sampling for understanding the ichthyoplankton composition and assemblage, night sampling was not applied mainly for safety considerations. Moreover, adhesive eggs are not able to collect using plankton nets. In the future, sampling methods need to be modified to obtain more ichthyoplankton samples.

The abundance of ichthyoplankton species (proportion of individuals) in Sansha Bay has changed over time. For example, a high abundance was found in the black sea bream *Acanthopagrus schlegelii* (Bleeker, 1854) (22%) and the bighead hairtail

*Trichiurus lepturus* Linnaeus, 1758 (16%) in 1990, changed to Labridae sp. (47.1%) in 2007, to Sciaenidae spp. (80.63%) and Cynoglossidae spp. (14.18%) in 2008, and to Sciaenidae (41.19%), Sparidae (33.67%), and Engraulidae (11.36%) in this study (Dai, 2006; Wang et al., 2010; Shen, 2011). The shift of major ichthyoplankton composition may be driven by intensive fishery pressure, habitats loss, or climate change (Bui et al., 2010; Fodrie et al., 2010; Shen, 2011; McCain et al., 2016; Curran et al., 2021). In contrast, the sampling frequency (monthly





or seasonally), spawning ground, and station setting may also influence the ichthyoplankton composition. The temporal and spatial variation of high ichthyoplankton density was detected from 1990 to 2019 (**Figure 8**) in Sansha Bay.

# Spawning Activities in Sansha Bay

This study confirmed that Sansha Bay is an important area for fish reproduction, for pelagic, demersal, and benthic species, including some commercially important species. One of the most traditionally important fishery species in Sansha Bay was *L. crocea*, a well-known species from spawning and overwintering aggregations in Chinese coastal waters (Liu and Sadovy de Mitcheson, 2008). It was documented that *L. crocea* migrated into Sansha Bay in May and June to spawn through the narrow Dongchong Channel (Chu and Wu, 1985). Eggs and larvae of *L. crocea* were collected in May, June, August, October, and November (Dai, 2006; Shen, 2011; Xu, 2018), confirming the existence of two spawning seasons (spring and autumn) in the region (Liu and Sadovy de Mitcheson, 2008). In this study, eggs and larvae of *L. crocea* were collected in April–June because only spring spawning season was focused (**Supplementary Tables 1, 2**), and mature females and mature males were also

Factors	Explains %	Contribution %	F	P-value	VIF	Axis 1	Axis 2
Temperature (T)	8.6	47.5	12.1	0.002	7.35	-0.9865	0.1135
Salinity (S)	2.0	11.0	5.9	0.002	2.79	-0.5773	0.3198
Dissolved oxygen (DO)	1.1	6.1	9.0	0.002	6.90	0.8229	-0.3384
рН	1.3	7.2	6.0	0.002	2.24	0.6401	-0.0375
Chlorophyll a (Chla)	2.4	13.3	4.7	0.002	1.42	-0.4133	0.8048
Phytoplankton (Phy)	1.5	8.3	2.4	0.004	1.38	0.3291	0.0533
Zooplankton (Zoo)	1.2	6.6	2.5	0.02	1.51	0.2159	-0.2252

TABLE 3 Results of Monte Carlo test of *F*-ratios and the interset correlations of environmental variables with the first two canonical correlation analysis (CCA) axes.

Explains %: the percentage of the total variation explained by the explanatory variable; contribution %: the percentage of the variable contribute to the explanatory power.

TABLE 4 | Canonical correlation analysis relating ichthyoplankton assemblages to abiotic and biotic factors in Sansha Bay of Fujian Province, China.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.5551	0.1818	0.1537	0.1097	6.3351
Species-environment correlations	0.9458	0.7120	0.7086	0.5972	
Cumulative percentage variance of species data	8.76	11.63	14.06	15.79	
Cumulative percentage variance of species-environment relation	48.35	64.18	77.57	87.12	
Sum of all unconstrained eigenvalues					6.3351
Sum of all canonical eigenvalues					1.1482
Sum of all canonical eigenvalues					1.14

caught in April–June by fixed nets in Sansha Bay following the confirmation by gonadal histology (Liu et al., 2020a). It is the first record that *L. crocea* also spawned in April. Further understanding the reproductive dynamic and migration pattern for *L. crocea* in the Sansha Bay will help us assess the stock status of this critically endangered species (Liu et al., 2020b).

Two sciaenid species, namely, the bighead croaker Collichthys lucidus (Richardson, 1844) and N. albiflora, have been of commercial importance in Fujian waters (Chu and Wu, 1985). Juveniles and adults can be caught by fixed nets in Sansha Bay throughout the sampling period of April-September (Liu et al., 2020a). Ichthyoplankton samples (eggs as majority) of C. lucidus and N. albiflora were collected in May, June, and August and in April-September, respectively, with dominant in May and June, and in May-September, respectively (Supplementary Table 1 and Table 2). However, ichthyoplankton of C. lucidus and N. albiflora were not collected in previous studies in 1990, 2007, 2008, and 2010 (Dai, 2006; Wang et al., 2010; Shen, 2011; Xu, 2018). Based on the external morphology identification of these previous studies, it was possible that the eggs and larvae of the two species were grouped as Sciaenidae species. In contrast, the reproductive dynamics of C. lucidus and N. albiflora have not been examined in Sansha Bay; therefore, it is unclear if their reproductive behavior has changed over time. For C. lucidus, the spawning and peak spawning seasons in Pearl River Estuary, approximately 800 km south of Sansha Bay, were December-July and May, respectively (Ou et al., 2012). For N. albiflora, the spawning and peak spawning seasons in Xiangshan Bay (Zhejiang Province), approximately 400 km north of Sansha Bay, were May-July and June-July, respectively (Lin et al., 2013). The variation on spawning seasons of the same species in different geological locations merits further assessments.

In Fujian waters, seabreams (Sparidae) such as *A. schlegelii* and the red seabream *Pagrus major* (Temminck and Schlegel, 1843)

mainly spawned in February–April and October–December, respectively (Chu, 1985). The eggs and larvae of *A. schlegelii* were collected from April to August in Sansha Bay (Wang et al., 2010; Shen, 2011; Xu, 2018; this study), indicating the species has a longer spawning season, extending from spring to summer. For *P. major*, the eggs and larvae were collected in November 1990 (Dai, 2006) and in April and May 2019 (this study) in Sansha Bay, indicating the existence of spring and autumn spawning seasons of the species.

In the East China Sea, the spawning season of *T. lepturus* is March–August, producing pelagic eggs, and the spawning grounds are known offshore of Chinese waters (Chu, 1985; Nakamura and Parin, 1993; Xu and Chen, 2015). However, *T. lepturus* was dominant in ichthyoplankton samples (eggs) in May and August 1990 in Sansha Bay (Dai, 2006), inferring its possible spawning grounds in nearshore and semi-closed bays. It was not collected in 2007, 2008, 2010, and 2019 surveys covering its spawning season in Sansha Bay (Wang et al., 2010; Shen, 2011; Xu, 2018; this study). Nearly 100% of *T. lepturus* collected in Sansha Bay using fixed nets were young juveniles (3.2–46.1 cm total length, TL) in May–September 2019 (Liu et al., 2020a). Although the spawning ground function of *T. lepturus* in the Sansha Bay is still not clear, its nursery ground function is clear.

The Indo-Pacific king mackerel *Scomberomorus guttatus* (Bloch and Schneider, 1801) and the Japanese Spanish mackerel *S. niphonius* are pelagic, forming spawning migrations from deep waters to shallow waters in spring and spawning in May and June in Sansha Bay (Wu, 1985). Ichthyoplankton of *S. guttatus* and *S. niphonius* were collected in June 2010 (Xu, 2018), and in April and May 2019 (this study), confirming the spawning ground function of the Sansha Bay for the two species.

Ichthyoplankton of two alien species were first collected in Sansha Bay in this study; eggs of *S. ocellatus* in August



FIGURE 7 | Canonical correspondence analysis (CCA) diagram for ichthyoplankton assemblages (A) and species (B) with abiotic and biotic factors in Sansha Bay of Fujian Province, China. The abbreviations in panel (B) are species names shown in **Supplementary Table 1**. The dominant species are shown in blue and bold. Sten, *Setipinna tenuifilis*; Scom, *Stolephorus commersonnii*; Sova, *Solea ovata*; Eaka, *Epinephelus akaara*; Nnuc, *Nuchequula nuchalis*;, Pbin, *Photopectoralis bindus*; Cluc, *Collichthys lucidus*; Nalb, *Nibea albiflora*; Asch, *Acanthopagrus schlegelii*; Pmai, *Pagrus major*; T, temperature; S, salinity; DO, dissolved oxygen; Chla, chlorophyll *a*; Phy, phytoplankton; Zoo, zooplankton.

and September 2019, and larvae of *S. aurata* in June 2019 (**Supplementary Table 1**). The two species were introduced into China for mariculture purposes from United States in 1991 and from France in 2001, respectively, and juveniles and adults have dispersed in coastal waters of China (Wang and Ji, 1996; Liu

et al., 1998; Wang et al., 2006; Lin et al., 2020; Zhang, 2020). It is likely that *S. ocellatus* has established reproductive wild stocks in Chinese waters (Lin et al., 2020). Both species are commonly cultured in floating cages in Sansha Bay, and their juveniles (*S. ocellatus*: 35.8 cm TL, n = 1; *S. aurata*: 3.7–31.2 cm TL, n = 9) were collected using the fixed nets in 2019 (Liu et al., 2020a). This study revealed that *S. ocellatus* and *S. aurata* can reproduce and may be able to establish spawning population in Sansha Bay.

# Ichthyoplankton Assemblages

Five main temporal ichthyoplankton assemblages were apparently separately in Sansha Bay. The densities of ichthyoplankton along Dongchong Peninsula coastline into Dongwuyang (S12–S25) were higher than those in the northwest waters of Sandu Island (S01–S11) with the significant high salinity (this study) and high tidal currents speed (Lin et al., 2018), and the dominant species were from Engraulidae [*S. tenuifilis*], Soleidae (*Solea ovata* Richardson, 1846), Serranidae [*Epinephelus akaara* (Temminck and Schlegel, 1842)], Sciaenidae (*N. albiflora* and *C. lucidus*), and Sparidae (*A. schlegelii* and *P. major*), including pelagic, demersal, and benthic species. The results indicated that these species may prefer spawning in waters with high salinity and strong currents, or fish eggs and larvae were dispersed to there by currents.

The spatial distribution patterns of ichthyoplankton varied over the past three decades in Sansha Bay, and three zones can be considered as core areas (Dai, 2006; Wang et al., 2010; Shen, 2011; Xu, 2018; this study; **Figure 8**). First, it is around Sandu Island. The high ichthyoplankton density area was in the north in 1990, then, shifted to the east in the late 2000s, and was not important in 2019. Second, it is in Guanjingyang waters with an extension to the Dongchong mouth. The high ichthyoplankton density was found in 2008, 2010, and 2019. Third, it is in Dongwuyang waters. The high ichthyoplankton density was found in 1990, 2007, 2010, and 2019. Overall, the high ichthyoplankton density areas remain the same in Guanjingyang and Dongwuyang over the past three decades and reduce largely from 1990 in Sandu Island water.

# **Influence of Abiotic and Biotic Factors**

Studies revealed that both abiotic and biotic factors shaped the fish assemblages (including fish reproduction stocks and ichthyoplankton) (Olivar, 1990; Marshall and Elliott, 1998; Pombo et al., 2005; Zhang et al., 2015; Hsieh et al., 2016; Rodriguez, 2019). Temperature and salinity influence fish distribution through the different preferences and tolerances of the species. Temperature is likely to be the dominant factor influencing the variability of migration, spawning, and recruitment (Gibson et al., 1993; Marshall and Elliott, 1998) and the abundance and distribution of phytoplankton, zooplankton, and ichthyoplankton (Siokou-Frangou et al., 1998; Rautio, 2001; Hsieh et al., 2005; Gogoi et al., 2021). In this study, seven abiotic and biotic factors, including T, S, DO, pH, Chla, Phy, and Zoo, significantly structured the ichthyoplankton assemblages in Sansha Bay, and temperature was also the dominant factor and then salinity and Chla.

Fish spawning and nursing behavior could be affected by spatial and temporal distribution of preys (Cushing, 1990).

**TABLE 5** | The interannual variations of the number of species and the average density (ind./m<sup>3</sup>) (mean  $\pm$  SD, n = 4 in 1990 and 2007, n = 2 in 2008, and n = 6 in 2010 and 2019) of fish eggs and larvae throughout the years in Sansha Bay of Fujian Province, China.

Survey year (survey month)	No. of species	Detection rate at species level	Average egg density (ind./m <sup>3</sup> )	Average larva density (ind./m <sup>3</sup> )	Sampling stations	Sampling methods	References
1990 (Feb, May, Aug, and Nov)	26	69.2%	$0.042 \pm 0.031^{*}$	$0.036 \pm 0.041^{*}$	16	Vertical Horizontal	Dai, 2006
2007 (Feb, May, Aug, and Nov)	23	39.1%	$0.365 \pm 0.670^{*}$	$0.490 \pm 0.765^{*}$	12	Vertical Horizontal	Wang et al., 2010
2008 (May and Nov)	35	51.5%	$4.920 \pm 9.377^{*}$	$0.175 \pm 0.253^{*}$	14	Vertical Horizontal	Shen, 2011
2010 (May, Jun, and Aug–Nov)	40* 31**	67.5%* 74.2%**	1.310 ± 1.2058* 4.331 ± 8.564**	$0.928 \pm 0.940^{*}$ $0.131 \pm 0.171^{**}$	41	Vertical Horizontal	Xu, 2018
2019 (Apr–Sept)	31* 58**	87.10%* 87.93%**	$\begin{array}{c} 0.457 \pm 0.305^{*} \\ 0.855 \pm 0.686^{**} \end{array}$	$\begin{array}{c} 0.118 \pm 0.073^{*} \\ 0.024 \pm 0.011^{**} \end{array}$	25	Vertical Horizontal	This study

\*Data from vertical tow net.

\*\*Data from horizontal tow net.



Besides, food suitability and availability have been proposed as major factors to determine the survival of early-stage larval fishes, e.g., the main foods of fish larvae are phytoplankton (diatoms, flagellates, and ciliates) and zooplankton (pelecypods, euphausiids, Mysidacea, and copepods) (Govoni et al., 1983; MacKenzie et al., 1996; Platt et al., 2003; Guevara et al., 2005; Nakagawa et al., 2007; Ajiboye et al., 2011; Abo-Taleb, 2019). The dominant species of phytoplankton and zooplankton in May and June (peak spawning season) in Sansha Bay were mainly from Bacillariophyta and copepods (Liu et al., 2020a), all of which may play important roles as feeds for fish larvae and young juveniles to further impact the distribution pattern of ichthyoplankton in Sansha Bay.

Chla, representing the primary productivity, is associated with phytoplankton and zooplankton abundance and always has a positive correlation with phytoplankton abundance (Felip and Catalan, 2000). In this study, the red tide forming species *Noctiluca scintillans* (Macartney) (Kofoid and Swezy, 1921) bloomed in May 2019, which was without chloroplast and purely phagotrophic (Balch and Haxo, 1984; Zhang et al., 2020), resulting in apparently high abundance of phytoplankton and low concentration of Chla (Nakamura, 1998). Moreover, *N. scintillas* can feed on phytoplankton, zooplankton, and even fish eggs and larvae (Nakamura, 1998; Quevedo et al., 1999; Umani et al., 2004); therefore, the impact of biotic factor Chla related with *N. scintillas* might have a negative correlation with Phy, Zoo, and certain ichthyoplankton species (**Figure 7**).

Although seven abiotic and biotic variables were integrated for analysis, only 18.1% of the variability observed in ichthyoplankton was explained (**Table 3**), which suggested that other factors could influence the ichthyoplankton assemblage, e.g., ocean currents, substrates, and human activities (Bascompte et al., 2005; Lopes et al., 2006; Daskalov et al., 2007; Muhling et al., 2008; Vilchis et al., 2009; Zhou et al., 2011; Vandendriessche et al., 2016).

## CONCLUSION

In this study, 60 taxa ichthyoplankton were identified from horizontal and vertical tows by combining DNA barcoding and external morphology from April to September 2019 in Sansha Bay of Fujian Province, China. Among these, 52 taxa were identified at species level, 5 taxa at genus, and 3 taxa at family level. The 10 dominant species were from Engraulidae (S. tenuifilis and Stolephorus commersonnii), Serranidae (E. akaara), Leiognathidae (Photopectoralis bindus and Nuchequula nuchalis), Sciaenidae (N. albiflora and C. lucidus), and Sparidae (P. major and A. schlegelii). The temporal distribution of ichthyoplankton were divided into five assemblages, namely, April, May, June, July, and August-September with a high density occurred mainly in Guanjingyang and along the Dongchong Peninsula coastline into Dongwuyang. The temporal and spatial patterns were closely related to both abiotic and biotic factors. Temperature was the main factor influencing the assemblage structure and then Chla and salinity. Other factors, such as ocean currents, substrates, and other anthropogenic activities still need further investigation. Currently, little is explored to understand the entire life cycles of the dominant and commercially important fish species in Sansha Bay and its adjacent waters, the East China Sea. To achieve effective fishery stock management, understanding different

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life stages and their habitat uses, and the connectivity among different life stages are highly recommended.

# DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: NCBI (accession: OK012006-OK012065).

# **AUTHOR CONTRIBUTIONS**

YJ wrote the first draft and organized the sampling trips. YJ, B-AL, H-YH, G-MD, ML, and L-MZ conducted the sample collection. B-AL, H-YH, and GZ performed the molecular analysis. YJ, B-AL, and L-TY performed the data analyses. ML and L-MZ revised the manuscript. All authors contributed to the article preparation and approved the submission.

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# SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars. 2021.758089/full#supplementary-material

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