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Temporal succession and spatial segregation of clupeoid larvae in the coastal waters off the Tanshui River Estuary, northern Taiwan

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Abstract In the coastal waters off the Tanshui River Estuary in northern Taiwan, eight species of clupeoid larvae were observed. They exhibited a distinct temporal succession in association with seasonal temperature changing. The time of peak abundance of *Etrumeus teres* was in January, *Engraulis japonicus* in late April, *Sardinella* spp. in mid-May, *Dussumieria elopsoides* in early June, *Thryssa dussumieri* in late June, *Stolephorus insularis* in mid-September, *Encrasicholina heteroloba* in early October and *E. punctifer* in mid-November. The time intervals of the temporal succession of the fishes were approximately 15 to 25 d in the spring/summer and 25 to 35 d in the autumn/winter fishing seasons. Also, they showed spatial segregation by distributing in areas with different water depths: *Sardinella* spp. at a water depth of 10 to 20 m, *T. dussumieri* at less than 10 m, *E. heteroloba* at 20 to 50 m and *E. punctifer* at 10 to 40 m. The larvae of these sympatric clupeoid species segregated their nursing periods and areas apparently to reduce competition for habitat and thus to maximize the utilization of resources.

Introduction

Clupeoid larvae (anchovy, sardine and round herring) are the most abundant fishes in the coastal waters off Taiwan (Chen 1985, 1986; Tzeng and Wang 1986, 1992, 1993; Wang et al. 1991; Wang and Hwang 1992). They are named "bull-ard" in Taiwanese and "shirasu" in Japanese, are harvested for local consumption and constitute the bulk of the catch in coastal fisheries of Taiwan (Chen 1980, 1984; Young et al. 1992). Due to the economic importance of the larval clupeoid fishery, several studies have been conducted for species identification (Chen 1987; Yu and Chiu 1994; Young et al. 1995), species composition (Chen 1980), feeding habits (Chern and Tzeng 1993, 1994), and fishery oceanography (Lee et al. 1990, 1995).

Herring, sardine and anchovy, which constitute the major portion of the catch of world fisheries in temperate regions, have undergone drastic fluctuations in abundance in recent decades (Lluch-Belda et al. 1989; Kawasaki et al. 1991). Pioneer studies on the fluctuation of recruitment of fish stocks were conducted by Hjort (1913, 1926). He postulated that the amount of the recruitment is established at an early life stage soon after larvae absorb their yolk sac. Although there was some argument concerning Hjort's hypothesis (Ahlstrom 1965; May 1974; Smith 1981; Methot 1983), this critical-period hypothesis has stimulated considerable research and formed the basis for many attempts to explain interannual variability in recruitment of fish larvae and juveniles (Blaxter 1974; Cushing 1975; Lasker 1981). This work has led to many additional hypotheses on the failure of recruitment, such as match and mismatch between fish larvae and prey (Cushing 1969, 1990; Henderson et al. 1984; Anderson 1988; Chenoweth et al. 1989), advection of currents transporting fish larvae to favorable environments (Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair and Iles 1985; Fortier and Gagne 1990), and impact of the stable ocean environment on larval survival (Lasker 1975; Peterman and Bradford 1987; Peterman et al. 1988).

Anchovy and sardine are sympatric and may compete for the same resources. Often, anchovy are abundant when sardine are scarce and vice versa when they co-occur (Daan 1980; Lluch-Belda et al. 1992). Fluctuations in recruitment might be due to food or habitat competition at the early life stages. However, no evidence has been shown to support this hypothesis. Competition between sympatric species may be avoided through resource partitioning, by habitat segregation, temporal succession or food resource partitioning

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(Helfman 1978; Schoener 1983; Ross 1986). Temporal succession and spatial segregation have been intensively studied for fishes in freshwater (e.g. Post et al. 1995), estuaries (e.g. Humphries and Potter 1993), and open oceans (e.g. Lambert 1984; Hopkins and Gartner 1992). However, studies on the larvae of coastal pelagic fishes, such as clupeoid species, are still lacking.

The present study examined the temporal succession and spatial segregation of the clupeoid larvae in the coastal waters off the Tanshui River Estuary, northern Taiwan.

Materials and methods

Study area

Fish larvae were collected from 26 sites in the fishing grounds situated in the coastal waters off the estuary of Tanshui River (Fig. 1), the largest river in northern Taiwan. The physical and chemical characteristics of the fishing grounds are influenced by both river discharge and oceanic currents, particularly tidal currents, which flow southward in the flood tide and northward in the ebb tide. The contour of the fishing grounds is steeper in the northern part than in the southern part. The bottom is sandy to muddy. The beach is sandy in the south and stony to sandy north of the mouth of the river.

Sampling design

Fish larvae in the catches of commercial set-nets were sampled daily. Because the sea surface was rough, the fishing activity ceased in late summer and late winter. A total of 109 samples was randomly collected among the 26 sampling sites in the spring/summer and autumn/winter fishing seasons, 1992 and 1993. Sea surface temperature was measured in the field with a thermostat sensor and water depth with a fish finder.

The set-net used in the fishery had a body-net 25 m long, 10 m high and 10 m wide (at the net mouth) with two wings approximately 30 m long. The mesh size of the body-net is 11 cm at the frontal part and decreases gradually to 0.1 cm at the cod end. The net was set against the tidal current during daytime. A sample of about 40 g of larvae was collected from each catch, fixed in 5% formalin-seawater solution, and then preserved in 70% alcohol. Each individual larva was identified to species, if possible, according to published descriptions of fish larvae (Okiyama 1988). Some larvae of the genus *Sardinella* were difficult to identify to species and were combined together as *Sardinella* spp. The total lengths of 30 individuals of each species in the sample were measured to the nearest 0.1 mm.

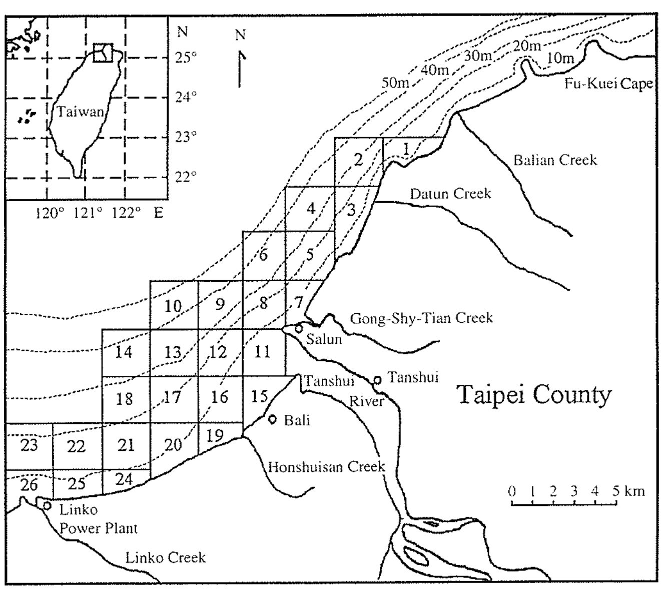

Fig. 1 Fishing grounds of larval fishes in the coastal waters off Tanshui River Estuary, northern Taiwan (*numerals* fishing sites)

Data analysis

According to daily catch (kg) and fishing effort (net-hour), catch per unit effort (CPUE, kg/net-hour) was calculated. The normality of the frequency distribution of total length was tested and the difference in mean total length among species was determined by one-way analysis of variance (ANOVA) with the combined data irrespective of years and seasons. Similarities in the species composition between fishing sites and between fishing dates were determined using Kimoto's (1976) overlap-degree index and then clustered using Mountford's (1962) average-linkage method. The index of overlap ($C\pi$) was calculated as follows:

$$C\pi = 2\Sigma n_{1i} \times n_{2i}/(\Sigma\pi_1{}^2 + \Sigma\pi_2{}^2) \times N_1 \times N_2 \ ,$$

where n_{1i} and n_{2i} were the number of individuals of the ith species in the 1st and 2nd samples, $\Sigma\pi_1{}^2$ and $\Sigma\pi_2{}^2$ the Simpson's index in the 1st and 2nd samples (Ludwig and Reynolds 1988), and N_1 and N_2 the total number of individuals for all species in the 1st and 2nd samples. A total of 78 consecutive samples collected from September 1992 through July 1993 was selected for the similarity analysis.

Mean (±95% confidence interval) sea surface temperature for the catch of the fish was calculated from the frequency of the temperature when the fish occurred. The differences in the temperature association among species were determined by Scheffé's homogeneity test; the relationships of CPUE to sea surface temperature and water depth for each species were determined by Pearson's correlation analysis (Johnson and Wichern 1982).

Results

Size and species composition

A total of 26 343 larval fishes belonging to 45 families and 124 species were collected from 109 samples in the spring/summer and autumn/winter fishing seasons, 1992 and 1993. The larvae were dominated by eight species of clupeoid fishes, and their composition differed significantly among seasons within years but was similar in the same season of different years (Fig. 2). In the spring/summer fishing season, *Sardinella* spp. was most abundant, comprising 33% and 36% of the total catch in 1992 and 1993, respectively. It was followed by *Thryssa dussumieri* (30% in 1992 and 27% in 1993), *Engraulis japonicus* (21% in 1992 and 17% in 1993), and five other clupeoid species (*Etrumeus teres*, *Dussumieria elopsoides*, *Encrasicholina punctifer*, *Encrasicholina heteroloba* and *Stolephorus insularis*; approximately 10%). The above eight species constituted approximately 90% of the total catch, and the remaining 116 species constituted only about 10%. On the other hand, in the au-

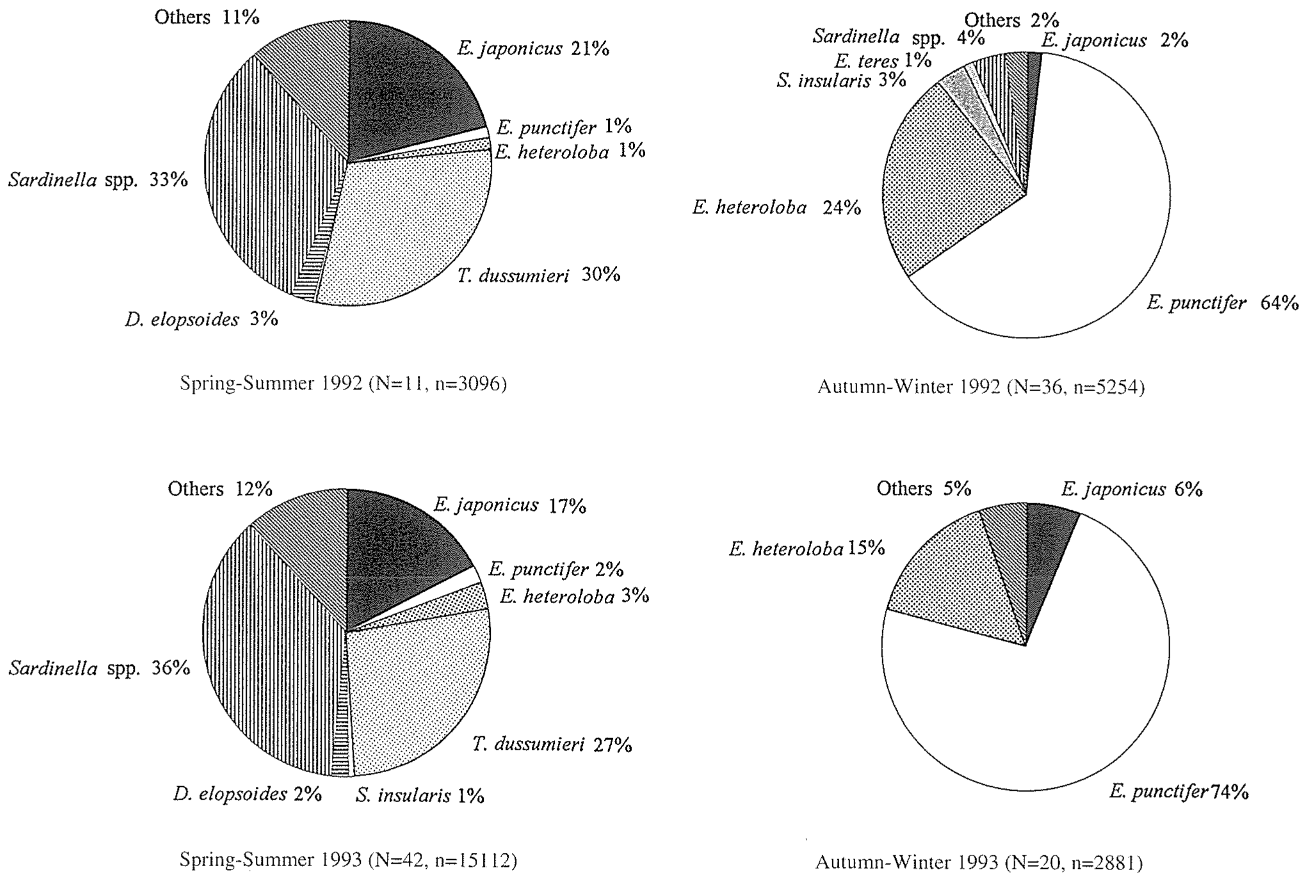

Fig. 2 Species composition (%) of larval fishes in commercial catches from the coastal waters off Tanshui River Estuary in the spring/summer and autumn/winter fishing seasons, 1992 and 1993 (*N* number of samples; *n* number of individuals)

tumn/winter fishing season, *E. punctifer* was the most dominant species comprising 64% and 74% of total catch in 1992 and 1993, respectively. It was followed by *E. heteroloba* (24% in 1992 and 15% in 1993). The remaining 122 species constituted only 12% of the total catch.

The length–frequency distributions of five clupeoid species are shown in Fig. 3. The total lengths ranged between 12 and 36 mm (21.6 ± 4.4 mm, mean ± standard deviation) for *Engraulis japonicus*, 16 and 40 mm (24.8 ± 4.2 mm) for *Encrasicholina punctifer*, 10 and 30 mm (18.2 ± 4.2 mm) for *E. heteroloba*, 8 and 22 mm (15.2 ± 3.9 mm) for *Stolephorus insularis*, and 8 and 26 mm (16.4 ± 4.6 mm) for *Thryssa dussumieri*. The ranges may relate to the retention time of each species in the fishing grounds. The means were significantly different among species (one-way ANOVA, $F_{1,4} = 749.27$, $p < 0.0001$).

Temporal succession

The species composition of 78 samples collected from September 1992 through July 1993 was clustered into five temporal groups: three in the spring/summer (A, B and C) and two in the autumn/winter (D and E) fishing seasons (Fig. 4). The percentage composition of clupeoid larvae of the above five groups are shown in Table 1. For the spring/summer fishing season, Group A was dominated by *Engraulis japonicus* (67% of the total catch) in March to June, Group B by *Sardinella* spp. (64%) in May to June, and Group C by *Thryssa dussumieri* (80%) in June to July. For the autumn/winter season, Group D was dominated by *Encrasicholina heteroloba* (67%) in September to October, and Group E by *E. punctifer* (83%) in October to January.

The temporal changes in abundance of the eight species of clupeoid larvae are shown in Fig. 5. In the spring/summer fishing season, *Engraulis japonicus* occurred from March to May (peak abundance in late April), *Sardinella* spp. from May to June (mid-May), *Stolephorus insularis* from May to June (late May), *Dussumieria elopsoides* from May to June (early June), and *Thryssa dussumieri* from June to July (late June). In the autumn/winter fishing season, *S. insularis* occurred in September (peak in mid-September), *Encrasicholina heteroloba* from September to November (early October), *E. punctifer* from October to February (mid-November), and *Etrumeus teres* from January to March (late January).

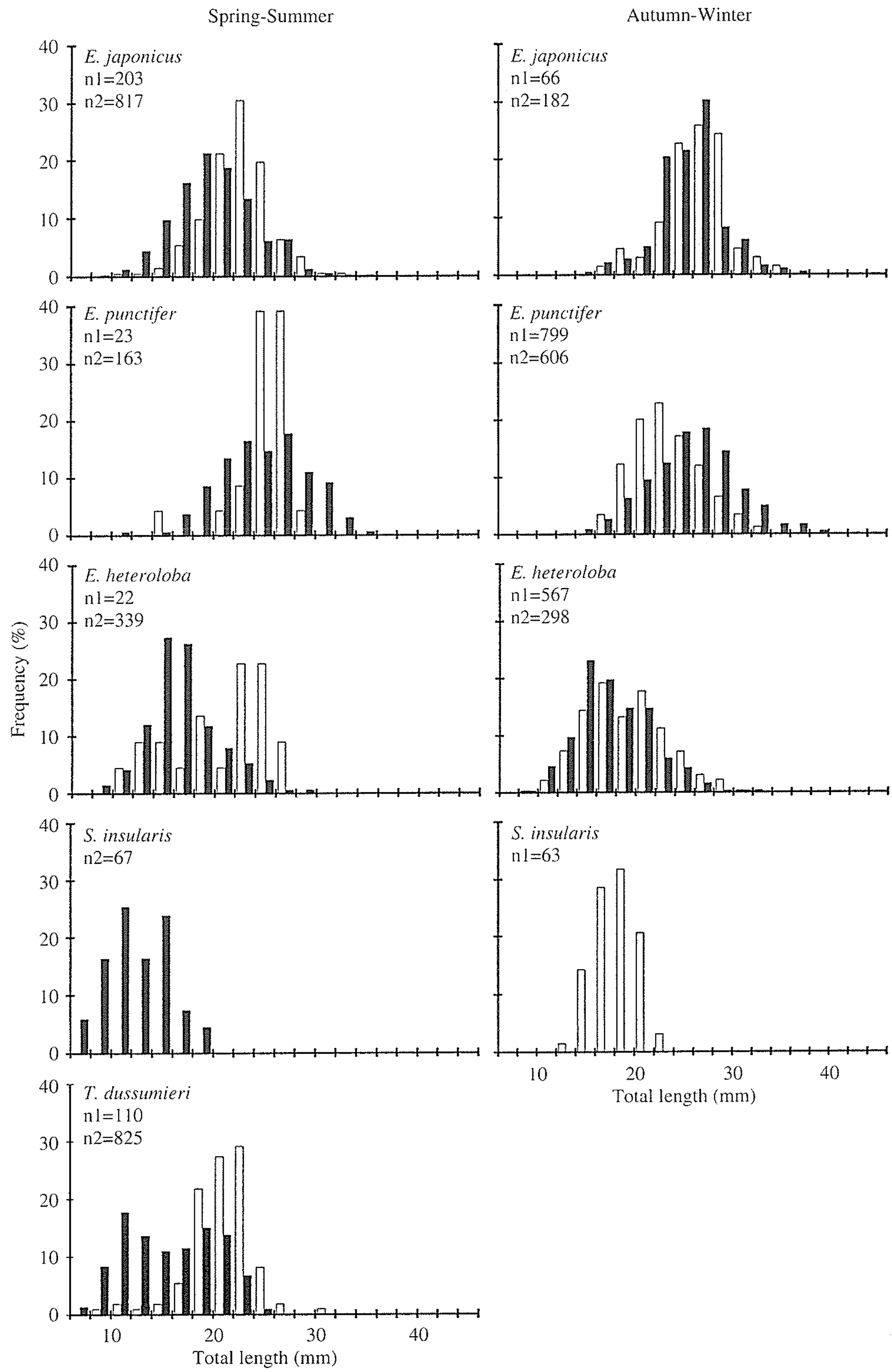

Fig. 3 Length–frequency distributions of clupeoid larvae collected from commercial catches in the coastal waters off Tanshui River Estuary, northern Taiwan, April 1992 to November 1993 (*open columns* 1992; *solid columns* 1993; *n1* sample sizes for 1992; *n2* sample sizes for 1993)

Based on the temporal changes in species dominance and the peaks of abundance of clupeoid larvae (Table 1; Figs. 4, 5), it is evident that there is a temporal succession in the dominant species in the coastal waters off the Tanshui River Estuary. The time intervals of the succession of the dominant species were 15 to 25 d in the spring/summer and 25 to 35 d in the autumn/winter fishing seasons. Also, when two species of clupeoid larvae co-occurred, one was dominant and the other was rare, such as the cases of *Sardinella* spp. versus *Stolephorus insularis* in May, *Thryssa dussumieri* versus *Dussumieria elopsoides* in June, and *Encrasicholina punctifer* versus *Etrumeus teres* in January.

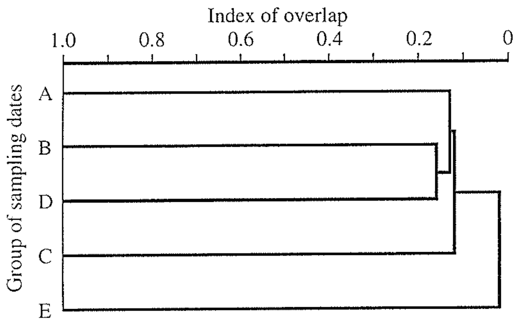

Fig. 4 Clustering of fish species composition of larval fish samples among fishing dates in autumn 1992 to spring 1993. Group A, March–June, *n* (number of samples) = 8; Group B, May–June, *n* = 23; Group C, June–July, *n* = 11; Group D, September–October, *n* = 8; and Group E, October 1992–January 1993, *n* = 28

Spatial distribution

The larval assemblages were divided into two groups in the spring/summer (Groups A and B) and in the autumn/winter (Groups C and D) fishing seasons. The species composition of clupeoid larvae is shown in Table 2 and their distribution in Fig. 6. In the spring/summer fishing season, Group A occurred at Sites 8, 11, 21 and 26 (Fig. 6), and was dominated by *Sardinella* spp. (42%), *Engraulis japonicus* (23%) and *Thryssa dussumieri* (13%) at the water depths around 10 to 20 m. Group B occurred at Sites 15 and 19 and was dominated by *T. dussumieri* (61%) and *Sardinella* spp. (23%) at less than 10 m. In the autumn/winter season, Group C occurred at Sites 8, 9, 10, 13 and 14, outside the mouth of the Tanshui River, at a water depth of between 20 and 50 m, and was dominated by *Encrasicholina heteroloba* (55%), *E. punctifer* (20%) and *Stolephorus insularis* (12%). Group D occurred at Sites 1, 3, 4, 5, 6, 7, 17 and 26 mainly in shallow water at 10 to 40 m in the coastal areas off small creeks. It was dominated by *E. punctifer* (80%) and *E. heteroloba* (12%).

Apparently, for each fishing season, there was a spatial segregation of dominant species in the larval assemblages in coastal waters in relation to water depth and the distance to the mouth of the Tanshui River.

Relationships of CPUE to sea surface temperature and water depth

The homogeneity test indicates that sea surface temperature when clupeoid larvae occurred was different among species (Table 3). The mean sea surface temperature was 19.2 °C for *Etrumeus teres*, 23.6 °C for *Encrasicholina punctifer*, 24.8 °C for *Engraulis japonicus*, 25 °C for *Encrasicholina heteroloba*, and approximately 26 °C for *Sardinella* spp., *Stolephorus insularis*, *Dussumieria elopsoides*, and *Thryssa dussumieri*.

Relationships between the correlation coefficients of CPUEs of eight species of clupeoid larvae to sea surface temperature and the correlation coefficients of CPUEs to water depth are shown in Fig. 7. *Sardinella* spp. and *Thryssa dussumieri* were significantly, positively correlated and *Encrasicholina punctifer* and *Etrumeus teres* were negatively correlated with temperature ($p < 0.05$). *Encrasicholina heteroloba* was significantly, positively correlated and *Sardinella* spp. was negatively correlated with water depth ($p < 0.05$).

Discussion and conclusions

In the coastal waters off northern Taiwan, the cold China Coastal Current flows southward to the study area in winter to early spring, while the warm South China Sea water intrudes northward to the area in mid-spring to autumn (Chu 1963; Fan 1982). Fish assemblages in the study area comprised the temperate species *Etrumeus teres* and *Engraulis japonicus* in winter and spring, and the tropical species *Sardinella* spp., *Thryssa dussumieri*, *Dussumieria elopsoides*, *Stolephorus insularis*, *Encrasicholina heteroloba*, and *E. punctifer* in spring, summer and autumn (Whitehead 1985; Whitehead et al. 1988). The seasonal differences in species may be primarily due to the seasonal changes in the coastal cur-

Table 1 Species composition of clupeoid larvae in the five temporal groups from the coastal waters off Tanshui River Estuary, 1992 to 1993 (Temporal Groups A to E as in Fig. 4)

Species	A		B		C		D		E	
	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
Engraulis japonicus	66.52	1	6.92	4	1.40	6	1.19	6	2.73	3
Sardinella spp.	12.53	2	63.55	1	2.05	4	10.04	3	0.13	6
Others	9.96	3	13.68	2	8.60	2	2.65	5	2.20	4
Thryssa dussumieri	6.28	4	8.22	3	80.34	1	0.14	7	0.05	7
Encrasicholina heteroloba	3.11	5	6.03	5	1.72	5	67.19	1	10.09	2
Encrasicholina punctifer	0.77	6	0.26	8	0.15	7	3.74	4	83.16	1
Dussumieria elopsoides	0.66	7	0.31	7	5.68	3	0.09	8	0.02	8
Etrumeus teres	0.17	8	0		0		0		1.60	5
Stolephorus insularis	0		1.02	6	0.05	8	14.97	2	0	
No. of individuals	2357		9884		2831		1273		4021	
No. of samples	8		23		11		8		28	

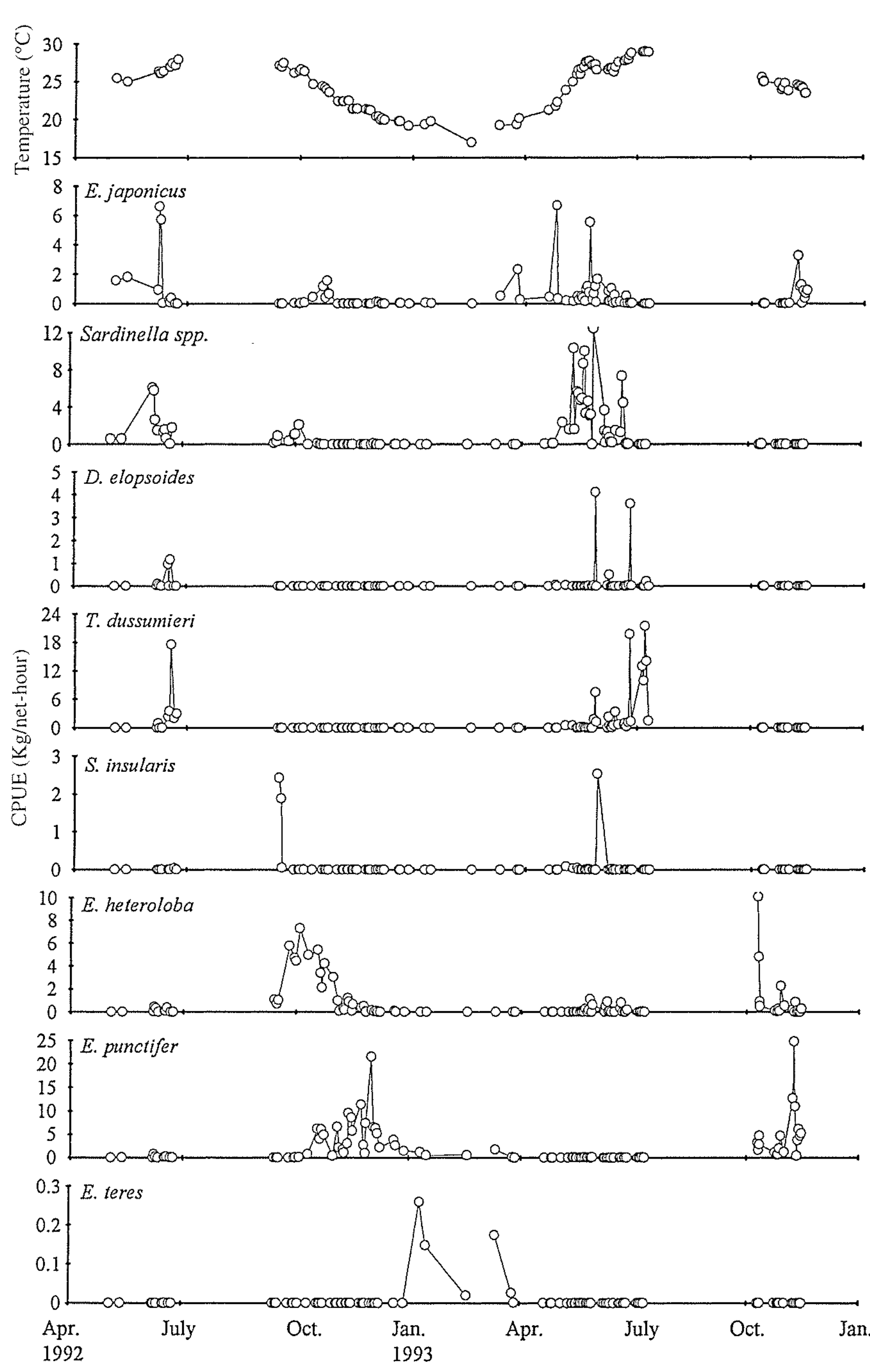

Fig. 5 Sea surface temperature (*upper panel*) and catch per unit effort (*CPUE*) for each species of larval clupeoid fish in commercial catches from the coastal waters off Tanshui River Estuary, April 1992 to October 1993

rents with which the species of clupeoid fishes are associated.

The results of this study showed that there was distinct temporal succession of clupeoid larvae in the coastal waters off the Tanshui River Estuary. Temporal succession has been well documented in larval fishes in lakes and streams (Faber 1967; Amundrud et al. 1974; Floyd et al. 1984; Post et al. 1995). The mechanism of temporal succession in freshwater species has been attributed to differences in temperature requirements for spawning, incubation and growth (Post et al. 1995). In the present study, the sea surface temperature associations of clupeoid larvae were found to be significantly different among species, and were probably the primary cause of the temporal succession of the larvae.

In general, fish larvae and juveniles in estuarine and coastal areas are relatively short-lived and represent a phase of inshore–offshore migration (Yàñez-Arancibia et al. 1980; Beckley 1984; Robertson and Duke 1987). The time intervals of succession of clupeoid larvae were shorter in the spring/summer (15 to 25 d) than in the autumn/winter (25 to 35 d) fishing seasons. This indicated that life-history transition was faster in the spring/summer than autumn/winter fishing season which was

Table 2 Species composition of clupeoid larvae in the four site groups from the coastal water off Tanshui River Estuary, 1992 to 1993 (Site Groups A to D as in Fig. 6)

Species	A		B		C		D	
	%	Rank	%	Rank	%	Rank	%	Rank
Sardinella spp.	42.15	1	23.17	2	8.08	4	1.74	4
Engraulis japonicus	23.36	2	2.30	4	2.46	6	1.53	5
Thryssa dussumieri	12.90	3	61.47	1	0.11	7	0	
Others	12.48	4	9.21	3	2.52	5	2.38	3
Encrasicholina heteroloba	3.82	5	1.54	6	54.71	1	12.4	2
Encrasicholina Punctifer	2.58	6	0.37	7	20.08	2	80.38	1
Dussumieria elopsoides	1.79	7	1.83	5	0.07	8	0	
Stolephorus insularis	0.65	8	0.12	8	11.97	3	0.11	7
Etrumeus teres	0.28	9	0		0		1.46	6
No. of individuals	10 966		4146		1381		3873	
No. of samples	30		12		10		26	

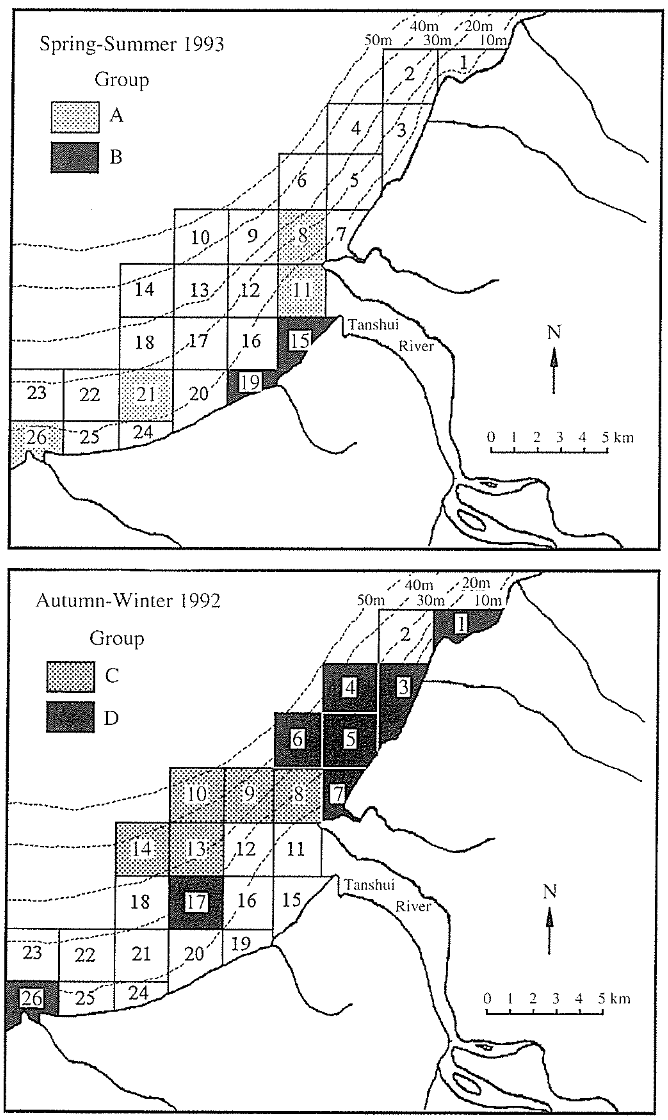

Fig. 6 Spatial distribution of larval fish assemblages in the coastal waters off Tanshui River Estuary in autumn 1992 and spring 1993 (Groups A to D as in Table 2)

probably due to the fact that the temperature was increasing from spring to summer and decreasing during the autumn and winter. Growth rate of the larvae is well known to be influenced by temperature.

Most of the coastal fishing grounds in the world rely upon river discharges to supply nutrients for fish production (Gunter 1967; Walme 1972). Also, salinity (Mitani and Hasegawa 1988; Lee et al. 1990, 1995) and turbidity (Uotani et al. 1993) have been suggested as major causes of the formation of fishing grounds of anchovy larvae in coastal waters. In this study, the fishing grounds of larval clupeoid fishes are located in the coastal waters off the Tanshui River Estuary. This area receives freshwater discharges from the river and other small creeks, which provide a favorable environment (water quality) for the formation of the fishing grounds and supply nutrients for the sustainment of its productivity.

Spatial segregation was observed in the clupeoid larvae in the coastal waters off the Tanshui River Estuary, and the abundance of many species was correlated with water depth. Spatial segregation of fishes may be due to water depth (Hixon 1980; Baker and Ross 1981; Kinoshita and Tanaka 1990; Hopkins and Gartner 1992), rate of water flow (Baltz et al. 1982; Matthews et al. 1982; Moyle and Vondracek 1985), occurrence of aquatic vegetation (Werner and Hall 1976; Magnhagen and Wiederholm 1982; Steffe et al. 1989; Humphries et al. 1992) and type of substratum (Paine et al. 1982; Humphries and Potter 1993). Tzeng and Wang (1993) indicated that different species of fish larvae and juveniles in the study areas distributed in different water depths with different salinities. Accordingly, the spatial segregation of larval clupeoid species in this study may be due to their salinity preference.

Temporal succession and spatial segregation may maximize food resource utilization for sympatric species. Chern and Tzeng (1994) indicated that *Encrasicholina punctifer* and *Stolephorus insularis* had a fairly similar diet, but they occurred in different seasons perhaps to avoid competition of food resources. In this study, we

Table 3 Sea surface temperature and homogeneous groups for the occurrence of the clupeoid larvae in the coastal waters off the Tanshui River Estuary, 1992 to 1993

Species	No. of samples	Sea surface temperature (°C)		Homogeneous groups	Season of occurrence
		Mean	95% confidence interval		
Etrumeus teres	6	19.2	17.2–21.1	A	Winter
Encrasicholina punctifer	74	23.6	23.0–24.2	B	Autumn to winter
Engraulis japonicus	79	24.8	24.3–25.4	C	Spring
Encrasicholina heteroloba	86	25.0	24.5–25.6	CD	Autumn
Sardinella spp.	64	26.0	25.4–26.6	DE	Spring
Stolephorus insularis	15	26.8	25.6–28.0	DE	Spring and autumn
Dussumieria elopsoides	32	26.5	25.7–27.4	E	Summer
Thryssa dussumieri	46	26.7	26.0–27.4	E	Summer

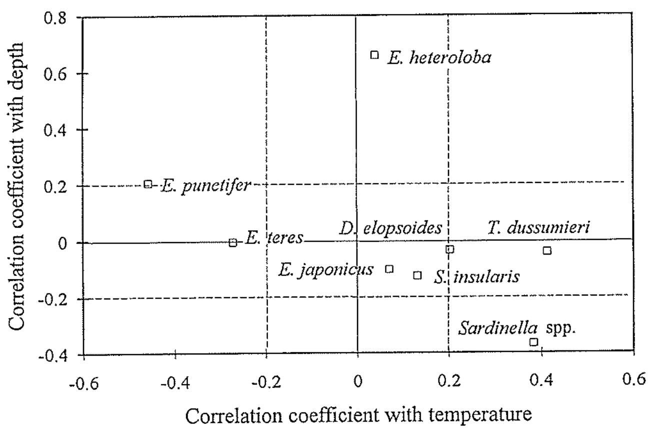

Fig. 7 Ordination of correlation coefficients between CPUE and sea surface temperature, and between CPUE and water depth for eight species of clupeoid larvae in the coastal waters off Tanshui River Estuary (*dashed lines* correlation at 5% significant level)

found that *Engraulis japonicus* and *Encrasicholina heteroloba* have a similar sea surface temperature preference but they occurred in different seasons: the former in spring and the latter in autumn. If the species occurred at the same sea surface temperature of their preference in the same season, such as *Sardinella* spp. (dominant) versus *Stolephorus insularis* (rare) in May, *Thryssa dussumieri* (dominant) versus *Dussumieria elopsoides* (rare) in June, and *E. punctifer* (dominant) versus *Etrumeus teres* (rare) in January, resource competition may result. In such cases, one species was dominant and the other species became rare, as described by Tilman (1982).

In conclusion, sea surface temperature and areas with different water depth are two important environmental variables associated with the temporal and spatial distribution of the clupeoid larvae in the coastal waters off the Tanshui River Estuary. Temporal succession and spatial segregation of the fishes may lead them to avoid or reduce competition for habitat and thus to maximize the utilization of resources.

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