

RESEARCH ARTICLE

Effect of freshwater discharge from Namgang Dam on ichthyoplankton assemblage structure in Jinju Bay, Korea

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Abstract – The movement of fish eggs and larvae in bay and estuarine systems is affected by freshwater discharge. In this study, the assemblage structures of ichthyoplankton eggs and larvae were assessed for the first time in Jinju Bay, South Korea, to identify the spawning and nursery functions of the bay. Fish eggs and larvae and several environmental parameters were sampled monthly from April 2015 to March 2016 inside and outside of the bay. Within the bay we collected eggs and larvae from 25 and 35 species, respectively, indicating greater diversity than outside the bay, where we collected eggs and larvae of 20 and 28 species, respectively. Fluctuations in water temperature and salinity were larger inside than outside of the bay, and chlorophyll-*a* concentration was higher within the bay, likely due to discharge from the Namgang Dam, which causes water to flow from the inside to the outside of the bay. This process influences fish larva abundance, such that more larvae are found outside than inside the bay. We also found that 28 fish species use Jinju Bay as a spawning ground. For some species, the timing of egg and larva appearance differed inside and outside of the bay, suggesting that the timing of spawning may differ between the two environments.

Keywords: Bay / egg / larva / spawning ground / nursery ground / freshwater discharge

1 Introduction

Despite their proximity to major cities and ports, bays and their catchments play important and complex roles in maintaining the health of coastal and marine environments. Bay environments are physiochemically more variable than most other aquatic systems, particularly in terms of water temperature, salinity, oxygen, sea level, and turbidity (Elliott and Whitfield, 2011). Arguably, the most important environmental factor influencing bays is freshwater inflow from rivers, which creates salinity gradients (Livingston et al., 2000; Stoichev et al., 2004; Kakehi et al., 2017). Such gradients can result in challenging conditions for the inhabiting organisms (Faria et al., 2006). Along with freshwater inflows, bays also supply nutrients of terrestrial origin, which can facilitate favorable conditions, resulting in an abundant supply of food for organisms such as fish larvae (Selleslagh et al., 2009; Newton et al., 2014; Álvarez et al., 2015). The physical structures of bays can also offer shelter and protection from predators of ichthyoplankton and juvenile fish (Allen, 1982;

Able and Fahay, 2010; Song et al., 2012) as well as facilitate larval movement by altering wave action (Swearer et al., 1999). Therefore, bays are generally considered to be important spawning and/or nursery grounds facilitating rapid growth and high survival rates for ichthyoplankton (Vasconcelos et al., 2010; Grol et al., 2011; Patrick and Strydom, 2014; Newton et al., 2014; Lin et al., 2016).

Bays are critically important to the function and structure of ichthyoplankton communities. Bays are used as a spawning and nursery grounds for a variety of fish (Van Guelpen et al., 2021). Fish egg and larva numbers increase dramatically during periods of intensive spawning. Understanding changes in ichthyoplankton species and populations in bays over time is essential for efficient marine ecosystem management (Santos et al., 2017). These changes are affected by a variety of factors including abiotic conditions and food availability (Leggett and Deblois, 1994; Costalago et al., 2011). Variability in the abiotic parameters associated with bay dynamics can influence the composition and demography of fish eggs, larvae, and juveniles (Maes et al., 2004; Elliott et al., 2007; Fox et al., 2009; Hufnagl et al., 2013; Temperonia and Viñas, 2013; Rezagholinejad et al., 2016). Such changes include larval seasonality (Ryu et al., 2011; Ribeiro et al., 2015), diversity

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(Álvarez et al., 2015), and distribution within the bay (Kim et al., 2003; Trembl et al., 2015). Ichthyoplankton are also important prey items for a range of predators (Shoji and Tanaka, 2006) and their success can have strong and immediate effects on the recruitment of juvenile fish into populations, some of which support fisheries (Dahlberg, 1979; Beck et al., 2001; Porch and Laretta, 2016). Ichthyoplankton communities are sensitive to salinity change associated with freshwater inflows in bays (Kim et al., 2003; Fuentes et al., 2016). The effects of freshwater on fish eggs and larvae have been well studied (Strydom et al., 2002; Landaeta et al., 2012; Spencer et al., 2020). However, the impacts of such inflows on ichthyoplankton movement and overall community structure within bays remain poorly understood.

Jinju Bay in the Korean Strait is semi-enclosed by three counties, Sacheon, Hadong, and Namhae Islands, and is greatly influenced by freshwater inflow from Namgang Dam, which discharges into the northern part of the bay (Kang et al., 2011). The flow from Namgang Dam is particularly heavy during the Korean rainy season (July to September) (Lee et al., 2015). In the absence of discharge by Namgang Dam, flow is affected by the Seomjin River (Kang et al., 2011). Jinju Bay is a spawning and nursery ground for a range of species and supports a shellfish industry due to its low-energy environmental conditions (Lee et al., 2001). Approximately one quarter of the bay is intertidal, which is thought to increase the accumulation of organic pollutants associated with human activity in the surrounding area. Despite the cultural, economic, and ecological importance of Jinju Bay to South Korea, especially the city of Sacheon on the banks of the bay, to date, the impacts of freshwater inflow on the ichthyoplankton community in the bay have not been examined.

The purpose of this study was to investigate the fish species using Jinju Bay as spawning and nursery grounds, and to evaluate the effect of freshwater discharge from Namgang Dam on ichthyoplankton migration. Because fish larvae have no movement ability (Schultz et al., 2000), and floating eggs are located in the surface layer and require about 2 days to hatch (Yang et al., 2007), we predicted that species diversity would be greater within Jinju Bay than outside during periods of increased nutrient supply from Namgang Dam. We also predicted that fewer eggs and larvae would be present within Jinju Bay than outside of the bay during the peak discharge season of Namgang Dam (July to September), when freshwater flow increases in strength. The results of this study will provide important basic data for resource management planning.

2 Materials and methods

2.1 Sampling

Samples were collected from six stations in the Jinju Bay area (34°48'19.36"–35°0'6.53" N, 127°53'45.88"–128°1'59.69" E): three within the bay (stations 1, 2, and 3) and three outside the bay (stations 4, 5, and 6, located between Changseon and Saryang Islands). Three additional stations were selected to replicate the sampling design. The boundary delineating the bay was based on previous studies that documented the extent of freshwater discharge stratification from Namgang Dam (Kim et al., 2010; Kang et al., 2011). Each station was a

minimum of 5 km from the nearest station and the distance between the inside and outside stations was approximately 15 km (Fig. 1).

Fish eggs and larvae were collected monthly at each station from April 2015 to March 2016 using an ichthyoplankton net (mouth diameter: 80 cm; mesh size: 330 µm). The net was towed horizontally at a speed of 1.5–2 knots for 10 min at a depth of 1–2 m below the surface layer. A mechanical flowmeter (General Oceanics, Inc., Miami, FL, USA) was attached at the center of each net mouth to estimate the water volume filtered in each tow. Organisms in the samples were immediately fixed in 99% ethanol and then transported to the laboratory. Environmental variables such as water temperature, salinity, and sampling depth were measured for each tow at each station using a conductivity–temperature–depth meter (SBE-19plus; Sea-Bird Electronics Inc., Bellevue, WA, USA). A 500-mL aliquot of seawater was also collected at the site of each tow, passed through a 0.45-µm Millipore filter, and then frozen for later chlorophyll-*a* (Chl-*a*) analysis using a fluorometer (AU-10.00; Turner Designs, Sunnyvale, CA, USA). The transparency of the water at the tow site was measured using a Secchi disk.

The area where fish eggs were collected was considered the spawning ground (Harada et al., 2015; Lin et al., 2016), while that where fish larvae were collected was considered the nursery ground of the species (Ellis et al., 2012; Hsieh et al., 2012). The period during which fish eggs were collected was considered their spawning season.

2.2 Taxonomic identification of fish eggs and larvae

Fish larvae were classified based on morphological characteristics outlined in Okiyama (2014) and Kim et al. (2011). Scientific names and classification of fishes followed Kim and Ryu (2016) and Nelson et al. (2016), respectively. With the exception of anchovy, fish eggs were photographed using a Moticam Pro 205A camera (Xiamen, China) attached to a stereomicroscope (Olympus SZX-16; Tokyo, Japan). Eggs were measured using the Active Measure imaging program (Shinhan Scientific Optics, Seoul, South Korea) and sorted based on diameter. Most fish eggs are round, whereas anchovy eggs are oval; therefore, oval fish eggs were classified as anchovy eggs.

Because in some cases the larval body morphology had not been described or the larva body was damaged, we performed molecular analysis using the left eye of the fish larva (Lee et al., 2019). Fish eggs were grouped by size, and then molecular analysis was performed by randomly selecting a group of five objects (Lin et al., 2016). If all five individuals were found to come from one species, the group was judged as a single species. If the results of the five specimens were different, then any fish eggs remaining in the group were used to divide the objects by shape for analysis. This method was repeated until the results of five specimens were concluded to be from the same species. Total DNA was extracted using 10% Chelex 100 Resin (Bio-Rad, Hercules, CA). A portion of the mitochondrial cytochrome oxidase subunit 1 (COI) gene was amplified using universal primers (Ward et al., 2005). Polymerase chain reaction (PCR) was performed in a 20-µL reaction volume containing 1 µL genomic DNA, 2 µL 10× PCR buffer, 2 µL

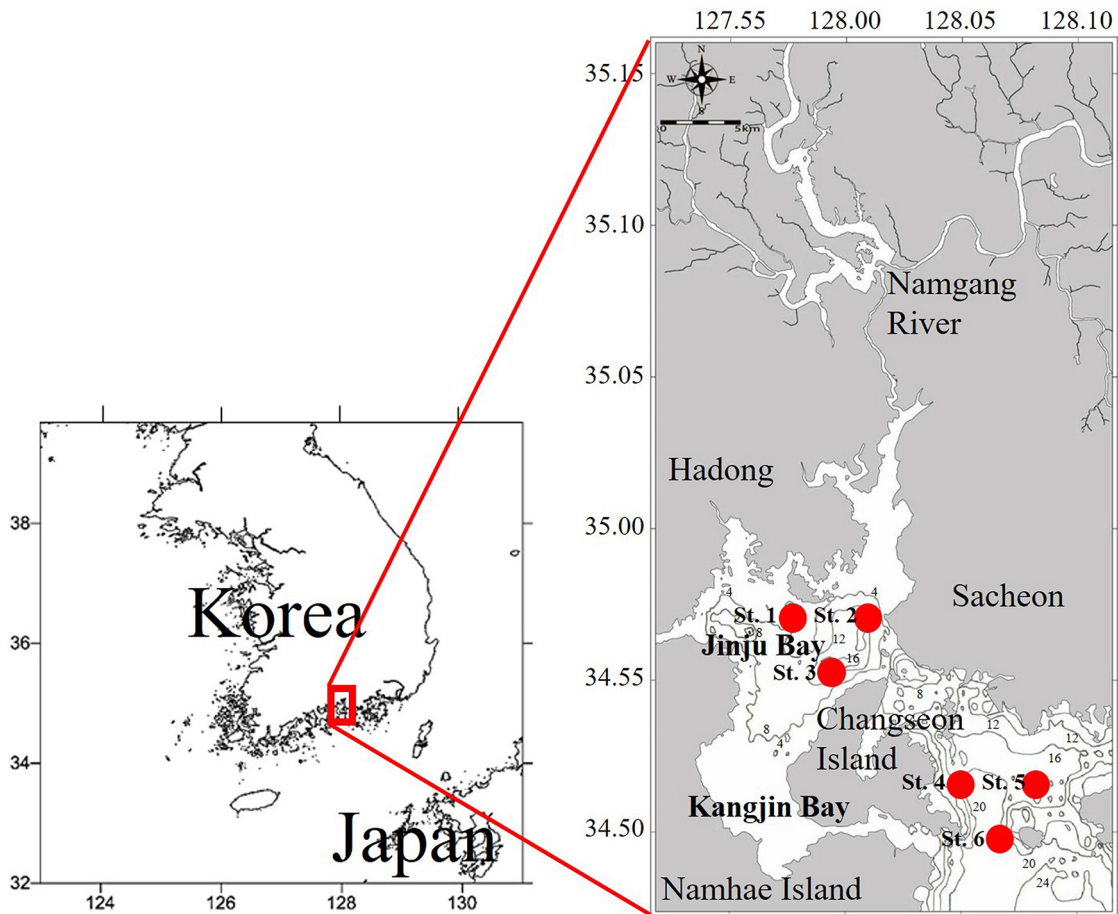


Fig. 1. Map showing the sampling stations of eggs and larvae of fish in Jinju Bay, Korea from April 2015 to March 2016.

2.5 mM dNTPs, 1 μ L of each primer, 0.1 μ L Ex-Taq DNA polymerase, and 12.9 μ L sterile distilled H₂O using a thermal cycler (MJmini PTC-1148; Bio-Rad). The PCR conditions were as follows: initial denaturation at 95 °C for 5 min, 34 cycles of PCR (denaturation at 95 °C for 60 s, annealing at 50 °C for 60 s, and extension at 72 °C for 60 min), and a final extension at 72 °C for 5 min. The PCR products were purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA) and sequenced using the ABI PRISM BigDye Terminator v3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystems Inc., Foster City, CA, USA) on an ABI 3730xl DNA Analyzer (Applied Biosystems Inc.). Sequences for the fish eggs and larvae were identified by comparison with reference sequences published in GenBank (National Center for Biotechnology Information, www.ncbi.nlm.nih.gov) and the Barcode of Life Data System (www.barcodinglife.com).

2.3 Data analysis

Differences in the number of fish species collected inside and outside of Jinju Bay were assessed by Mann–Whitney *U*-test with the SPSS v21 for Windows software (Chicago, IL, USA). To assess any changes in taxa, a similarity matrix was constructed depending on sampling location and species

composition using the Bray–Curtis index (Bray and Curtis, 1957). Prior to calculation, the data were normalized using logarithmic transformation [$\log_{10}(x + 1)$]. Cluster analysis was conducted using Bray–Curtis similarity. A similarity percentage (SIMPER) was used to determine which species had contributed most to the differences. Clusters were compared using similarity analyses (ANOSIM) to detect significant differences among groups. Non-metric multidimensional scaling (nMDS) ordination was performed to examine the cluster relationship on a two-dimensional map. Cluster analysis, SIMPER, ANOSIM, and nMDS ordination were performed using the PRIMER v6.0 statistical package (Clarke and Gorley, 2006). Monthly temperature, salinity, and Chl-*a* parameters were mapped using the Surfer v13.0 software (Golden Software, Inc., Golden, CO, USA). Fish eggs and larvae were analyzed separately.

Relationships between fish egg abundance and environmental factors (water temperature, salinity, Chl-*a*, depth, and transparency) were analyzed using canonical correspondence analysis (CCA). CCA could not be performed for larvae due to insufficient population size. A subset of fish collected from June to August 2015, when higher numbers of species and individuals were predicted, were used for CCA. To avoid overestimation of less frequently occurring species, only those

Table 1. Temporal variation in the number of individuals for fish eggs (unit: eggs 1000 m⁻³) collected inside of the Jinju bay, Korea from April 2015 to March 2016.

Scientific name	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Mean	%
<i>Engraulis japonicus</i>	10,228	112,664	205,363	294,457	11,900	2	1	–	–	–	–	–	52,884.6	68.8
<i>Thryssa kammalensis</i>	–	578	1,020	–	–	–	–	–	–	–	–	–	133.1	0.2
<i>Setipinna tenuifilis</i>	–	–	–	502	–	–	–	–	–	–	–	–	41.8	0.1
<i>Konosirus punctatus</i>	2,626	355	189	8,664	–	–	–	–	–	–	–	–	986.1	1.3
<i>Sardinella zunasi</i>	–	–	38	–	–	–	–	–	–	–	–	–	3.1	+
<i>Gadus macrocephalus</i>	–	–	–	–	–	–	–	–	–	48	–	–	4.0	+
<i>Inimicus japonicus</i>	–	–	705	13	–	–	–	–	–	–	–	–	59.9	0.1
<i>Platycephalus indicus</i>	–	445	5,566	–	265	–	–	–	–	–	–	–	523.0	0.7
<i>Lateolabrax maculatus</i>	–	–	–	–	–	–	2	–	–	–	–	–	0.1	+
<i>Epinephelus akaara</i>	–	–	–	13	–	–	–	–	–	–	–	–	1.0	+
<i>Sillago japonica</i>	–	2,531	16,064	3,089	2,907	–	1	–	–	–	–	–	2,050.0	2.7
<i>Nuchequula nuchalis</i>	–	3,689	4,225	27,423	273	–	–	–	–	–	–	–	2,967.5	3.9
<i>Acanthopagrus schlegelii</i>	9,228	6,319	4,917	–	–	–	–	–	–	–	–	–	1,705.3	2.2
<i>Pagrus major</i>	–	–	–	76	–	–	–	–	–	–	–	–	6.4	+
<i>Pennahia argentata</i>	–	–	7,598	–	42	–	–	–	–	–	–	–	636.6	0.8
<i>Nibea albiflora</i>	–	–	–	881	–	–	–	–	–	–	–	–	73.4	0.1
<i>Halichoeres poecilopterus</i>	–	–	2,366	21,418	–	–	–	–	–	–	–	–	1,981.9	2.6
<i>Repomucenus valenciennesi</i>	222	–	152,603	–	541	104	2	–	–	–	–	–	12,789.4	16.6
<i>Kareius bicoloratus</i>	–	–	–	–	–	–	–	–	194	1	–	–	16.3	+
<i>Pleuronichthys cornutus</i>	–	–	–	–	–	–	–	1	–	–	–	–	0.1	+
<i>Pseudaesopia japonica</i>	–	112	–	–	–	–	–	–	–	–	–	–	9.3	+
<i>Cynoglossus abbreviatus</i>	6	–	–	–	–	–	–	–	–	–	–	–	0.5	+
<i>Cynoglossus interruptus</i>	–	–	–	–	–	3	–	–	–	–	–	–	0.2	+
Unidentified fish egg A	4	–	–	–	–	–	–	–	–	–	–	–	0.4	+
Unidentified fish egg C	–	–	–	–	11	–	–	–	–	–	–	–	0.9	+
No. of species	6	8	12	10	7	4	3	2	1	2	0	0	25	
Total	22,314	126,694	400,652	356,535	15,938	119	5	3	194	49	0	0	76,875	100

+: <0.1%.

accounting for over 0.5% of the total abundance were used for this analysis. CCA was performed using the Excel XLSTAT v7.5.2 package (Addinsoft, Paris, France; <http://www.xlstat.com>). The data were log-transformed [$\log(x + 1)$] before the analysis.

3 Results

3.1 Ichthyoplankton species composition

Throughout the survey period, we collected 76,875 ± 145,704 eggs 1000 m⁻³ (mean ± standard deviation, SD) belonging to 25 species inside the bay, and 34,013 ± 57,122 eggs 1000 m⁻³ from 20 species outside of the bay. In total, 28 species were collected at the six stations (Tabs. 1 and 2). Among all collected fish egg specimens, *Engraulis japonicus* was the most abundant both inside (68.8%) and outside the bay (87.0%), followed by *Repomucenus valenciennesi* (16.6%) inside the bay and *Sillago japonica* (4.9%) outside the bay. Fish eggs were collected intensively inside and outside of the bay from April to August, and the numbers of species and populations declined thereafter (Tabs. 1 and 2).

A mean of 408 ± 1042 larvae 1000 m⁻³ (±SD) from 35 species was collected inside the bay and 730 ± 1716 larvae 1000 m⁻³ from 28 species were collected outside the bay, for a

total of 40 species collected in the survey area (Tabs. 3 and 4). As with the fish eggs, *E. japonicus* had the greatest abundance inside (70.9%) and outside the bay (77.9%). The second most abundant species was *S. japonica* both inside the bay (4.7%) and outside the bay (5.1%). The third most abundant species was *Omobranchus elegans* (4.2% and 4.4% inside and outside, respectively). Larvae were collected intensively both inside and outside the bay from June to September (Tabs. 3 and 4).

No significant differences in the total number of egg and larval species were observed inside (25 and 35 species, respectively; Tabs. 1 and 3) or outside the bay (20 and 28 species, respectively; Tabs. 2 and 4) (Mann–Whitney *U*-test, $U = 252$, $N_1 = 24$, $N_2 = 24$, $P = 0.76$).

Some fish egg and larvae species occurred only inside or outside of the bay. The numbers of species collected only within the bay (8 egg and 12 larval species) were greater than those that were uniquely found outside of the bay (3 egg and 5 larval species). *Thryssa kammalensis* was collected at a density of 4793 eggs 1000 m⁻³ in inside the bay, but was not found outside the bay. *Girella punctata* and *Halichoeres tenuispinis* were collected at densities of 10.1 and 2.3 eggs 1000 m⁻³, respectively, outside of the bay, but we found no evidence of these species within the bay. *Nibea albiflora* (2.7 larvae 1000 m⁻³) and *Pennahia argentata* (2.6 larvae 1000 m⁻³) larvae were the most abundant among 12 species collected

Table 2. Temporal variation in the number of individuals for fish eggs (unit: eggs 1000 m⁻³) collected outside of the Jinju bay, Korea from April 2015 to March 2016.

Scientific name	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Mean	%
<i>Engraulis japonicus</i>	7,641	28,211	165,621	68,625	84,744	–	111	–	–	–	–	–	29,579.4	87.0
<i>Konosirus punctatus</i>	21	3	–	74	–	–	–	–	–	–	–	–	8.1	+
<i>Inimicus japonicus</i>	–	–	36	24	–	–	–	–	–	–	–	–	5.0	+
<i>Platycephalus indicus</i>	–	–	500	–	533	–	–	–	–	–	–	–	86.1	+
<i>Lateolabrax maculatus</i>	–	–	–	–	–	–	–	4	–	–	–	–	0.4	+
<i>Sillago japonica</i>	–	337	1,092	5,725	12,810	8	1	–	–	–	–	–	1,664.4	4.9
<i>Nuchequula nuchalis</i>	–	27	–	9,983	152	–	–	–	–	–	–	–	846.8	2.5
<i>Acanthopagrus schlegelii</i>	872	542	938	–	–	–	–	–	–	–	–	3	196.2	0.6
<i>Pagrus major</i>	–	–	–	48	1,119	–	–	–	–	–	–	–	97.2	+
<i>Pennahia argentata</i>	–	–	451	2,064	304	–	–	–	–	–	–	–	235.0	0.7
<i>Girella punctata</i>	–	–	–	–	–	–	–	–	–	–	–	3	0.3	+
<i>Halichoeres poecilopterus</i>	–	–	2,862	4,883	695	42	–	–	–	–	–	–	706.7	2.1
<i>Halichoeres tenuispinis</i>	–	–	–	–	–	–	–	–	1	–	–	–	0.1	+
<i>Repomucenus valenciennesi</i>	773	1,757	1,773	–	42	91	3	–	–	–	–	–	370.0	1.1
<i>Kareius bicoloratus</i>	–	–	–	–	–	–	–	–	1,678	3	2	–	140.2	+
<i>Pleuronichthys cornutus</i>	–	–	–	–	–	–	–	1	–	–	–	–	0.1	+
<i>Pseudoesopia japonica</i>	–	–	24	–	–	–	–	–	–	–	–	–	2.0	+
<i>Cynoglossus interruptus</i>	–	–	–	–	–	107	–	–	–	–	–	–	8.9	+
Unidentified fish egg B	–	–	701	–	25	–	–	–	–	–	–	–	60.6	+
Unidentified fish egg C	–	–	–	–	63	–	–	–	–	–	–	–	5.2	+
No. of species	4	6	10	8	10	4	3	2	2	1	1	2	20	
Total	9,307	30,877	173,998	91,425	100,487	247	115	5	1,679	3	2	6	34,013	100

+: <0.1%.

only within the bay. Based on the fish eggs identified to species level, more species spawned inside ($n=25$) than outside the bay ($n=20$) during the sampling period.

3.2 Spawning seasons of dominant species

We found 25 species spawning within Jinju Bay, and 20 species spawning outside the bay. When the water temperature was high, *E. japonicus* and *R. valenciennesi* spawned inside and outside the bay from April to October, and *Nuchequula nuchalis* and *S. japonica* spawned inside and outside the bay from May to August. *Halichoeres poecilopterus* spawned inside the bay from June to July and outside the bay to June and September. When the water temperature was low, *Gadus microcephalus* (January) and *Kareius bicoloratus* (December, January) spawned inside the bay, and *K. bicoloratus* (December to February) spawned outside the bay.

3.3 Assemblage structure

A total of 58 species (eggs and larvae) were collected during the survey period. nMDS revealed that the communities of fish eggs and larvae collected from the six stations were distinctly divided into two groups of stations, those inside and outside of the bay (Fig. 2). Communities of stations inside the bay (stations 1, 2, and 3) were more widely dispersed than those outside the bay (stations 4, 5, and 6) (Fig. 2). However, the ANOSIM results showed no significant difference between the two groups ($R=0.926$, $P=0.1$).

According to SIMPER analysis, the degree of similarity among the three sampling stations inside the bay was 72.7%, with two main species contributing to this assemblage: *E. japonicus* (9.8%) and *R. valenciennesi* (9.1%). Higher similarity was observed within the three sampling stations outside the bay (79.7%), and two species contributed substantially to this assemblage: *E. japonicus* (10.7%) and *S. japonica* (8.0%). Species that contributed to the distinction between the inside and outside of the bay were *T. kammalensis* (6.5%) and *Konosirus punctatus* (4.5%), perhaps due to the larger proportion of common species collected at stations outside the bay than inside the bay.

3.4 Environmental variables

Changes in water temperature, salinity, and Chl-*a* between April 2015 and March 2016 are shown in Figure 3. The mean depth of the three stations inside the bay was 10.6 ± 5.6 m (\pm SD), whereas that of the stations outside the bay was 18.6 ± 3.5 m. The average surface water temperatures inside and outside of the bay during the study period were 17.3 ± 6.6 °C and 17.2 ± 6.1 °C, respectively. Fluctuations in water temperature were greater inside (7.0–25.7 °C) than outside (7.6–24.8 °C) of the bay. Differences in surface water temperature inside and outside the bay were greatest in May and December, but no significant difference was observed in March (Mann–Whitney *U*-test, $U=71$, $N_1=12$, $N_2=12$, $P=0.56$, Fig. 4). A greater temporal difference in temperature between the surface and bottom layers was observed in water

Table 3. Temporal variation in the number of individuals for fish larvae (unit: larvae 1000 m⁻³) collected inside of the Jinju bay, Korea from April 2015 to March 2016.

Scientific name	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Mean	%
<i>Engraulis japonicus</i>	–	12	–	143	3,255	42	15	–	–	–	–	–	288.90	70.9
<i>Syngnathus schlegeli</i>	–	18	14	–	–	–	–	1	–	–	–	–	2.77	0.7
<i>Hippocampus mohnikei</i>	–	–	–	–	–	2	–	–	–	–	–	–	0.15	+
<i>Sebastes pachycephalus</i>	–	2	–	–	–	–	–	–	–	–	–	–	0.18	+
<i>Sebastes inermis</i>	–	–	–	–	–	–	–	–	1	14	1	–	1.27	0.3
<i>Sebastes marmoratus</i>	–	–	–	–	–	–	–	–	–	–	1	–	0.06	+
<i>Platycephalus indicus</i>	–	–	8	26	–	–	–	–	–	–	–	–	2.83	0.7
<i>Hexagrammos otakii</i>	–	–	–	–	–	–	–	–	46	50	–	–	7.96	2.0
<i>Pseudoblennius cottoides</i>	–	–	–	–	–	–	–	–	–	2	–	–	0.14	+
<i>Furcina ishikawae</i>	–	–	–	–	–	–	–	–	1	1	–	–	0.18	+
<i>Sillago japonica</i>	–	–	8	135	49	34	2	–	–	–	–	–	19.07	4.7
<i>Nuchequula nuchalis</i>	–	–	–	22	8	–	–	–	–	–	–	–	2.55	0.6
<i>Johnius grypotus</i>	–	–	–	–	1	–	–	–	–	–	–	–	0.07	+
<i>Pennahia argentata</i>	–	–	–	9	22	–	–	–	–	–	–	–	2.64	0.6
<i>Nibea albiflora</i>	–	–	–	–	32	–	–	–	–	–	–	–	2.67	0.7
<i>Ernogrammus hexagrammus</i>	–	–	–	–	–	–	–	–	–	–	–	2	0.20	+
<i>Chirolophis saitone</i>	–	–	–	–	–	–	–	–	1	–	–	–	0.04	+
<i>Stichaeidae sp.</i>	–	–	–	–	–	–	–	–	–	82	6	–	7.35	1.8
<i>Pholis nebulosa</i>	–	–	–	–	–	–	–	–	1	–	–	–	0.04	+
<i>Pholis crassispina</i>	–	–	–	–	–	–	–	–	–	33	2	–	2.93	0.7
<i>Ammodytes japonicus</i>	–	–	–	–	–	–	–	–	1	2	1	–	0.25	0.1
<i>Omobranchus elegans</i>	–	–	51	99	5	40	9	–	–	–	–	–	17.06	4.2
<i>Repomucenus valenciennesi</i>	–	8	6	3	12	5	4	–	–	–	–	–	3.20	0.8
<i>Amblychaeturichthys hexanema</i>	–	–	9	–	54	–	–	–	–	–	–	–	5.19	1.3
<i>Periophthalmus modestus</i>	–	–	–	–	–	1	–	–	–	–	–	–	0.08	+
<i>Cryptocentrus filifer</i>	–	–	–	46	–	2	–	–	–	–	–	–	3.98	1.0
<i>Pseudogobius masago</i>	–	–	–	–	–	5	–	–	–	–	–	–	0.41	0.1
<i>Acentrogobius pflaumi</i>	–	–	–	28	105	–	–	–	–	–	–	–	11.08	2.7
<i>Luciogobius guttatus</i>	3	9	–	–	–	–	–	–	–	–	–	–	0.95	0.2
Gobiidae sp.A	–	–	4	17	103	50	1	–	–	–	–	–	14.61	3.6
Gobiidae sp.B	–	–	–	11	–	–	–	–	–	–	–	–	0.91	0.2
Gobiidae sp.C	–	–	51	–	–	–	–	–	–	–	–	–	4.21	1.0
Gobiidae sp.D	–	–	–	9	23	–	–	–	–	–	–	–	2.67	0.7
<i>Pseudopleuronectes yokohamae</i>	–	–	–	–	–	–	–	–	–	–	–	1	0.06	+
<i>Cynoglossus robustus</i>	–	–	–	–	10	–	–	–	–	–	–	–	0.87	0.2
No. of species	1	5	8	12	13	9	5	1	6	7	5	2	35	
Total	3	50	150	548	3,681	181	31	1	49	183	11	3	408	100

+: <0.1%.

outside the bay ($\pm 4.8^\circ\text{C}$) than inside of the bay ($\pm 2.9^\circ\text{C}$; Fig. 4). Thermoclines occurred in both areas during the sampling period but differed temporally in their presence. In April 2015 a thermocline began to form a depth of 2–3 m inside the bay, which increased in stratification to a depth of 3–5 m in May, and then disappeared in October (Fig. 4). Outside the bay, a thermocline formed at a depth of 12–15 m in May 2015, which intensified in July and then disappeared in November (Fig. 5).

Salinity was consistently lower inside the bay than outside throughout the year, with the highest values occurring in June 2016 (inside, 32.7; outside, 33.1) and the lowest occurring in July 2016 (30.2 and 31.2, respectively; Fig. 4). Surface layer salinity was consistently lower than that in the bottom layers. A halocline formed at a depth of 2–3 m inside the bay in April and disappeared in August (Fig. 5). Stations outside the bay

formed haloclines at depths of 1–4 m in August 2015, but were less affected than their shallower counterparts in the bay.

Chl-*a* concentrations exceeded 2.5 $\mu\text{g/L}$ from June to October 2015 inside the bay, with a maximum value of 8.6 $\mu\text{g/L}$ recorded during this period. Stations outside the bay exhibited maximum Chl-*a* concentrations (4.3 $\mu\text{g/L}$) in September, which then decreased from November 2015 to April 2016 (0.3–0.9 $\mu\text{g/L}$). The difference in Chl-*a* values inside and outside of the bay was large from June to August, with higher values inside than outside the bay (Fig. 4).

3.5 Correlations with environmental variables

Among the four environmental variables assessed, water temperature and Chl-*a* showed higher values inside than

Table 4. Temporal variation in the number of individuals for fish larvae (unit: larvae 1000 m⁻³) collected outside of the Jinju bay, Korea from April 2015 to March 2016.

Scientific name	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Mean	%
<i>Engraulis japonicus</i>	–	1	570	1,305	4,897	47	–	–	1	–	–	–	568.33	77.9
<i>Syngnathus schlegeli</i>	–	–	–	–	–	–	–	1	–	–	–	–	0.08	+
<i>Hippocampus mohnikei</i>	–	–	–	–	–	–	1	–	–	–	–	–	0.09	+
<i>Sebastes inermis</i>	–	–	–	–	–	–	–	–	19	1	3	–	1.96	0.3
<i>Sebastes marmoratus</i>	–	–	–	–	–	–	–	1	–	–	–	–	0.09	+
<i>Sebastes longispinis</i>	–	–	–	–	–	–	–	6	–	–	–	–	0.53	0.1
<i>Platycephalus indicus</i>	–	–	1	4	124	–	–	–	–	–	–	–	10.78	1.5
<i>Hexagrammos otakii</i>	–	–	–	–	–	–	–	–	42	128	3	–	14.41	2.0
<i>Liparis tanakae</i>	–	–	–	–	–	–	–	–	–	–	3	–	0.21	+
<i>Sillago japonica</i>	–	–	4	110	237	94	–	–	–	–	–	–	37.12	5.1
<i>Nuchequula nuchalis</i>	–	–	1	11	14	–	–	–	–	–	–	–	2.17	0.3
<i>Acanthopagrus schlegelii</i>	–	–	–	2	–	–	–	–	–	–	–	–	0.17	+
<i>Chirolophis saitone</i>	–	–	–	–	–	–	–	–	3	4	–	–	0.59	0.1
<i>Stichaeidae sp.</i>	–	–	–	–	–	–	–	–	–	11	9	–	1.71	0.2
<i>Pholis crassispina</i>	–	–	–	–	–	–	–	–	–	1	–	–	0.07	+
<i>Ammodytes japonicus</i>	–	–	–	–	–	–	–	–	44	1	–	–	3.72	0.5
<i>Omobranchus elegans</i>	–	–	61	87	186	39	10	–	–	–	–	–	31.95	4.4
<i>Repomucenus valenciennei</i>	–	–	2	22	133	–	25	–	–	–	–	–	15.25	2.1
<i>Amblychaeturichthys hexanema</i>	1	–	–	4	213	–	–	–	–	–	–	–	18.23	2.5
<i>Cryptocentrus filifer</i>	–	–	–	2	–	1	–	–	–	–	–	–	0.26	+
<i>Acentrogobius pflaumi</i>	–	1	–	–	–	–	–	–	–	–	–	–	0.10	+
<i>Luciogobius guttatus</i>	1	1	–	–	–	–	–	–	–	–	–	–	0.16	+
<i>Luciogobius sp.</i>	2	–	–	–	–	–	–	–	–	–	–	–	0.14	+
Gobiidae sp.A	–	–	3	16	167	45	–	–	–	–	–	–	19.32	2.6
Gobiidae sp.B	–	–	6	–	–	–	–	–	–	–	–	–	0.47	0.1
Gobiidae sp.D	–	–	–	–	14	–	–	–	–	–	–	–	1.17	0.2
<i>Kareius bicoloratus</i>	–	–	–	–	–	–	–	–	–	–	2	–	0.21	+
<i>Pseudopleuronectes yokohamae</i>	–	–	–	–	–	–	–	–	–	–	1	5	0.45	0.1
No. of species	3	3	8	10	9	5	3	3	5	6	6	1	28	
Total	3	4	649	1,564	5,986	227	36	8	109	146	21	5	730	100

+: <0.1%.

outside of the bay, whereas salinity and water transparency showed the opposite pattern (Fig. 6). Eggs of *R. valenciennei* and *Platycephalus indicus* collected inside the bay were positively associated with Chl-*a* and negatively associated with salinity and transparency, whereas *E. japonicus* and *P. argentata* displayed the opposite pattern. No significant correlation was observed between the four environmental variables for the other five species (*N. nuchalis*, *S. japonica*, *H. poecilopterus*, *Acanthopagrus schlegelii*, and *K. punctatus*).

4 Discussion

In this study, we found that the inside of Jinju Bay, which is more heavily affected by Namgang Dam, was used as a spawning ground by more fish species than the outside of the bay, which is less affected by the dam. This is the first study to assess the influence of freshwater discharge on fish eggs and larvae in this area. The lack of ichthyological information for this area makes such baseline data valuable for our understanding and management of fisheries and ecosystem

health in the region. Our results are consistent with those of other studies that reported that bay interiors serve as important fish spawning grounds (Able and Fahay, 2010; Chen et al., 2014; Ribeiro et al., 2015; Lin et al., 2016). We found greater species richness among larvae and eggs in waters inside the bay, but higher numbers of larvae outside the bay (Tabs. 1–4). Concentrations of Chl-*a*, a reliable predictor of nutrient and carbon concentrations (Jakobsen and Markager, 2016) and food availability for larval fishes (phytoplankton, zooplankton, and fish larvae), which drives predator–prey interactions (Cowan and Shaw, 2002; Irigoien et al., 2004), were higher inside than outside of the bay during freshwater discharge from Namgang Dam. We also found species composition differences inside and outside the bay, which were related to changes in environmental factors (water temperature and salinity). Freshwater discharge was strongly correlated with fish egg and larva abundance in the area because the water temperature, salinity, and Chl-*a* content differ between the inside and outside of Jinju Bay due to the influence of discharged freshwater from Namgang Dam (Figs. 4 and 5). More species were found inside than outside Jinju Bay when nutrients from

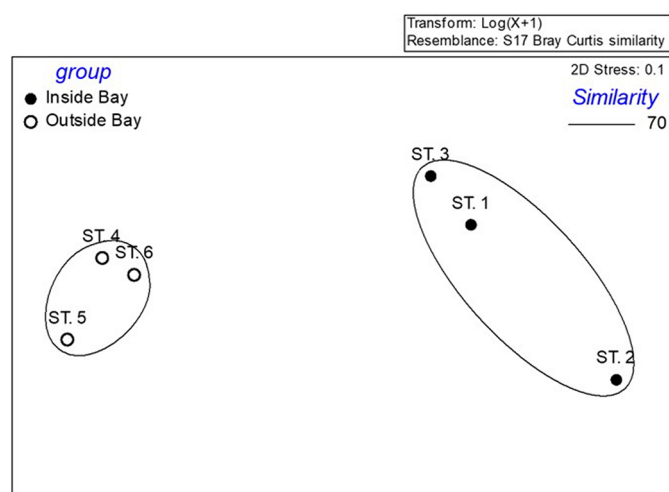


Fig. 2. Dendrogram plots of the community similarity of the six stations using composition and abundance data for fish species found in Jinju Bay, Korea.

the dam were present, and fewer fish eggs and larvae were present in the bay when water flows peaked in strength. Thus, both of our hypotheses were supported by our findings.

From June to September, the numbers of fish eggs and larvae showed similar patterns of increase and decrease to Chl-*a* content and ichthyoplankton abundance. Phytoplankton availability is linked to larval fish health (Lasker, 1975; Hsieh et al., 2012). A study of summer Chl-*a* concentrations in China showed higher values inshore (mean, $2.4 \pm 1.4 \text{ mg m}^{-3}$) than offshore ($0.3 \pm 0.3 \text{ mg m}^{-3}$) (Lin et al., 2016), and a similar study in Jinhae Bay, South Korea, showed that August Chl-*a* concentrations were high near the coast and lower with distance seaward (Yoo et al., 2007). When precipitation was high, primary and secondary production (zooplankton) increased in Ariake Bay and the Chikugo River estuary, enhancing larval fish growth (Shoji et al., 2006). High phytoplankton abundance fuels zooplankton reproduction, which provides a food source for larval fish (Kim et al., 2015). The shallower water depth and higher turbidity within the bay may protect fish larvae from predators, thereby increasing survival rates (Braverman et al., 2009; Zhang et al., 2015). This difference in the environments inside and outside the bay increases the survival of larvae of fish that spawn inside the bay, such that more species use the bay interior as spawning and nursery grounds.

The most dominant species found among our egg and larval samples was *E. japonicus*, which is a well-known coastal species in Korea (Kim et al., 2009; Kwak et al., 2013). The next most common species were *R. valenciennei* (inside) and *S. japonica* (outside), whose abundances varied according to location. Some species occurred either solely inside or outside the bay, suggesting that some spawning and nursery grounds in each of these habitats were species-specific. Fluctuations in water temperature and salinity were greater inside ($7.0\text{--}25.7^\circ\text{C}$; $30.2\text{--}32.7$) than outside of the bay ($7.6\text{--}24.8^\circ\text{C}$; $31.2\text{--}33.1$) (Fig. 5). These differences in environmental variation inside and outside the bay may have

influenced the selection of spawning grounds in the fish species sampled in this study. Thus, our results support the findings of previous studies suggesting that mature fish are limited to spawning within the bay by temperature and salinity gradients (Fincham et al., 2013). Among the fish eggs collected in this study, eight and three species were collected solely inside and outside of the bay, respectively (Tabs. 1 and 2), which indicates species-specific selection of spawning grounds. Future studies should perform more surveys according to spawning season to identify spawning ground locations more accurately.

Our results are consistent with previous reports of a positive relationship between the number of eggs and water temperature (Laprise and Pepin, 1995; Park et al., 2005; Kwak and Park, 2014; Harada et al., 2015; Fig. 6). Higher water temperature can enhance larval growth and increase survival during the first winter (Denit and Sponaugle, 2004; Kim et al., 2015; Veale et al., 2015), thereby conferring an advantage to eggs from fish that spawn inside the bay over those that spawn outside. The increased supply of nutrients from freshwater influxes during the rainy season (June–August) in this region can result in phytoplankton blooms (Yeo and Park, 1997; Oh et al., 2007; Han et al., 2015; Moon et al., 2010), which can further promote larva growth within the bay through nutrient provision. The mean discharge ($135.96 \text{ m}^3/\text{s}$) from Namgang Dam was highest in July (Water Resources Management Information System; <http://www.wamis.go.kr>) during our sampling period. Therefore, we infer that the interior Jinju Bay environment was more favorable for the early fish stages during this season than that outside of the bay. High water temperature and freshwater inflow are good for larval growth and increase survival rates, leading to greater diversity in the species spawning within the bay, as we observed in terms of egg and larval abundance and diversity in Jinju Bay.

Water discharged from Namgang Dam appeared to have a negative impact on larval presence and density in the bay. Unlike eggs, the number of larvae collected outside of the bay was 1.8 times greater than that inside the bay. Although larvae typically swim faster than the low current (Genin, 2004) and their distribution can be similar to that of their food organisms (Garrido et al., 2009; Staaterman and Paris, 2014), the larvae in this study may have been strongly influenced by the rapid flow of water discharged from Namgang Dam (Kim et al., 2003; Jung and Ro, 2010; Patrick and Strydom, 2014). Kang et al. (2011) reported that Jinju Bay experiences two-layered water circulation in summer, with surface water flowing from the inside to the outside of the bay due to high freshwater discharge from the dam and bottom water flowing in the opposite direction. Freshwater discharge from a river 3 km away, which is considered a major factor in changing the physical environment of the bay (Stoichev et al., 2004), likely also influences its water circulation (Kakehi et al., 2017). In this study, greater anchovy fish egg abundance was observed inside the bay ($52,884 \text{ eggs } 1000 \text{ m}^{-3}$) than outside ($29,579 \text{ eggs } 1000 \text{ m}^{-3}$), but more larvae were collected outside the bay, likely due to the influence of surface layer flow. Since the hatching time of anchovy eggs is short (1–3 days; Zweifel and Lasker, 1976), any eggs that were transported outside of the bay through surface layer flow would hatch and be collected as larvae outside of the bay.

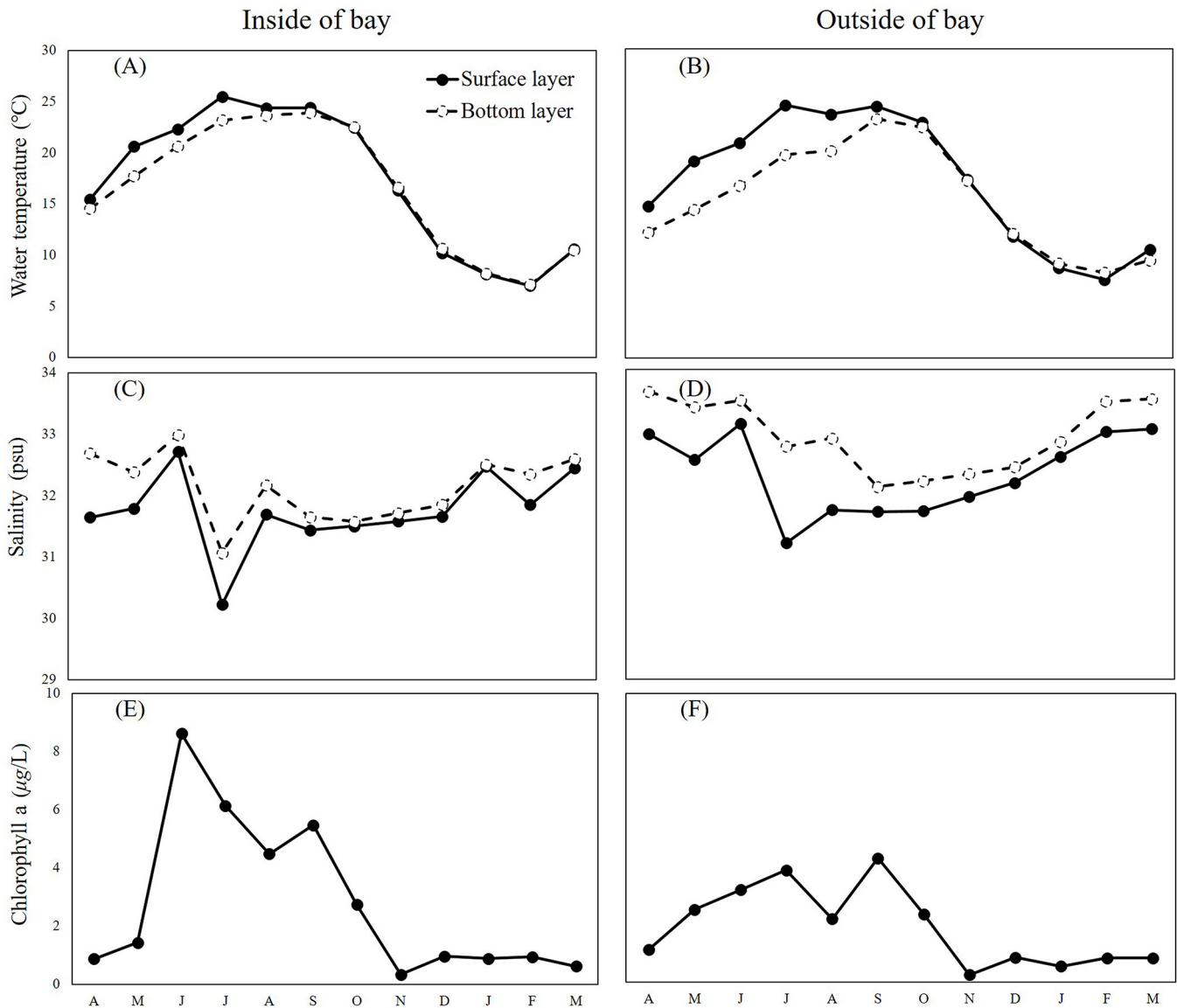


Fig. 3. Monthly variations in the sea water temperature (A, B), salinity (C, D), and Chlorophyll a (E, F) from inside and outside of the Jinju-bay, Korea from April 2015 to March 2016.

Egg buoyancy greatly affects fish demography within the bay. Many pelagic eggs are buoyant, occurring on seawater surface layers in coastal ecosystems (Dethlefsen et al., 2001; Ospina-Álvarez et al., 2012). After hatching, the larvae remain at the surface for a few days until their high concentration of oil decreases, then move to bottom water for growth (Toledo et al., 2002; Saborido-Rey et al., 2003; Hinrichsen et al., 2016). Therefore, pelagic eggs spawned within the bay flow outward with exiting surface waters, which in part explains the large numbers of larvae collected outside of the bay (Tab. 4). Demersal eggs are more likely to remain in bottom water within the bay until hatching (Ziadi-Künzli and Tachihara, 2016). As newly hatched larvae have poor swimming capability, their movements depend on current direction and/or velocity (Schultz et al., 2000). The species found to spawn demersal eggs in this study were *Pholis crassispina* (inside, 2.9 larvae 1000 m⁻³; outside, 0.1 larvae 1000 m⁻³),

Cryptocentrus filifer (inside, 4.0 larvae 1000 m⁻³; outside, 0.3 larvae 1000 m⁻³), *Luciogobius guttatus* (inside, 1.0 larvae 1000 m⁻³; outside, 0.2 larvae 1000 m⁻³), Gobiidae sp. B (inside, 0.9 larvae 1000 m⁻³; outside, 0.5 larvae 1000 m⁻³), and Gobiidae sp. D (inside, 2.7 larvae 1000 m⁻³; outside, 1.2 larvae 1000 m⁻³). More of their larvae were collected within the bay than outside; we conclude that they spawned within the bay and were collected as they emerged from the surface layer while hatching.

Environmental factors differed inside and outside of Jinju Bay during sampling, which may explain some of the differences observed between these habitats. Depth was shallower and salinity lower inside than outside of the bay; however, water temperature was warmer in April–September, when many fish eggs and larvae were collected, and Chl-*a* concentrations were higher inside than outside of the bay. Changes in such environmental factors are well documented to

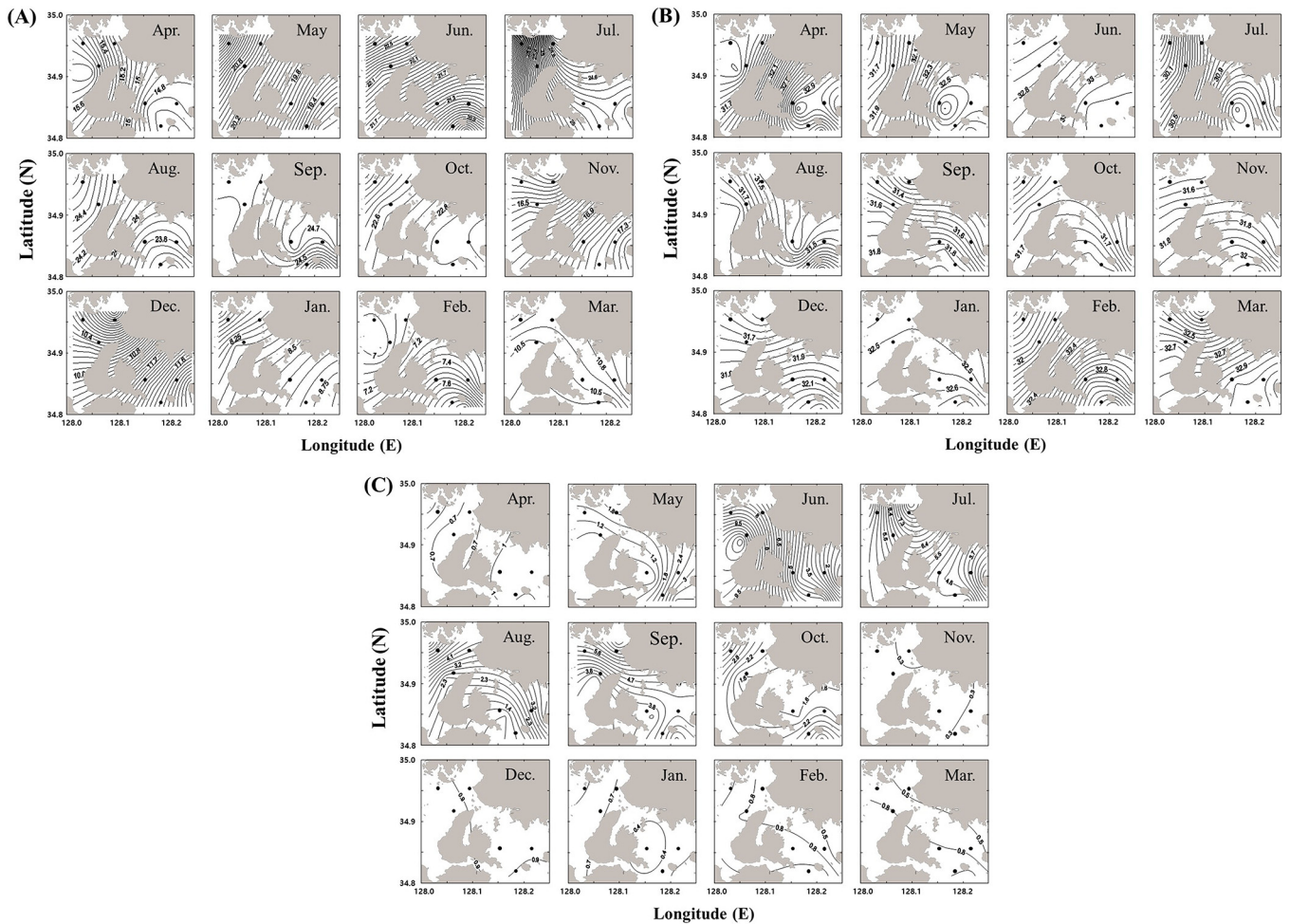


Fig. 4. Horizontal distributions of temperature (A), salinity (B), and chlorophyll-*a* (C) at 1 m depth at Jinju Bay, Korea, from April 2015 to March 2016. Dots indicate stations.

influence fish egg and larval distributions in bay systems and many species have preferential environmental niches for optimal survival and growth (Nahas et al., 2003; Taylor et al., 2010; Zhang et al., 2015; Zhang et al., 2016), potentially due to their different adaptive capacities (Jiang et al., 2006). In this study, 25 fish species spawned within the bay, where environmental fluctuations were greater, whereas 20 species spawned outside, where there was little environmental change. For example, salinity can affect spawning behavior and location, but in a species-dependent manner (Boccanfuso et al., 2019). Generally, diadromous species require an environment with a high salinity gradient to spawn (Haddy and Pankhurst, 2000). We observed a larger salinity change in the waters within Jinju Bay than outside of it. Three species (*T. kammalensis*, *K. punctatus*, and *N. nuchalis*) spawned inside the bay, and their ecology is suited to brackish water (Froese and Pauly, 2019). Thus, species that require increased salinity for spawning, or whose spawning is not substantially impacted by salinity changes, may have favored spawning within the bay.

Interestingly, water temperature was positively correlated with ichthyoplankton abundance in Jinju Bay in our study. Spawning behaviors are often species-specific (Duffy-Anderson et al., 2006; Rodríguez, 2008), and water

temperature is a main spawning cue for many ecologically and economically important fish species (Fage, 1920; Russell, 1976; Bye, 1984; Palomera, 1992; Heyman and Kjerfve, 2008; Selleslagh et al., 2009; Feeley et al., 2018). Water temperature may also be a driving factor of differences in spawning times between the two areas. The bay is semi-enclosed and highly affected by freshwater discharge from Namgang Dam. In particular, the two-layered water circulation becomes stronger during the rainy season (July–September) than in other seasons, with surface layer water flowing from the inside of the bay, but bottom water flowing in the opposite direction. The water temperature inside Jinju Bay was consistently $\sim 2^{\circ}\text{C}$ higher than in the deeper waters outside the bay from April to August during our study period, and fish spawning occurred earlier inside Jinju Bay than outside. Abundant *P. indicus* and *S. japonica* fish eggs were collected inside the bay in June (5,566 eggs 1000 m^{-3} and 16,064 eggs 1000 m^{-3} , respectively). However, outside the bay, the largest populations were collected in August (533 eggs 1000 m^{-3} and 12,810 eggs 1000 m^{-3}). *A. schlegelii* was collected most intensively inside the bay in April (9,228 eggs 1000 m^{-3}) and outside the bay in June (938 eggs 1000 m^{-3}). This finding indicates a difference of about 2 months in the spawning period inside and outside of the bay, even within the

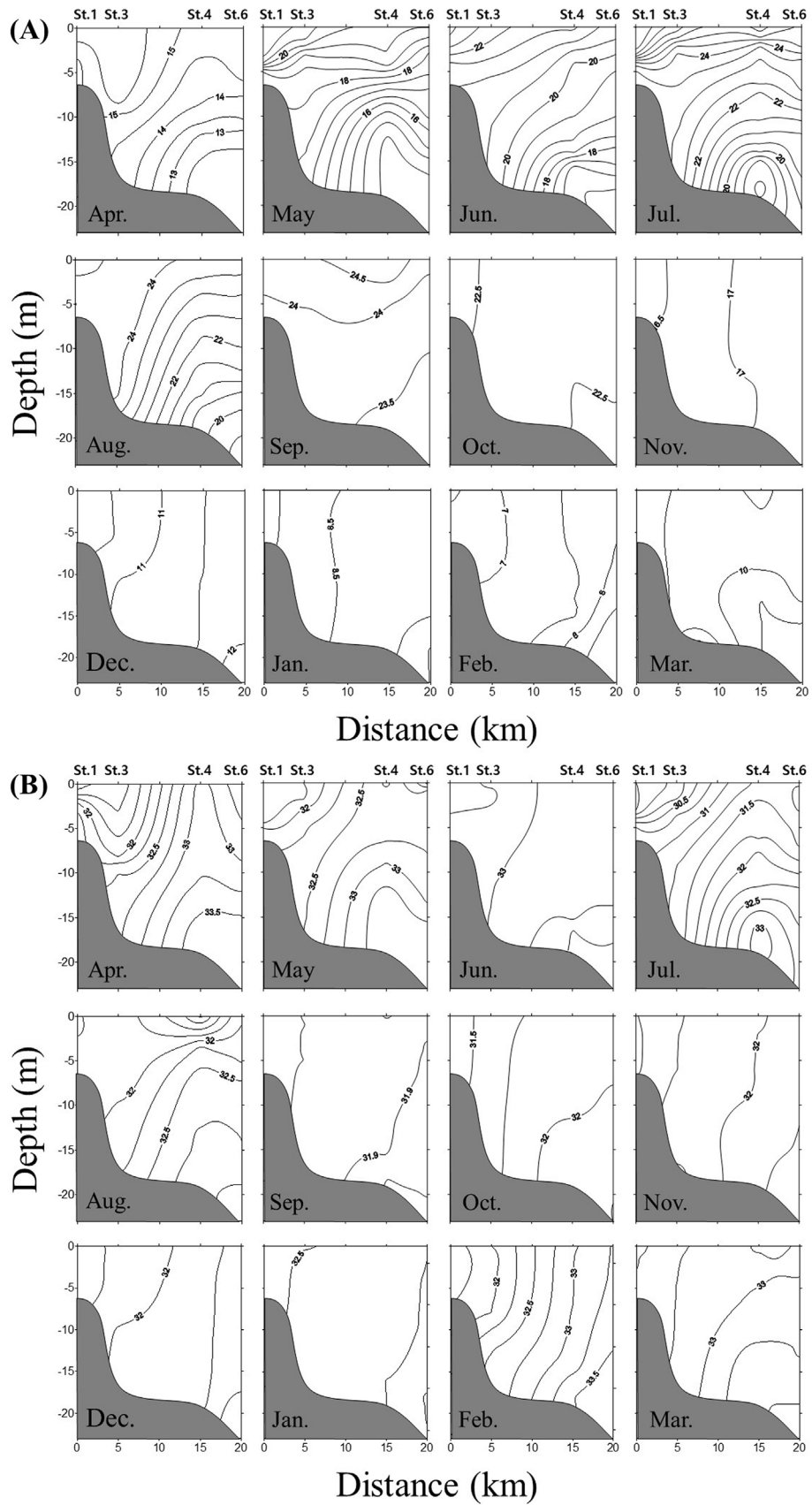


Fig. 5. Monthly variations in seawater temperature (A) and salinity (B) with depth at Jinju Bay, Korea, from April 2015 to March 2016. Contour intervals (solid line) are at 0.5°C for temperature and 0.25 for salinity.

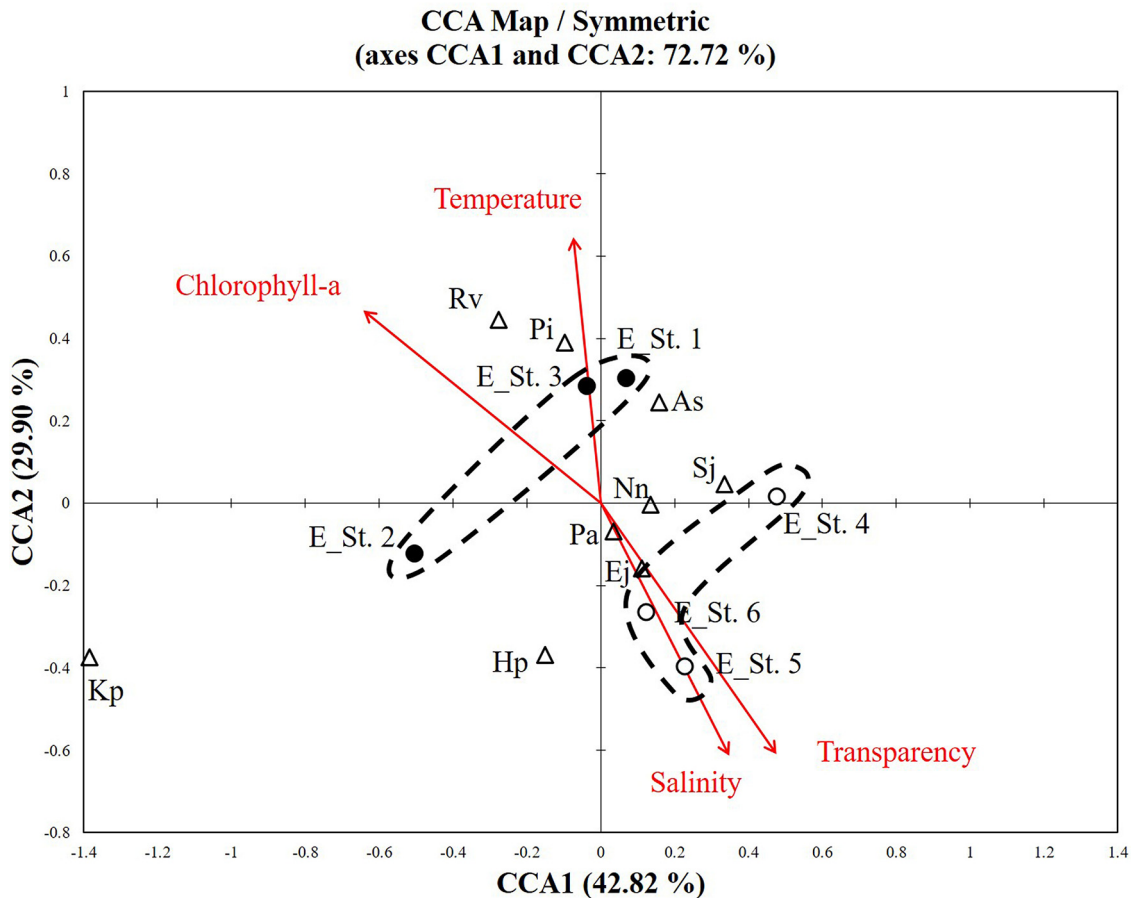


Fig. 6. Canonical Correspondence Analysis (CCA) ordination diagrams of fish egg species in relation to environmental variables (temperature, salinity, transparency, chlorophyll-*a*) inside (black circle) and outside (white circle) in the Jinju bay, Korea (Species codes: Ej, *Engraulis japonicus*; Rv, *Repomucenus valenciennesi*; Nn, *Nuchequula nuchalis*; Sj, *Sillago japonica*; Hp, *Halichoeres poecilopterus*; As, *Acanthopagrus schlegelii*; Kp, *Konosirus punctatus*; Pa, *Pennahia argentata*; Pi, *Platycephalus indicus*).

same species. During the period when fish eggs and larvae were collected most intensively, eggs of *P. argentata*, *Pseudaesopia japonica*, and *Pagrus major* were collected 1 month earlier in the bay (Tabs. 1 and 2). Larvae of *S. japonica*, *O. elegans*, *P. indicus*, and *N. nuchalis* were collected 1 month earlier inside the bay than outside (Tabs. 3 and 4). The flow of currents into the bay due to its shape, depth, and the amount of water discharged from the dam can be used predict the migration paths of eggs and larvae, which will be useful for resource management (Soares et al., 2019). Changes in water depth and differences in Chl-*a* concentration may also influence spawning behavior in these areas (Duffy-Anderson et al., 2006; Rodríguez, 2008). Further research is required to elucidate the mechanisms driving spawning behavior in this region.

One limitation of this study is the relatively short duration of fish egg and larva collection. As our sampling efforts were restricted to within 1 year, seasonal trends in egg and larval demography could not be established. Such trends are important for understanding fish recruitment in this region. Their impacts on local fisheries should be studied in future multi-year research projects on the early life history stages of fishes within the Jinju Bay region. Patterns of fish egg and larval distribution can vary sporadically among years, and it

can be difficult to understand true patterns within ecological noise (Able and Fahay, 2010; Ospina-Alvarez et al., 2015; Baptista et al., 2020). Understanding trends in such data is important for managing the spawning and nursery grounds of these fishes.

An understanding of movement dynamics in the early life history stages of the fishes associated with Jinju Bay is useful for identifying the parameters important to successful spawning and larval dispersal of the ichthyoplankton community. Such parameters are critical to the sustainable management of these species and their associated fisheries. Further research is required to understand the larval dispersal and recruitment of fish species in this region.

Supplementary Material

Table S1. Morphological and DNA barcode identification of fish eggs in Jinju Bay, Korea.

Table S2. Morphological and DNA barcode identification of fish larvae in Jinju Bay, Korea.

The Supplementary Material is available at <https://www.alr-journal.org/10.1051/alr/2021017/olm>.

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