

1 **Ichthyoplankton community associated with oceanic fronts in early**
2 **winter on the continental shelf of the southern East China Sea**

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16
17 **ABSTRACT**

18 Ichthyoplankton communities associated with oceanic features on the continental
19 shelf of the southern East China Sea (ECS) were studied in early winter of the years
20 2006 to 2009. Species composition of ichthyoplankton and its spatial distribution
21 were classified and compared with oceanic fronts. In total, 1809 fish larval individuals
22 belonging to 76 families and 137 taxa were identified from 5 field surveys. Using the
23 Bray-Curtis dissimilarity index, the identified taxa with abundances of > 0.5% from
24 36 stations were classified into 4 groups: China coastal group, mixed shelf group,
25 Taiwan Strait group, and Kuroshio group. The shallow-water species of *Sebastiscus*
26 *marmoratus* dominated the China coastal group; different species components were
27 found in the mixed shelf group (*Saurida* spp., *Trichiurus lepturus*, *Bregmaceros* spp.,
28 etc.) and Taiwan Strait group (*Engraulis japonicus* and *Benthoosema pterotum*). The
29 dominant species in the Kuroshio group could also be distinguished from the 3 other
30 groups, including *Gonostoma gracile*, unidentified Myctophid larvae, etc. Spatial
31 distributions of ichthyoplankton community groups were further superimposed on a
32 thermal front map in the study area. It clearly revealed that the China coastal front
33 could be a boundary which separated the China coastal group on the west and the
34 mixed shelf group on the east side. In addition, the abundance and diversity of
35 ichthyoplankton were higher in the region close to the Kuroshio front.

36
37 *Key words:* Ichthyoplankton, East China Sea, Kuroshio front, China coastal front.

38 1. Introduction

39

40 The early life stage is the most important stage for determining annual
41 recruitment of fishes supporting various major commercial fisheries, and many studies
42 focused on ecological aspects of the larval stage, such as the distribution, growth, and
43 survival (Houde, 2008). An oceanic condition, such as currents, eddies, and fronts,
44 play important roles in determining the spatial and temporal distributions of
45 ichthyoplankton in the various seas of the world (Okazaki et al., 2002; Richardson et
46 al., 2010). Several studies suggested fronts that occur at shelf break served as
47 retention mechanisms by aggregating ichthyoplankton within the spawning area or
48 drifting towards the coast (Huang and Chiu, 1998; Ross and Rhode, 2004; Sassa and
49 Konishi, 2006; Wang et al., 1991). These biological-physical linkages are frequently
50 observed the shelf break regions where a boundary between coastal and oceanic
51 waters occurs. For example, dynamic interactions between the Kuroshio Current (KC)
52 and shelf waters at the frontal boundary were thought to potentially affect larval fish
53 transport, distribution, and prey availability (Hsieh et al., 2007a; Okazaki and Nakata,
54 2007; Sassa et al., 2008a, b).

55 The complexity of hydrographic conditions in the southern East China Sea (ECS)
56 is influenced by seasonal changes in currents (Tang et al., 2000). Well-known physical
57 processes in the ECS are the mechanism of the KC between the ECS and the east of
58 Taiwan, which flows northeasterly along the edge of the continental shelf. It
59 transports warm, saline Kuroshio waters and oceanic materials across the shelf into
60 the southern ECS, which means that the Kuroshio front is an important factor
61 affecting this area. Furthermore, the China Coastal Current (CCC) and Taiwan Strait
62 (TS) water (TSW) also determine the major temperature-salinity structure for water
63 masses in the study area. The upwelling caused by the intrusion of Kuroshio
64 subsurface water to the northeast of Taiwan also provides large amounts of nutrients
65 (Chen et al., 2004; Gong et al., 2003). The ECS features extremely stable, primarily
66 wintertime fronts formed by a broad range of physical processes. These fronts were
67 relatively well studied from satellite data (Belkin et al., 2009; Chang et al., 2008;
68 Hickox et al., 2000) and in situ measurements (Chen, 2009; Lee et al., 2005a).

69 In winter, the TSW originates from an overshooting of the KC across the
70 continental shelf northeast of Taiwan, and it flows northeasterly over the middle shelf
71 of the ECS (Lie and Cho, 2002), which provides warm and saline water to the area off
72 the southeastern Chinese coast. The CCC, associated with the Changjiang discharge,
73 flows southward along the Chinese coast (Gong et al., 1995; Gong et al., 2003). The
74 southern ECS (Fig. 1) is thus characterized by strong hydrodynamic front effects
75 caused by these currents along the Chinese coast and Kuroshio edge. The China

76 coastal front (CCF) is a boundary of cold coastal water and mixed waters on the shelf
77 (Chang et al., 2008). In addition, the Kuroshio front to the northeast of Taiwan forms
78 between the KC and shelf water, and reflects large variabilities in the path of the KC
79 (Tang et al., 2000).

80 A previous study revealed that the KC flow pattern to the north of Taiwan
81 migrates seasonally (Tang et al., 2000). In summer, the Kuroshio generally moves
82 offshore from the southern edge of ECS, and splits into northeasterly mainstream and
83 westerly currents. In winter, the KC moves closer to and sometimes onto the northern
84 shelf of Taiwan. The intrusion of the Kuroshio dominates the flow pattern in the
85 region, causing the disappearance or obscuring of the counterclockwise circulation
86 and cold dome (Tang et al., 2000). The Kuroshio flow pattern north of Taiwan was
87 found to vary by season. Variations in transport from the TS and the east of Taiwan
88 have considerable effects on the intrusion of the Kuroshio onto the shelf. Front
89 intrusion studies discussed how the Kuroshio in the present case produces a
90 comprehensive (Gong et al., 1997), objectively derived, year-round climatology of
91 ocean thermal fronts in seas east of China (Hickox et al., 2000) and identified the
92 previously known fronts (Ning et al., 1998). Lan et al. (2008) indicated that seasonal
93 exchanges between coastal and offshore waters could influence the zooplankton, the
94 distribution of which can be divided into 2 distinct communities (inshore and offshore)
95 defined by the dominance of different species. Okazaki and Nakata (2007) also
96 suggested that the Kuroshio frontal eddy may affect larval distributions, due to
97 variations in primary production in the frontal region. However, a comprehensive and
98 definitive pattern of the thermal front and its relationship with fish larvae cannot yet
99 be constructed.

100 Two major oceanographic research projects in Taiwan, the Kuroshio Edge
101 Exchange Processes (KEEP) (Wong et al., 2000) and Long-term Observations and
102 Research of the East China Sea (LORECS), focused on investigating seasonal
103 variations in hydrographic conditions in the ECS (Gong et al., 2006). The KEEP
104 project has been ongoing since 1989 is a multidisciplinary study, focusing on the
105 physical and chemical oceanography within the ECS Shelf and the exchange of
106 material between this Shelf and its adjoining Kuroshio (Gong et al., 1997; Wong et al.,
107 2000). A number of the KEEP studies investigated in the abundance, distribution and
108 diversity of ichthyoplankton of the study area (Chiu and Hsyu, 1994; Huang and Chiu,
109 1998; Lee et al., 1990). Hsieh et al. (2007a) first tried to evaluate the ichthyoplankton
110 distribution in relation to thermal fronts from a single late winter survey. However, the
111 relation between the structure of the larval fish communities and the spatial variability
112 of the thermal front in the continental shelf of southern ECS are still not well
113 described in early winter. Therefore, we tried to examine spatial distributions of fish

114 larval assemblages and their relationships to satellite-derived thermal front on the
115 continental shelf of southern East China Sea.

116

117 **2. Material and methods**

118

119 Oceanic measurements and organism samples used in this study were collected
120 from cruises 1400, 1503, 1598, 1600, and 1692 in December in 2006 to 2009 on board
121 the *Ocean Research II* (Table 1). Hydrographic data and ichthyoplankton samplings
122 were taken at 9 fixed stations on each cruise (Fig. 1). Ichthyoplankton was sampled
123 using an ORI plankton net with a mouth diameter of 1.6 m and a mesh size of 330 μm .
124 A flow meter was tied at the center of the mouth of the net to measure the filtered
125 water volume. The ORI net was towed at ca. 1 m s^{-1} in an oblique way from 200 m
126 deep to the surface. At shallower stations, the net was towed from 10 m above the
127 bottom to the surface. The ichthyoplankton samples were preserved in seawater with
128 5% formalin. Finally, larval fishes were brought to the laboratory for further
129 identification to the lowest taxonomic level as possible.

130 Water temperature and salinity at different depths for every station were obtained
131 by lowering a CTD profiler from the sea surface to a depth near the bottom.
132 Satellite-derived sea surface temperature (SST) observed by National Oceanic and
133 Atmospheric Administration/Advanced Very High Resolution Radiometer
134 (NOAA/AVHRR) sensors were also used from the Department of Environmental
135 Biology and Fisheries Science, National Taiwan Ocean University in this study.
136 Satellite-derived SSTs were validated with a small bias of $0.009 \text{ }^\circ\text{C}$ and root mean
137 square deviation of $0.64 \text{ }^\circ\text{C}$ (Lee et al., 2005b). An entropy-based edge detection
138 method (Shimada et al., 2005) was used to detect the monthly frontal SST gradient
139 magnitude (GM) in the southern ECS. This method is independent of annual
140 variations in geophysical parameters which can detect and retain finer-scale SST
141 fronts, and has been used efficiently in coastal seas (Shimada et al., 2005). The GM is
142 calculated by the following formula:

$$143 \text{ GM (}^\circ\text{C/km)} = \sqrt{(\partial T/\partial x)^2 + (\partial T/\partial y)^2};$$

144 where T is the SST, and the x and y axes are directed toward the east and north,
145 respectively. The GM is computed at all frontal pixels for each image, and then the
146 monthly mean of the GM is computed pixel-wise. The GM map enhances frontal
147 patterns and reveals frontal areas more clearly.

148 Shannon's diversity index was used to calculate the species diversity, and
149 Simpson's evenness was further used to estimate the relative abundances of species at
150 each station. Shannon's diversity index and Simpson's evenness were calculated using

151 the PRIMER (vers. 6) program. A cluster analysis was used for log (X+1)
152 transformation performed with the STATISTIA 7 statistical software package. A
153 cluster analysis with normalized Euclidean distances was used to investigate levels of
154 similarity in species compositions among sampling stations, and Ward's method was
155 used to illustrate the relation of these stations in a dendrogram.

156

157 **3. Results**

158 *3.1. Hydrographic conditions*

159

160 The temperature-salinity (T-S) diagram of the study area is shown in Fig. 2 and
161 compared with the results of previous studies (Gong et al., 1995; Jan et al., 2006).
162 According to Gong et al. (1995), the range of the mainstream KC was denoted by a
163 solid line, and the TSW was distributed to the west of the KC. The dashed line also
164 denotes the KC mainstream (Jan et al., 2006). Most stations in the offshore region in
165 our survey were considered to be KC and TSW with high water salinities (Fig. 2).
166 Inner stations adjacent to the Chinese coast were considered to be China coastal water,
167 with low temperatures and various salinities.

168 Figure 3 shows vertical profiles of water temperature and salinity along the
169 transect of sampling stations during the study period. In December 2006 (Fig. 3a, b),
170 water in the middle of the shelf (at stations K4~K7) was composed of warm shelf
171 water (temperature > 22 °C, salinity < 34.4 psu), while the offshore region, to the east
172 of station K7, was blocked by KC upwelling water with temperatures of < 20 °C and
173 salinities of > 34.4 psu. It was noted that in 2007, the KC had obviously intruded onto
174 the shelf of the southern ECS (stations K5~K7, Fig. 3c, d), which resulted in clear
175 upwelling of Kuroshio subsurface water with temperatures of < 20 °C and salinities of
176 > 34.4 psu. However, the profiles in 2008 and 2009 (Fig. 3e, h) revealed that the KC
177 had intruded onto the shelf, but the subsurface upwelling water (temperatures of > 20
178 °C, salinities of < 34.4 psu) was repressed at the same time and to the east of station
179 K7. This suggests that the intrusion of the KC might have occurred in early winter, but
180 upwelling of the subsurface water did not necessarily occur. The vertical profiles can
181 clearly reveal annual variations in water masses between the CCC and KC. In 2006,
182 the study area was characterized by warm water from the TS.

183

184 *3.2. Distributions of SST fronts and ichthyoplankton abundances*

185

186 Marked thermal fronts, shown in Fig. 4, detected from satellite-derived SST data
187 of December, were averaged to produce a 4-year monthly composite. Two significant
188 frontal bands were found, one in the vicinity of the Chinese coast and another to the

189 northeast of Taiwan. The former frontal band was defined as the China coastal front,
190 and the latter was referred to as the Kuroshio front. The China coastal front was
191 obvious along the 50-m isobath with an SST gradient > 0.15 °C/km, while the
192 Kuroshio front was located between the 100- and 200-m isobaths. However, it was
193 noted that the Kuroshio front was a combination of 2 separate frontal bands: one was
194 a curving, blurred band on the shelf and the other was a straight, sharp band near the
195 shelf break (white arrow) with an SST GM of > 0.2 °C/km. This short band of the
196 Kuroshio front began near the northern tip of Taiwan and then extended northeasterly
197 along the shelf break; we thus suggest that this frontal band is the Kuroshio shelf
198 break front. However, this short front showed its strongest SST GM only to the west
199 of 123°E, but it was rarely found in offshore waters.

200 The 4-year monthly mean abundances of larval fish species a cumulative
201 abundance of $> 50\%$ at each station were superimposed on the SST frontal map (Fig.
202 4); the different scales of the circles indicate different abundances. The abundance
203 near the China coastal front was distinctively lower (with an average abundance of $<$
204 80 individuals (ind.)/1000 m³), but the abundance clearly increased (average
205 abundance of > 150 ind./1000 m³) at stations close to the Kuroshio front, and in the
206 middle of the shelf was ca. 100 ind./1000 m³. Larval fish species with a cumulative
207 abundance of $> 50\%$ were abundant at the Kuroshio front. This suggests that the
208 Kuroshio front was an exceptional phenomenon which made the water very suitable
209 for some species.

210 The maximum value of the SST GM for every frontal boundary in each year
211 from 2006 to 2009 was extracted as frontal boundary lines and superimposed on Fig.
212 5. The boundaries of the China coastal front, Kuroshio front, and Kuroshio shelf break
213 front are respectively denoted by dotted, solid, and dashed lines. We determined that
214 the boundaries of the China coastal front was permanently distributed along the 50-m
215 isobath with slightly variations and the Kuroshio shelf break front existed along the
216 shelf break. However, the curving Kuroshio front on the shelf significantly varied
217 with year. It was noted that the Kuroshio front moved offshore in 2006 (gray curve),
218 but it intruded more inshore in 2007 (black curve). For 2008 and 2009, the Kuroshio
219 front exhibited normal distributions near the 100-m isobath.

220

221 3.3. *Distribution of ichthyoplankton assemblages*

222

223 In total, 1809 fish larval individuals representing 76 families and 137 taxa were
224 collected in the 5 surveys. In the oblique net tows in December of the years 2006 to
225 2009, 6060.39 ind./1000 m³ larvae were captured (Table 2). Thirteen taxa contributed
226 approximately 75% to the total catch: Myctophid larvae, *Gonostoma gracile*,

227 *Sebastiscus marmoratus*, *Benthosema pterotum*, *Bregmaceros* spp., *Engraulis*
228 *japonicus*, *Saurida* spp., *Encrasicholina punctifer*, *Trichiurus lepturus*, Apogonid
229 larvae, Callionymid larvae, *Scomber* spp. and Serranid larvae. In the dendrogram
230 using Bray-Curtis dissimilarity, identified taxa with > 0.5% abundance from 36
231 stations for tows that caught at least 1 larva were classified into 4 groups: A, B, C, and
232 D (Fig. 6). According to geolocations of every single station comprising each group,
233 the defined 4 groups were further referred to as the China coastal group (A), mixed
234 shelf group (B), Taiwan Strait group (C), and Kuroshio group (D). The dominant
235 species in the China coastal group was *Sebastiscus marmoratus*; this differed from the
236 species in the mixed shelf group (*Saurida* spp., *Trichiurus lepturus*, and *Bregmaceros*
237 spp.) and Taiwan Strait group (*Engraulis japonicus* and *Benthosema pterotum*). The
238 dominant species in the Kuroshio group could also be distinguished from the other 3
239 groups (*Gonostoma gracile* and Myctophid larvae; Table 2, boldface).

240 Stations of the China coastal group were located in the region of cold fresh
241 waters that were influenced by the CCC. Hydrographic features where the mixed shelf
242 group was distributed were distinctive with wide variations in water temperatures and
243 salinities. The Taiwan Strait group was only identified from sampling data in 2006,
244 where the T-S diagram showed the stations were surrounded by the TSW (Figs. 2, 3).
245 Stations of the Kuroshio group were located between the Kuroshio front region and
246 the edge of the continental shelf. The water in this region was warm and saline and
247 was supplied from an intrusion of the KC. In 2007 to 2009, the Kuroshio front
248 intruded more inshore and varied between stations K7 and K8 (Fig. 5), and the
249 Kuroshio groups were mostly to the east of the front. Fish congregated in the mixing
250 zone, where the CCC and the KC blended, creating a complex temperature and
251 salinity structure, as the mixed shelf group. However, a special case occurred in 2006
252 that the KC receded onto the shelf as the Taiwan Strait warm water intruded into the
253 middle shelf area. In our results, the annual variation in water masses caused the
254 discrepancy on the larval cluster analysis.

255 In contrast, a water mass of approximately 23 °C intruded into the southern ECS
256 where waters of the TSW intruded in 2006. The larval fish distribution in 2006 was
257 densest in the middle shelf region from stations K3 to K8, and only a few larval fish
258 were distributed in the China coastal area. Therefore, our results divided the fish
259 distributions in the middle shelf region into 2 groups: the China Coastal group in 2007
260 to 2009 and the Taiwan Strait group in 2006. The China coastal group located in the
261 area surrounded by the Chinese coast in 2007 to 2009 clearly revealed that the
262 Chinese coastal front could be the boundary, which separated the China coastal group
263 to the west and the mixed shelf group to the east. In addition, the Kuroshio front on
264 the shelf bounded the Taiwan Strait group in the northern end of the TS, and separated

265 the Kuroshio group in the Kuroshio region in the east.

266

267 3.4. Specific taxon distributions, abundances, and diversity

268

269 The abundances of the larval assemblages were relatively high in the Kuroshio
270 region and were low in coastal regions (Fig. 4, Table 2). We examined the cross-shelf
271 distribution of dominant fish larvae from 2006 to 2009 (Fig. 7) with vertical dashed
272 lines indicating the China Coastal front and solid line indicating the Kuroshio front
273 (standards marked as the place closest to the Chinese coast referring to Fig. 5). It
274 should be noted that *Sebastiscus marmoratus* was mostly found in 2008 and 2009 at
275 stations K1 and K2, where an inshore surface intrusion of low-temperature water
276 occurred. On the other hand, Myctophid larvae were abundant in the warm water
277 stream from the Kuroshio in the shelf region. As shown in Fig. 7, *Benthosema*
278 *pterotum* had the highest abundances on both sides of the Kuroshio front region,
279 although part of its assemblage was also distributed at stations K3 to K8 in 2006.
280 *Engraulis japonicus* was distributed at stations K4 to K7 only in 2006, and *Trichiurus*
281 *lepturus* was abundant at stations K5 and K6 in 2007. *Bregmaceros* spp. were found
282 in waters of all stations, and *Gonostoma gracile* was abundant in the warm Kuroshio
283 stations in 2007, when the surface water of the KC had intruded further onto the shelf.

284 The variation of larval fish abundance and diversity in relation to the position of
285 Kuroshio front were shown in Fig. 8. The x-axis shows the distance of each station in
286 reference to the Kuroshio front, with negative values indicating the distance of
287 stations to the west of the front, and positive values revealing the region to the east of
288 the front. It was interesting that the abundance of larvae (Fig. 8a) was usually lower in
289 the western region far from the Kuroshio front, but higher at stations close to the front.
290 Shannon's diversity index value of larval fishes (Fig. 8b) gradually increased at
291 stations closer to the Kuroshio front.

292

293 4. Discussion

294

295 The survival of larval fishes greatly depends on environmental factors such as
296 fronts and currents (Grioche and Koubbi, 1997; Okazaki et al., 2003), frontal eddies
297 (Okazaki and Nakata, 2007; Okazaki et al., 2002), and tides (Epifanio and Garvine,
298 2001). In this study, the spatial distributions and species components of larval fishes
299 may have been strongly affected by variations in water masses on the continental shelf
300 of the southern ECS. The hydrographic features on the shelf of the ECS during the
301 early winter are strongly influenced by the KC and CCC. These features associated
302 with the topography contribute to the formation of thermal fronts between the water

303 masses. The China coastal front is a long frontal band along the Chinese coast, which
304 acts as a boundary between cold, fresh coastal water and warm, saline mixed shelf
305 water (Chang et al., 2006). On the other hand, the Kuroshio front forming on the shelf
306 could be attributed to the Kuroshio intrusion, and its subsurface upwelling interacted
307 with mixing shelf water, thus simultaneously resulting in thermal fronts and high
308 chlorophyll concentrations (Chang et al., 2008). Although the curving part of this
309 front was well defined by Hickox et al. (2000) and Chang et al. (2006, 2008), the
310 straight, sharp band was rarely discussed previously. It is suggested that the short
311 distribution of the Kuroshio shelf break front on the west side of 123°E might resulted
312 from the interaction between the KC and uplifted topography at the northern tip of
313 Taiwan. While the Kuroshio flows into the Okinawa Trough from 123°E, the
314 topography sharply decreases, which would made the water mass more stable,
315 resulting in a rarely occurring thermal front.

316 In addition, 4 major assemblages of larval fishes were defined based on
317 hydrographic features and thermal fronts in this study. They are the China coastal
318 group, mixed shelf group, Taiwan Strait group, and Kuroshio group. During sampling
319 periods, abundances varied significantly in each group, while the Kuroshio group had
320 higher abundances than the China coastal group. Moreover, species components also
321 revealed significant differences among the groups, with detail comparisons described
322 bellow.

323

324 4.1. China coastal group

325

326 The China coastal assemblage was distinguished by a greater abundance of
327 *Sebastiscus marmoratus* (i.e., rockfish), which prefers shallow near-shore water or
328 rocky bottoms (Okiyama, 1988). This ovoviviparous species has a long spawning
329 period. Its larvae can be found from November to May (Okiyama, 1988); but it is
330 abundant during December to March in waters near Taiwan (Takano et al., 1991).
331 Although fish eggs and larvae may have been transported from elsewhere or
332 aggregated by environmental factors (Sassa et al., 2006), the distribution of the larval
333 fish relative to the front suggests adaptive spawning strategies in response to
334 environmental conditions (Ross and Rhode, 2004). However, because it is
335 ovoviviparous, there were no eggs of *S. marmoratus*, but larval fishes after hatching
336 were at the pre-flexion stage. Nevertheless, pre-flexion stage larvae still have no
337 swimming ability. Therefore, the survival of *S. marmoratus* larvae still depends on
338 environmental factors. Wu (2000) studied the effect of several environmental factors
339 on the life, growth, and survival of *S. marmoratus* larvae. His results showed that *S.*
340 *marmoratus* larvae schooled, were attracted to weak light, and were transported by

341 currents. Results also suggested that the optimal survival temperature of this species
342 was in a water mass at 10~14 °C. To compare hydrographic data in our study, the
343 CCC (temperature < 19 °C, salinity < 33 psu) flowed southward and extended more
344 offshore in 2008 and 2009 (Fig. 3e-h) than in the other 2 years. The spatial
345 distribution of dominant species in Fig. 7 also revealed that abundances of *S.*
346 *marmoratus* were higher at stations K1 and K2 in 2008 and 2009 (Fig. 7c, d), which
347 was bounded by the China coastal front (gray dashed line) to the west. As a
348 consequence, the temporal-spatial distribution of the southerly CCC and abundance of
349 *S. marmoratus* seemed to be highly related. In addition, brood fishes of *S.*
350 *marmoratus* ascribed as being ovoviviparous would select a beneficial environment
351 for their larvae to survive and remain. As a result, the shallow, low-temperature
352 water along the Chinese coast is the best choice for them. We thus suggest that the
353 southerly movement of the CCC with temperatures of < 19 °C might make a suitable
354 environment for *S. marmoratus*, such that its great abundance was found near the
355 Chinese coast in years with strong intrusion of the CCC.

356

357 4.2. Mixed shelf group

358

359 The mixed shelf assemblage was distinguished by *Trichiurus lepturus*, *Saurida*
360 spp. and *Bregmaceros* spp. In general, *T. lepturus* is found throughout the tropical and
361 temperate waters of the world, and its larvae are usually inhabited in muddy bottoms
362 of shallow coastal waters and often enter estuaries for feeding. *Saurida* spp. are
363 usually distributed in shallow waters and estuaries on the shelf (Leis and Rennis,
364 1983). *Bregmaceros* spp. larvae are distributed from shallow to deep waters around
365 Taiwan (Hsieh et al., 2007b; Lo et al., 2010), but most adults of *Bregmaceros* spp. are
366 distributed in deeper waters. In addition, the environment of the mixed shelf region
367 was complex, where mixing of inner-shore and outer-shore waters occurred.
368 Therefore, *T. lepturus*, *Saurida* spp., and *Bregmaceros* spp., were widely distributed
369 on the ECS shelf, so these 3 taxa were defined as mixed shelf group in this study.
370 However, the distribution of these fish larvae seemed to be associated with
371 topographic features and currents. *T. lepturus* was distributed at the northern end of
372 Taiwan Strait, to the west of the Kuroshio front during the study period. Abundances
373 of *T. lepturus* reached a maximum at stations K5 and K6 (Fig. 7b), which are
374 occupied by mixed shelf water. High abundances of *T. lepturus* were also found by
375 Hsieh et al. (2007a) at similar locations. Our results further revealed that *T. lepturus*
376 was more abundant in 2007 than in other years. Adult *T. lepturus* is widely distributed
377 with multi-spawning times in the ECS and Taiwan Strait (Chiou et al., 2006; Hsieh et
378 al., 2007b; Wang et al., 2006); however, such annual variations of its larval fish

379 abundances in this region were rarely discussed. We thus suggest that the intrusion of
380 the KC might compress the space where *T. lepturus* larvae exist thus increasing the
381 density of the larvae in the shelf region. This might have caused the great abundance
382 found in the middle shelf in the year with strong intrusion of the KC. However,
383 studying the detail mechanisms of larval spatial distributions related to oceanography
384 still remains for the future.

385

386 4.3. Taiwan Strait group

387

388 The Taiwan Strait assemblage was distinguished by *Engraulis japonicus* and
389 *Benthoosema pterotum* larvae, which were only abundant in the northern end of the TS
390 in 2006. In general, *B. pterotum* is a kind of lanternfish, the habitat of which is in
391 benthopelagic and mesopelagic areas of the slope and in continental and island waters.
392 According to [Huang and Chiu \(1998\)](#) and [Chiu and Hsyu \(1994\)](#), *B. pterotum* is
393 abundant in winter and is the most common lanternfish species in the southern ECS.
394 [Huang and Chiu \(1998\)](#) also indicated that *B. pterotum* was widely distributed around
395 the waters of Taiwan, especially in the TS, which corresponds with our results.
396 However, the warm TSW only appeared in 2006 and showed the TS larval group.

397 It was also found that *E. japonicus* was abundant in the northern end of the TS
398 where the water temperature was about 22 °C. It is well known that *E. japonicus* is a
399 major species in the inshore waters of the continental shelf area. It comes in large
400 schools near the surface, mainly in coastal waters but as far out as over 1000 km from
401 the shore. Spatial patterns in the distribution and abundance of *E. japonicus* eggs were
402 studied in the area off the Changjiang River, China where a large spawning ground
403 exists ([Iseki and Kiyomoto, 1997](#)). In addition, [Takasuka et al. \(2007\)](#) examined the
404 growth rate of larval samples at the optimal temperature of 22.0 °C collected at
405 different locations during various seasons. They generally moved to and aggregated in
406 estuarine areas for feeding, where water temperatures varied 22.6~30 °C ([Lee et al.,](#)
407 [1990](#)). According to the circulation patterns of the TS in winter ([Jan et al., 2002](#)), a
408 portion of the southward penetration of the CCC is deflected by the Chang-Yuen
409 Ridge and turns back northeastward. As show in SST images ([Fig. 9a](#)), it was noted
410 that in 2006, the TSW significantly intruded northward to the northern TS, while the
411 feature was not found in the other 3 years. The northward TSW might bring a reflux
412 of the CCC (arrows) from the northern Chang-Yuen Ridge to the northern TS.
413 Therefore, the interaction between the northerly intrusion of TSW and a portion of the
414 CCC could play an important role in ichthyoplankton transport in the study area.
415 Judging from the fish larval distributions and hydrographic features in this study, we
416 suggest that *E. japonicus* which spawns offshore of the Changjiang area may be

417 driven southerly to the TS by the CCC after the fish have hatched. In addition, the
418 northward current mixed with a reflux portion of the CCC and TSW could thus
419 transport *E. japonicus* and *B. pterotum* to the southern ECS from the TS.

420

421 4.4. Kuroshio group

422

423 The Kuroshio assemblage was distinguished by *Gonostoma gracile* and
424 Myctophid larvae, and was unique from the other groups. Figure 7b shows that in
425 2007, the major species of *G. gracile* in the Kuroshio group was significantly
426 abundant at stations to the east of the Kuroshio front. Abundant *G. gracile* and
427 Myctophid larvae observed in the present study corresponded to spatial distributions
428 reported by Hsieh et al. (2007b) and Tzeng (1989). Indeed, *G. gracile* and Myctophid
429 larvae are both lanternfishes, a kind of mesopelagic species among the most widely
430 distributed, populous, and diverse of all vertebrates, which play important ecological
431 roles as prey for larger organisms. Some species of the Myctophidae and
432 Gonostomatidae are used as indicator species of the KC because they mostly occur
433 within the KC and adjacent areas (Hsieh et al., 2010). However, in 2006, the Kuroshio
434 group was not observed in the southern ECS as the Kuroshio front had formed far
435 from the shelf (gray contour in Fig. 5).

436 The schematic map in Fig. 5 reveals that the straight-sharp Kuroshio shelf break
437 front was persistent near the 200-m isobath; however, the curving Kuroshio front on
438 the shelf changed with clear annual variations. It is well known that the frontal band
439 caused by the topographic uplift and Kuroshio intrusion is a unique feature in waters
440 northeast of Taiwan (Tang et al., 2000), an important region for the transport of
441 marine organisms. Previous studies indicated that the Kuroshio collides with the
442 continental shelf break of the ECS with different scales of temporal variations from
443 daily, monthly to annually (Chang et al., 2008; Lee et al., 2005a; Tang et al., 2000).
444 Lee et al. (2005a) further suggested that the more-northerly intrusion of TSW from the
445 Strait can result in a more-offshore distribution of the Kuroshio front in northeastern
446 Taiwan. This corresponds well with the SST images in this study (Fig. 9a), i.e., the
447 TSW current had intruded further northward in 2006. According to Okazaki and
448 Nakata (2007), the abundance and diversity of larval fishes were less at lower
449 temperatures and increased with increasing temperature of these waters. Lan et al.
450 (2008) also indicated the abundance and Shannon's diversity index value of plankton
451 increased near the Kuroshio front area. Figure 8 thus provides clearer features of the
452 relationship between the Kuroshio front and spatial distribution of biodiversity. As a
453 consequence, we suggest that when the Kuroshio front forms more inshore, a greater
454 abundance of *G. gracile* will be found in the Kuroshio region.

455 5. Conclusion

456

457 The spatial distribution of the dominant species of *Sebastiscus marmoratus* was
458 higher in the region close to the Chinese coast and was bounded by the China coastal
459 front. Our data further showed that abundance of *S. marmoratus* was highly related to
460 the strong southerly movement of the CCC where the environment may be suitable for
461 the survival of *S. marmoratus* larvae. Although *Trichiurus lepturus* is widely
462 distributed on the ECS shelf, which was defined as the mixed shelf group in this study,
463 its distribution seemed to be associated with the Kuroshio front intrusion. However,
464 the relationship between the mixed water and larval assemblage of *T. lepturus* is not
465 understood yet. In addition, the unique distribution of *Engraulis japonicus* observed
466 in 2006 was suggested to be caused by an interaction between a portion of the CCC at
467 the Chang-Yuen Ridge and the northward TSW. We suggest that larval *E. japonicus* is
468 driven southerly along the Chinese coast by the CCC, and is transported to the
469 northern end of the TS by a reflux portion of the CCC and TSW. Based on the above
470 information, the front plays an important part in larval fishes. The migration of the
471 Kuroshio front causes annual variability in the spatial distributions of *Gonostoma*
472 *gracile* and Myctophid larvae. The Kuroshio front is accompanied by an interaction
473 with KC intrusions into the inner shelf and the mixed shelf water flowing from the TS;
474 thus, generation of the Kuroshio front may result in cross-frontal transport of marine
475 organisms and larval fishes in the study area. As a consequence, abundances of
476 Kuroshio group dominant species were strongly related to the intrusion intensity of
477 the KC. In other words, the more the KC intruded, the more abundant were Kuroshio
478 species.

479 The CCC front and its reflux water caused different patterns of larvae belonging
480 to the China coastal group. *Sebastiscus marmoratus*' distribution and the latter
481 contribute to the abundance of *Engraulis japonicus*. In summary, our results indicate
482 that the horizontal distribution of larval fish in the shelf region of the southern ECS is
483 highly influenced by the dynamics of Kuroshio front intrusions. In addition, although
484 we did not examine larval fish distribution in other seasons, it is likely that different
485 patterns of seasonal variations in the water would affect the horizontal distributions of
486 larval fishes. Moreover, larval fish abundances were higher in the Kuroshio front
487 region than in the inner shelf region, but abundances of relatively different species
488 significantly varied between the shelf and off the shelf. Thus, cross-shelf advection
489 associated with the Kuroshio front was concluded to strongly affect the survival
490 strategy of the early life stages by larval transport. Future studies need to clarify
491 seasonal variations of fish larvae in relation to hydrographic conditions in the
492 southern ECS.

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494

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499

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