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Hydrography and distribution dynamics of larval and juvenile fishes in the coastal waters of the Tanshui River estuary, Taiwan, with reference to estuarine larval transport

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Abstract. Distribution dynamics of fish larvae and juveniles in the coastal waters of the Tanshui River, Taiwan was studied fortnightly using surface horizontal tows with a larval net in daytime during the period from early April through early June 1991. Environmental factors, including water temperature, salinity, dissolved oxygen, pH, transparency and depth at sampling stations, were also monitored. A total of 10737 fish eggs and 1387 individuals, representing 43 families and 93 species, was collected during five cruises from 12 stations in the coastal waters. Most fish were estuarine-dependent marine species. *Liza macrolepis*, *Ambassis gymnocephalus*, *Terapon jarbua*, Mullidae and Gobiidae were the most dominant, making up 64.7% of the total catch. Early life stages, including egg, preflexion, flexion and postflexion larvae were abundant in surface samples. However, yolk-sac larvae were absent in the surface water, probably due to an ontogenetic behavioral shift as a consequence of a change in specific weight during early development. The species composition of fish larvae and juveniles was related to the microhabitats found in the coastal waters. The physico-chemical conditions, along with ontogenetic behavior, played an important role in larval fish distribution in the coastal waters.

Introduction

The coastal waters adjacent to the Tanshui River estuary make up a commercial fishing ground important for harvesting the juveniles of engraulids and clupeids for local consumers, as well as anguillid elvers for cultivation. There are rare mangroves, *Kandelia candel* (Rhizophoraceae), in the lower estuary of the river (Chou et al. 1987), which provide plentiful organic detritus and a link to the food web of the estuarine-dependent marine fish population during their early life stages (McErlean et al. 1973, Haedrich and Haedrich 1974, Bell et al. 1984, Robertson and Duke 1987, Blaber and Milton 1990). Consequently, the study area functions as a nursery and feeding ground for the onshore-offshore migratory fish.

Due to rapid economic and population growth, the river has been severely polluted, receiving domestic sewage from Taipei city and industrial wastewater from factories in the immediate area (Chou et al. 1987). Thus, the production of larval fishes in the Tanshui River estuary seems to be decreasing and the fishing grounds shifting seaward. In order to begin restoration of the river, a sewage and wastewater processing plant is now under construction at Bali. Treated wastewater will be discharged into the nearshore waters off the Tanshui River, a nursery ground for many commercially important fishes. In order to evaluate the effect of this discharge on distribution and abundance of fish larvae and juveniles in the ecosystem, baseline information, including hydrography, fauna and flora of the estuary is essential. Accordingly, a multidisciplinary team of scientists was formed, supported by the National Science Council, Republic of China, to study the mangrove estuarine ecosystem in the Tanshui River (Chou and Bi 1990).

The temporal and spatial use of estuaries and nearshore waters by estuarine, marine, freshwater and estuarine-dependent marine species has been schematically described by Deegan and Thompson (1985). A conceptual model of the transport of fish larvae and juveniles between nearshore and estuarine nursery areas was proposed on the basis of physical processes, activity and behavior of the fish, and environmental cues (Boehlert and Mundy 1988). In addition, the movement and vertical distribution of the fish larvae and juveniles from offshore to estuaries in relation to spawning mode and development of the fish were also suggested (Tanaka 1976).

The occurrence, abundance and species composition of fish larvae and juveniles in the estuary and nearshore waters varies with the spawning season of the fish and their seasonal onshore-offshore migrations, as well as the physico-chemical conditions during estuarine transportation (Blaber and Whitfield 1977a, b, Weinstein 1979, Bell 1980, Blaber and Blaber 1980, Quinn, 1980, Yáñez-Arancibia et al. 1980, Bell et al. 1984, Loneragan et al. 1986, Mukai 1987, Powell et al. 1989, Blaber and Milton 1990, Robertson and Duke 1990, Sebatés 1990, Drake and Arias 1991 b). The estuarine orientation of the fish is dependent on swimming ability and tolerance of the fish to the extremes of the environmental variables, which differs considerably among species (Kinne 1964, Whitfield et al. 1981), as well as between size and developmental stages of each species (Kinne 1964, Holliday 1971).

The species composition, structure and seasonal dynamics of the larval and juvenile fish community in the mangrove estuary of the Tanshui River has previously been studied (Wang et al. 1991, Tzeng and Wang 1992). The present paper aims to clarify the distribution and abundance of fish larvae and juveniles in relation to environmental factors in the coastal waters adjacent to the Tanshui River estuary.

Materials and methods

Study area

The Tanshui River, approximately 159 km long, is the largest river in northern Taiwan. The river flows through the Taipei basin and meets the sea at the town of Tanshui. The river mouth faces the shallow continental shelf in the northern part of the Taiwan Strait. The estuary belongs to a coastal plain estuary, its hydrography being greatly influenced by tidal currents. The direction of the tidal current is southward during flood and northward during ebb, with a tidal range in the river inlet from approximately 3.0 m at spring tide to 1.5 m at neap tide (Lee and Chu 1965). Twelve stations in the nearshore waters of the Tanshui River were selected for larval and juvenile fish sampling (Fig. 1). These stations were chosen because they will probably be affected by the treated wastewater discharged from the Bali wastewater processing plant.

The topography is deeper in the northern, offshore areas and shallower in the river inlet and in the southern part of the studied habitat. The depth of the sampling stations ranged from 10 to 50 m (Fig. 1).

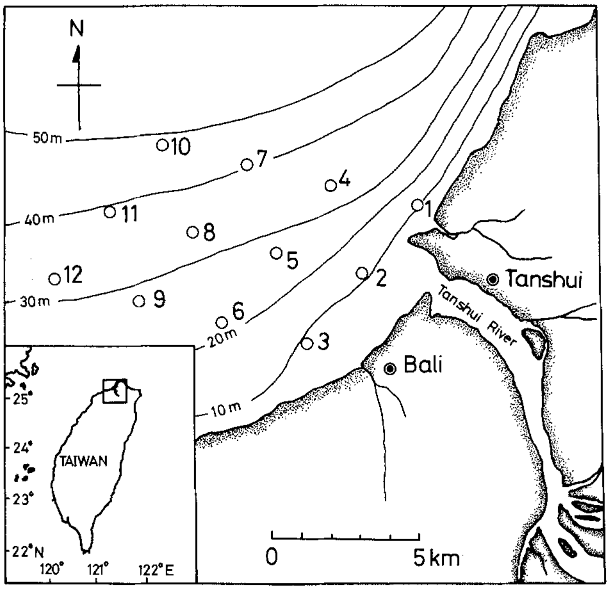

Fig. 1. Map showing sampling stations (1–12) and isodepth in the nearshore waters of the Tanshui River, Taiwan

Sampling design

Fish larvae and juveniles were collected fortnightly from the 12 stations in the nearshore waters of the Tanshui River, during the period from early April to early June 1991. The investigation period is consistent with the main fishing season of the larval and juvenile fish. Sampling was conducted using surface horizontal tows with a larval net during the daytime flood tide. The duration of sampling was pre-set at 5 min for each station at a speed of ca. 2 knots. The larval net was a modified Maruchi-D larval net, net mouth diameter 1.3 m, length 4.5 m and mesh size 0.5 × 0.5 mm (Nakai 1962). A flowmeter mounted in the net mouth recorded filtered water volume. The fish collected were fixed immediately in 10% formalin seawater solution. Fish larvae and juveniles were identified to the lowest possible taxon, the developmental stages of the fish determined according to Kendall et al. (1984).

The environmental factors were monitored during sampling. Temperature was measured with a mercury thermometer, salinity with a salinometer (WTW: microprocessor conductivity meter, Model: LF 196), DO (dissolved oxygen) with Winkler's method, pH with a pH meter (Coring: pH meter, M107), transparency with a secchi disc, and the depth at station was measured with an echo sounder.

Patchy distribution, gear selection, net avoidance, and diel vertical migration of the larvae in relation to ontogenetic behaviour of the fish, and their influence on the accuracy of the estimation of fish abundance, has frequently been debated by many researchers. It has been suggested that replicated and vertically stratified samplings can reduce the sampling bias (e.g. Clutter and Anruku 1968, Smith and Richardson 1977, Omori and Hamner 1982, Leis 1986, Brander and Thompson 1989). However, sampling in the present study was not replicated because the environmental conditions changed rapidly due to tidal currents. In addition, stratified sampling was difficult due to the shallow waters. The difference between night and day collections, gear selection and the vertical distribution of the larvae will be studied in a separate paper. The present study emphasized the horizontal distribution of the fish larvae in relation to environmental factors.

Data analysis

The density of fish eggs and larvae was calculated from the flowmeter reading, then standardized according to the number of fish per 1000 m^3 seawater filtrated. The homogeneous and heterogeneous relationships of the environmental factors among stations were analyzed using multivariate analysis: principle coordinate analysis (PCA). To explain the zonation of the fish community according to habitat, the 12 stations were clustered and the dominant species ordinated based on species density data using PCA. For purposes of comparison, the similarities of species composition among stations was also calculated using Kimoto's (1976) overlap-degree index, and then clustered into different groups using the Mountford's (1962) method.

The community structure of fish larvae and juveniles was evaluated using Shannon-Weaver's species diversity (H') and Pielou's evenness (J') indices (Pielou 1966). The relationship between biotic and environmental factors was analyzed by canonical (Dillon and Goldstein 1984) and Spearman rank correlations (Siegel 1956).

Results

Physico-chemical conditions

The environmental factors in the estuary changed with tidal conditions and season. Hence, environmental conditions not only differed between the five surveys but also among the 12 stations themselves (Fig. 2).

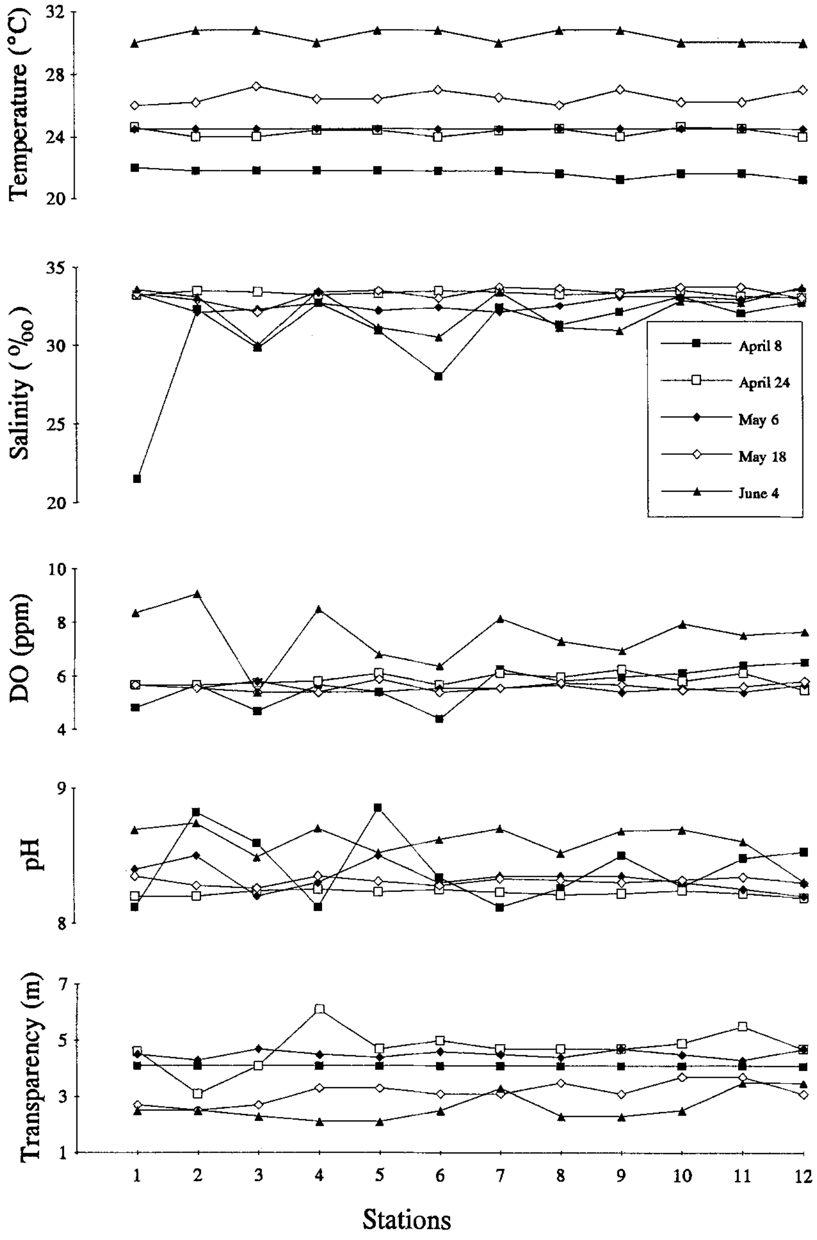

Fig. 2. Temporal and spatial variations of temperature, salinity, DO (dissolved oxygen), pH and transparency measured in the nearshore waters of the Tanshui River on 8 and 24 April, 6 and 18 May, and 4 June 1991

Water temperatures increased from 21 °C on 8 April to 31 °C on 4 June 1991. The temperatures in the southern stations were lower before and higher after 18 May (Stns 3, 6, 9, and 12) than in the northern and offshore stations of the studied habitat. This indicated that seawater temperatures were more variable in the shallower areas.

Salinity varied with sampling dates and fluctuated between the 12 stations (Fig. 2). Salinity was higher on 24 April and 18 May (greater than 33‰), moderate on 6 May (32 to 33‰) and less than 32‰ at some of the stations on 8 April and 4 June. The lower salinity was due to a strong river discharge, more greatly affecting the shallower, southern stations (Stns 3, 6, and 9). Therefore, the outflow of freshwater from the Tanshui River tended to be diverted to the southern part of the studied habitat during flood tides.

DO also varied with sampling dates and stations, and ranged from 4.5 to 9.0 ml l^{-1} (Fig. 2). This range was above the minimal requirements of the fish. DO was higher both during cold water mixing period (8 April) and during increased photosynthesis during the summer (6 June), but lower when affected by strong fluvial discharge, pH values were close to that of normal seawater (8.1 to 8.3), their fluctuations following those of DO. When DO increased, pH increased. DO and pH were related to biological activity and river discharge. Transparency was higher in offshore than in inshore waters but decreased with temperature and DO. This phenomenon indicated that transparency was correlated to plant biomass, as well as being influenced by the turbidity loading in the estuary.

Relationships among the five environmental factors at the 12 stations in the nearshore waters were analysed by PCA ordination. They indicated that physico-chemical conditions at these stations were very dynamic, differing on all five successive surveys. The 12 stations were classified into different groups according to the attributes of the five changing environmental factors (Fig. 3).

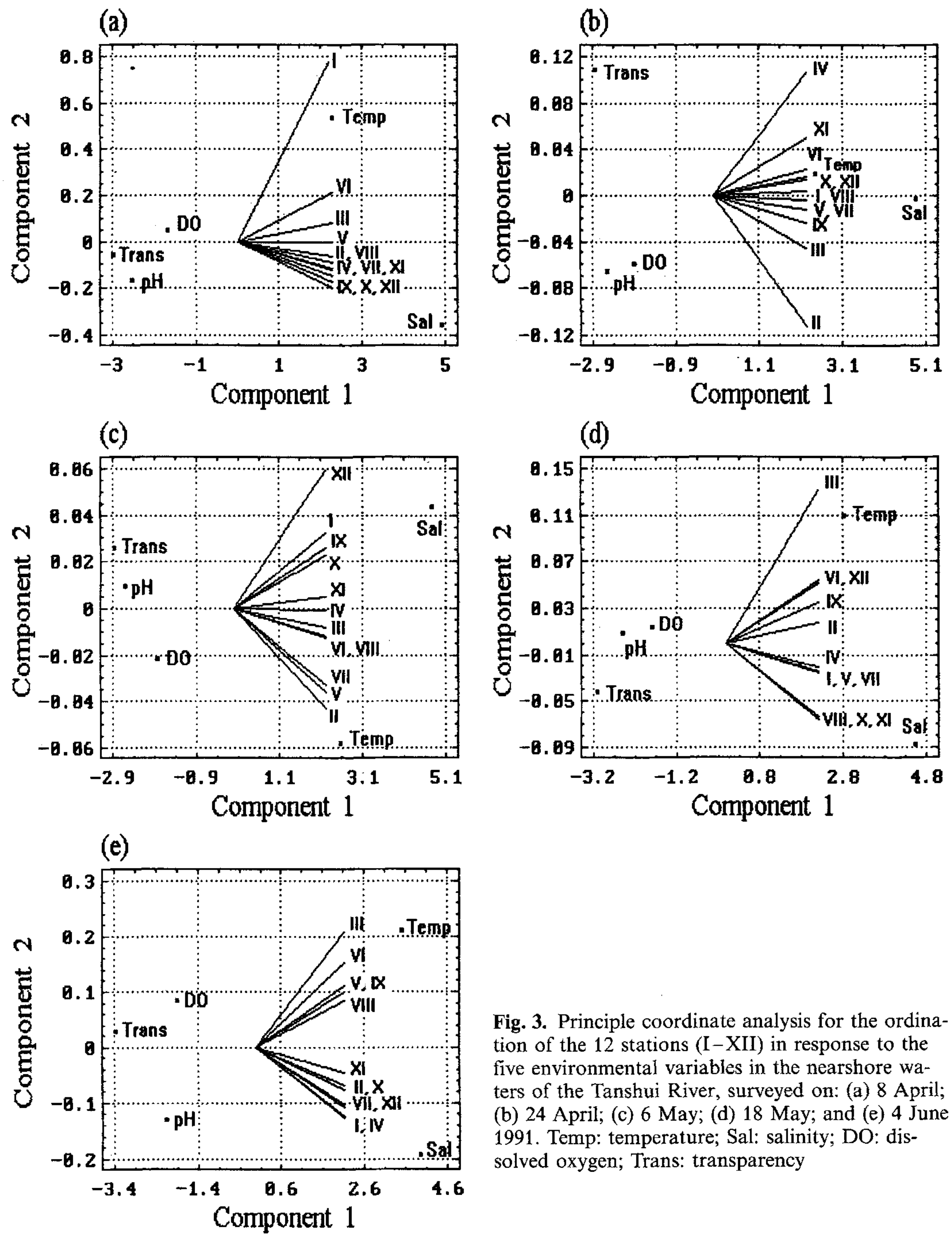

Fig. 3. Principle coordinate analysis for the ordination of the 12 stations (I–XII) in response to the five environmental variables in the nearshore waters of the Tanshui River, surveyed on: (a) 8 April; (b) 24 April; (c) 6 May; (d) 18 May; and (e) 4 June 1991. Temp: temperature; Sal: salinity; DO: dissolved oxygen; Trans: transparency

The ordination of the 12 stations as indicated from the first component of PCA in Fig. 3a, surveyed on 8 April 1991 was positively correlated to temperature and salinity, and negatively correlated to DO, transparency and pH. But the ordination of the 12 stations as indicated from the 2nd component was slightly divergent, the ordination of the shallower stations (Stns 1, 3, 6) being positively correlated to temperature and DO, and negatively correlated to salinity, pH and transparency; at the remaining nine stations, the relationships were reversed. This situation changed in each of the other four surveys (Fig. 3b–e).

Abundance and distribution of fish eggs and larvae

Fish eggs were more abundant at the deeper stations than at the shallower stations, except at Stn 1 on 8 April (Fig. 4). Fish eggs were probably spawned in the studied area or drifted with the current from offshore into the studied area. Fish larvae were more abundant in the deeper offshore stations (Stns 11 and 12) than in the shallower, more nearshore stations (Stns 1, 2, 3, and 6). This suggested that most fish eggs and larvae probably originated from the offshore-spawning marine species.

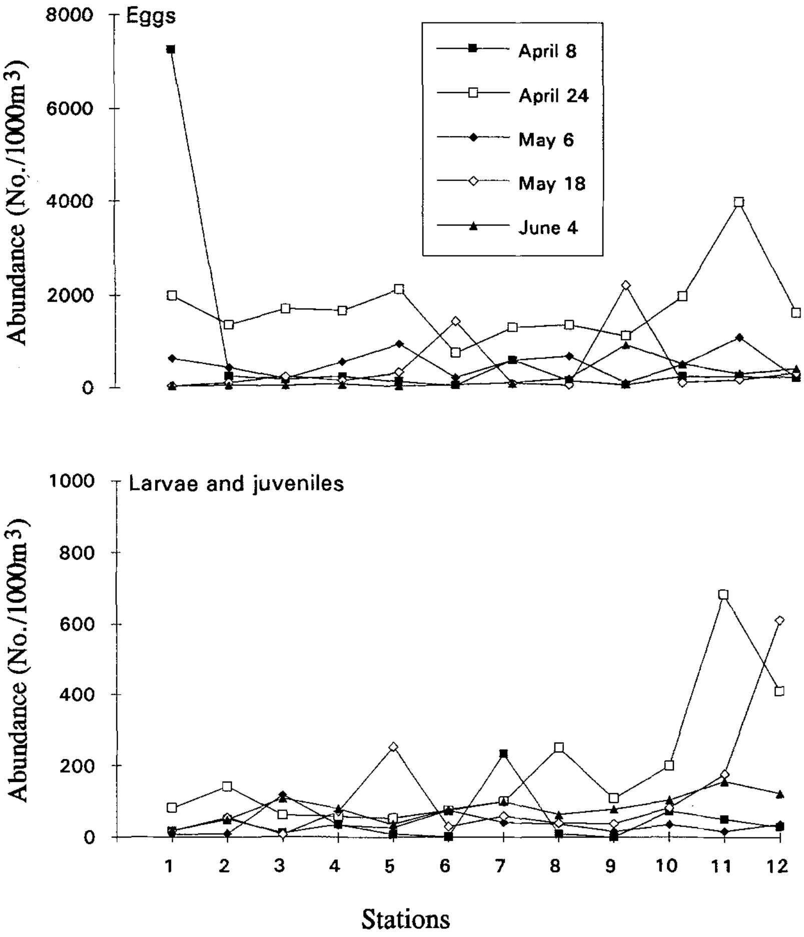

Fig. 4. Temporal and spatial variations in abundance of fish eggs and larvae collected in the nearshore waters of the Tanshui River on 8 and 24 April, 6 and 18 May, and 4 June 1991

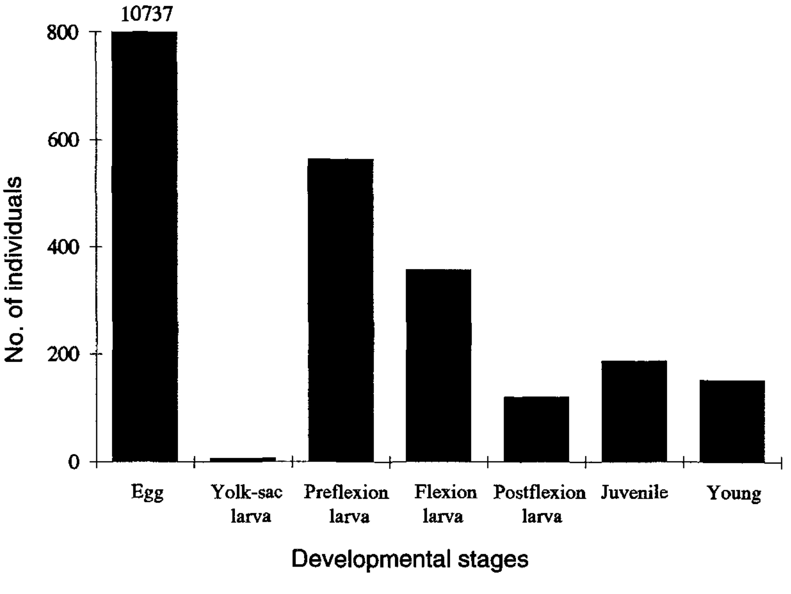

Fig. 5. Relative abundance at different developmental stages of the fish collected from the 12 stations in the nearshore waters of the Tanshui River on 8 and 24 April, 6 and 18 May, and 4 June 1991

Fish abundance associated with developmental stages

In general, due to mortality, the number of fish gradually decreased from egg to young. However, the number of yolk-sac larvae from surface sampling in the studied area was dramatically less than that of the next developmental stage (Fig. 5, Table 1). The number of yolk-sac larvae was significantly lower than that of preflexion, flexion, and postflexion larvae. This indicates that the abundance of yolk-sac larvae does not fit the standard survival curve of fish in the early stages. This discontinuous phenomenon was probably due to ontogenetic behavioral changes. The specific weight of yolk-sac larvae has been reported to be greater than that of pelagic eggs (Tanaka 1990). Yolk-sac

Table 1. Species composition, life stage and frequency occurrence of fish larvae and juveniles collected from 12 stations in the nearshore waters of the Tanshui River estuary, surveyed on: 8 (A) and 24 (B) April; 6 (C) and 18 (D) May; and 4 (E) June 1991. Ys: yolk-sac larva; Pr: preflexion larva; Fl: flexion larva; Po: postflexion larva; Ju: Juvenile; Yg: young

Serial no.	Species and family	No. of fish at life stage						Total no. of fish	Frequency of occurrence (5 surveys at 12 stns)		
		Ys	Pr	Fl	Po	Ju	Yg		Date	Sum for all Stns	%
	Clupeidae										
1	*Sardinella melanura*			1		1		2	C	2	3.33
2	sp. 3					1		1	B	1	1.67
	Engraulidae										
3	*Stolephorus buccaneeri*	1	24	3	1	2		31	A B C	10	16.67
4	*Thryssa kammalensis*					2		2	C	1	1.67
	Myctophidae										
5	*Benthosema pterotum*		1	2				3	A	2	3.33
6	sp. 3			1				1	E	1	1.67
7	sp. 4		5					5	E	4	6.67
8	sp. 5					1		1	E	1	1.67
	Synodontidae										
9	*Trachinocephalus myops*		1		1			2	D	1	1.67
	Bregmacerotidea										
10	*Bregmaceros nectabanus*		1					1	B	1	1.67
11	Antennariidae sp. 1						1	1	D	1	1.67
12	Atherinidae sp. 1			2				2	C D	2	3.33
13	Holocentridae sp. 1		7	1				8	B C D	7	11.67
14	Scorpaenidae sp. 2		1					1	C	1	1.67
	Platycephalidae										
15	sp. 2		1					1	B	1	1.67
16	sp. 3			1				1	E	1	1.67
17	sp. 4		1					1	B	1	1.67
	Centropomidae										
18	*Ambassis gymnocephalus*	1	62	5	36	52		156	A B C D E	38	63.33
19	Serranidae sp. 1		1					1	B	1	1.67
	Teraponidae										
20	*Terapon jarbua*	1	35	93	1	9		139	B C D	13	21.67
21	Priacanthidae sp. 1		1					1	D	1	1.67
	Apogonidae										
22	*Apogon notatus*		21	2				23	A B C E	15	25.00
23	sp. 3		37	10				47	A B C D E	12	20.00
24	sp. 5					1		1	C	1	1.67
25	sp. 6				1	1		2	C	2	3.33
26	sp. 7			1				1	B	1	1.67
	Sillaginidae										
27	*Sillago sihama*		1	5				6	B E	4	6.67
28	*Sillago japonica*		5	10	1			16	B C D E	11	18.33
29	*Sillago maculata*				1	1		2	B C	2	3.33
	Carangidae										
30	*Trachurus japonicus*		12	1				13	A B C D	12	20.00
31	*Decapterus maruadsi*		4	1	11	2		18	C E	10	16.67
32	*Scomberoides tol*	2	26			1		29	A E	8	13.33
	Coryphaenidae										
33	*Coryphaena hippurus*					1		1	D	1	1.67
	Formionidae										
34	*Formio niger*		11					11	B	3	5.00
	Menidae										
35	*Mene maculata*			1				1	D	1	1.67
	Leiognathidae										
36	sp. 1				2		1	3	C E	3	5.00
37	sp. 2			1				1	B	1	1.67
	Nemipteridae										
38	sp. 1		3					3	E	2	3.33
39	sp. 2		7	18	10			35	B C D E	16	26.67
40	sp. 3		8	6				14	D E	2	3.33
	Gerreidae										
41	*Gerres abbreviatus*			6	4	2		12	E	5	8.33
42	*Gerres macrosoma*					2		2	E	1	1.67
43	Caesionidae sp. 1			1	2	1		4	B E	3	5.00
	Sciaenidae										

Table 1 (continued)

Serial no.	Species and family	No. of fish at life stage						Total no. of fish	Frequency of occurrence (5 surveys at 12 stns)						
		Ys	Pr	Fl	Po	Ju	Yg		Date					Sum for all Stns	%
44	sp. 1		1					1				D		1	1.67
45	sp. 3			1				1		B				1	1.67
46	sp. 6		3					3		B		D		2	3.33
47	sp. 7		6					6	A					3	5.00
48	sp. 8		2					2	A					2	3.33
	Mullidae														
49	sp. 1		43	36	15	7	5	106		B	C	D		16	26.67
50	sp. 2		69	22				91		B	C	D	E	16	26.67
51	Pempheridae sp. 1		3					3	A					1	1.67
	Scatophagidae														
52	*Scatophagus argus*		1		1			2				D	E	2	3.33
	Pomacentridae														
53	sp. 1					4		4				D		2	3.33
54	sp. 2						1	1					E	1	1.67
	Mugilidae														
55	*Liza macrolepis*		31	83	16	60	143	333		B	C	D	E	28	46.67
56	Sphyraenidae sp. 1		3	5				8		B		D	E	8	13.33
57	Scaridae sp. 1				2			2				D		1	1.67
58	Mugiloididae sp. 2		1					1		B				1	1.67
59	Percophididae sp. 1				1	1		2			C	D		2	3.33
	Blenniidae														
60	*Entomacrodus niuafooensis*					6		6			C	D	E	6	10.00
61	sp. 2			1	1	4		6			C	D	E	6	10.00
62	sp. 3		32	1				33	A	B	C	D		17	28.33
63	sp. 4						1	1				D		1	1.67
64	sp. 5		7	1				8	A		C		E	7	11.67
65	sp. 7		1					1					E	1	1.67
66	Tripterygiidae sp. 1		1					1			C			1	1.67
	Gobiidae														
67	sp. 1		5			1		6	A					4	6.67
68	sp. 8		5					5	A					3	5.00
69	sp. 14		1					1	A					1	1.67
70	sp. 15		1					1	A					1	1.67
71	sp. 16		44	22	5	2		73		B		D	E	19	31.67
72	sp. 17					2		2			C	D		2	3.33
73	sp. 18		1	2	1			4			C		E	3	5.00
74	sp. 19					2		2			C			2	3.33
75	sp. 20			1	2			3		B		D		3	5.00
76	sp. 21					1		1					E	1	1.67
77	sp. 22		1			1		2	A				E	2	3.33
	Scombridae														
78	*Scomber japonicus*			1				1		B				1	1.67
	Callionymidae														
79	sp. 1				2			2			C			2	3.33
80	sp. 2		19	6	1	1		27	A	B	C	D	E	16	26.67
	Bothidae														
81	sp. 1		3		1			4		B	C	D		4	6.67
82	sp. 2				1			1				D		1	1.67
83	sp. 4					1		1			C			1	1.67
84	Cynoglossidae sp. 1		2					2		B				2	3.33
	Monacanthidae														
85	*Stephanolepis cirrhifer*					9		9		B			E	3	5.00
86	sp. 2		1					1				D		1	1.67
87	sp. 3					4		4					E	4	6.67
	Tetradontidae														
88	*Fugu niphobles*					1		1			C			1	1.67
89	sp. 2			1				1					E	1	1.67
	Unidentified														
90	sp. 1	1						1		B				1	1.67
91	sp. 2	1						1		B				1	1.67
92	sp. 3		1					1				D		1	1.67
93	sp. 4			2				2		B				1	1.67
Total		7	564	357	120	187	152	1387	18	38	35	36	35	60	100.00

Table 2. Spearman rank correlation between fish abundance and abiotic factors for five surveys. A: 8 April; B: 24 April; C: 6 May; D: 18 May; E: 4 June. TEMP: temperature; SAL: salinity; DO: dissolved oxygen; DEP: depth of station; TRANS: transparency; DIST: distance from coast; H': Shannon-Weaver's species diversity index; J': Pielou's evenness index

	Abiotic factors																																		
	TEMP					SAL					pH					DO					DEP					TRANS					DIST				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Community variables																																			
No. of species	±	±	±	±	±	±	±	±	±	±	±	−*	±	±	±	±	±	±	±	±	±	±	±	+*	+*	±	±	±	+*	±	±	±	±	+*	+*
H'	±	−*	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	+*	±	±	±	±	±	±	±	+*	+*	+*
J'	±	±	±	±	±	±	±	±	±	±	±	+*	+*	±	±	−*	±	±	±	±	±	±	±	±	±	±	±	+*	±	±	±	±	±	±	±
Abundance (no./1000 m^3)																																			
Liza macrolepis		±	±	±			−*	±	±			±	±	±			±	±	±			+*	±	±			±	+*	±			+*	±	±	
Ambassis gymnocephalus		±	±	±	±		−*	±	±	±		±	±	±	±		±	±	±	±		±	±	±	±		±	±	±	±		±	±	±	±
Terapon jarbua		+**		±			±		±			±		±			±		±			+*		±			±		±			+*		±	
Mullidae sp. 1		±	±	±			±	±	±			±	±	±			±	±	±			+*	±	±			±	±	±			+*	±	±	
Mullidae sp. 2		±		±			−*		±			±		±			±		±			+*		+*			±		±			+*		±	
Gobiidae sp. 16		−**			±		±			±		±			±		±			±		±			±		±			±		±			±
Nemipteridae sp. 2		±			±		−*			±		±			±		±			±		±			±		±			±		±			±
Decapterus maruadsi			±		±			±		±			±		±			±		±			±		±			±		±			+*		±
Stephanolepis cirrhifer					±					±					±					±					−*					±					±
Overall species	±	±	±	±	±	+*	±	±	±	±	±	±	−*	±	±	±	±	±	±	±	±	±	±	+*	±	±	±	±	±	±	±	+*	±	±	±
Eggs	±		±	+*	±	±		±	±	±	±		±	±	±	±		±	±	±	±		±	±	+*	±		−**	±	±	±		±	±	+*

± no significant correlation; + positive correlation; − negative correlation; ** $p<0.01$; * $0.01<p<0.05$; blank: no catch

larvae usually sink to the bottom at this stage. Therefore, yolk-sac larvae were not as accessible to surface sampling.

Species composition and retention

A total of 1387 individuals, representing 43 families and 93 species, was collected from 12 stations through five surveys, during the period from early April to early June 1991 (Table 1). The number of fish captured was consistent with their frequency of occurrence. The dominant species was widely distributed among the 12 stations and occurred with higher frequency in the five surveys. The top five dominant taxa – *Liza macrolepis*, *Ambassis gymnocephalus*, *Terapon jarbua*, Mullidae and Gobiidae – made up 64.7% of the total catch. Most species occurred in low numbers and at an early life stage, indicating that most species occurring in the area were short-term, temporary residents or rare species (Bell et al. 1984). In contrast, the dominant species, *Liza macrolepis* and *Ambassis gymnocephalus*, may be long-term, temporary residents, because of their higher frequency of occurrence in the nearshore waters and the larger number of life history stages in comparison with the other species. They may live in the nearshore waters for extended periods as juveniles before leaving.

Ordination of station by species density

The 12 stations clustered by PCA according to the species density data (Fig. 6), are similar to those clustered by Kimoto's (1976) index and Mountford's (1962) method (Fig. 7). The classification of the stations was not always consistent between surveys (Fig. 6).

According to species composition of fish larvae and juveniles, the 12 stations surveyed on 8 April can be classified into three groups: A (Stns I, II, IV, VII and X), B (Stns V and XI) and C (Stns III, VIII and XII). The dominant species in each group was different. Group A consisted mainly of *Scomberoides tol* and *Stolephorus buccaneeri*; Group B of Gobiidae sp. 1, Apogonidae sp. 3; and Group C of Callionimidae sp. 2 and Blenniidae sp. 3, respectively. Group A was mainly made up of pelagic fishes, while Groups B and C were mainly benthic fishes (Fig. 6a). Similarly, the same stations surveyed on 24 April were classified into only two groups: A (Stns I, IV, V, VII, VIII, X, XI and XII) and B (Stns II, III, VI and IX). The dominant species in the stations changed, Group A dominated by *Liza macrolepis* and *Terapon jarbua*; and Group B by Gobiidae sp. 16 and *Formio niger*, respectively (Fig. 6b). The stations of the other three surveys can also be classified into different groups, in which the dominant species again changed (Figs. 6c–e). These changes of station groupings and dominant species indicated that species composition of fish larvae and juveniles in the nearshore waters changed rapidly. This phenomenon was probably due to the seasonal succession of the species and/or environmental conditions.

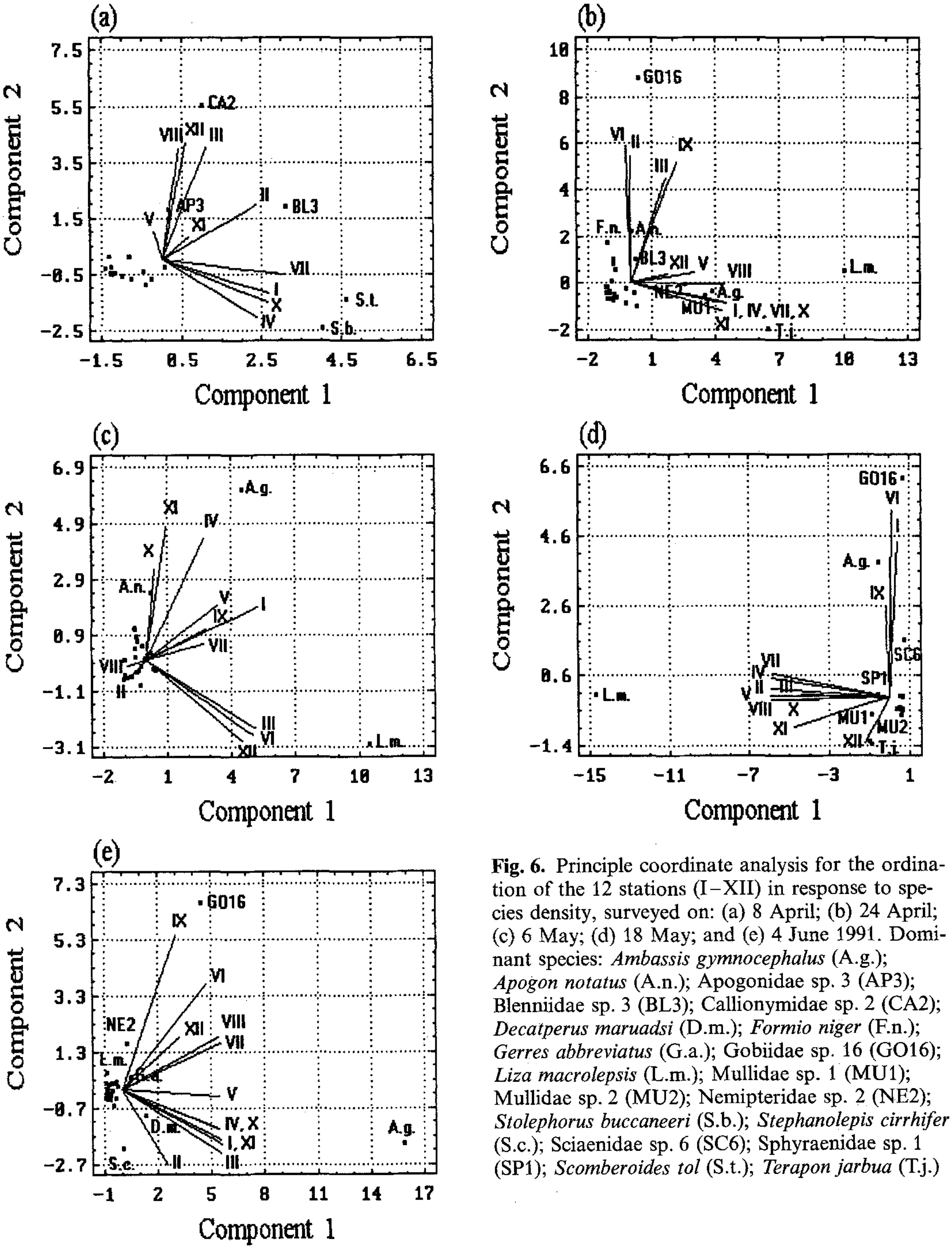

Fig. 6. Principle coordinate analysis for the ordination of the 12 stations (I–XII) in response to species density, surveyed on: (a) 8 April; (b) 24 April; (c) 6 May; (d) 18 May; and (e) 4 June 1991. Dominant species: *Ambassis gymnocephalus* (A.g.); *Apogon notatus* (A.n.); Apogonidae sp. 3 (AP3); Blenniidae sp. 3 (BL3); Callionymidae sp. 2 (CA2); *Decatperus maruadsi* (D.m.); *Formio niger* (F.n.); *Gerres abbreviatus* (G.a.); Gobiidae sp. 16 (GO16); *Liza macrolepsis* (L.m.); Mullidae sp. 1 (MU1); Mullidae sp. 2 (MU2); Nemipteridae sp. 2 (NE2); *Stolephorus buccaneeri* (S.b.); *Stephanolepis cirrhifer* (S.c.); Sciaenidae sp. 6 (SC6); Sphyraenidae sp. 1 (SP1); *Scomberoides tol* (S.t.); *Terapon jarbua* (T.j.)

Relationships between biotic and abiotic factors

A canonical correlation of the relationships between biotic and abiotic factors indicated that the abundance of fish eggs and larvae as well as species diversity indices were influenced by multiple abiotic factors (Fig. 8). The first two canonical correlations between six abiotic and five biotic factors were both significant ($r_1 = 0.7298$, DF = 30, $\chi_1^2 = 74.917$ $P < 0.00001$; $r_2 = 0.5959$, DF = 20, $\chi_2^2 = 36.88$, $0.01 < P < 0.05$). In the first canonical variate, abundance of fish egg and larvae, and species diversity index (H') were positively correlated with temperature, DO, depth and transparency, but negatively correlated with salinity and pH, as well as number of species and species evenness index (J'). While in the second canonical variate, the relationship between biotic and abiotic factors was more complicated. Larval abundance was positively correlated with all the abiotic factors except pH, and negatively correlated with egg abundance and number of species (Fig. 8).

Furthermore, the community variables and abundance of dominant species in relation to each of the abiotic factors for each of the five surveys were conducted by Spearman rank correlation (Table 2). The community structure was more complicated with increasing pH, depth, transparency and the distance from the coast. Of the 18 selected species, half were significantly correlated with the abiotic factors. The abundance of most domi-

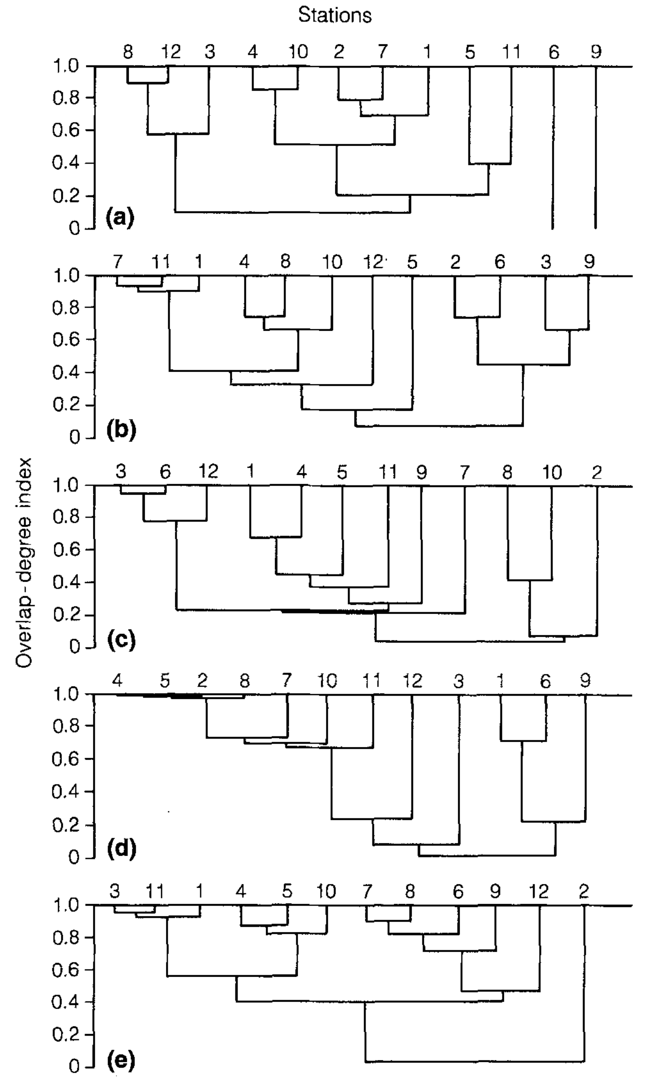

Fig. 7. Clustering of the 12 stations by Mountford's (1962) method based on Kimoto's (1976) overlap-degree index ($C\pi$) of species composition between stations, surveyed on: (a) 8 April; (b) 24 April; (c) 6 May; (d) 18 May; and (e) 4 June 1991

nant species was positively correlated to depth and location of the station. *Ambassis gymnocephalus*, Nemipteridae, Mullidae and *Liza macrolepis* tended to live in low salinity water. Fish abundance was not significantly correlated with DO, probably due to the fact that DO was not lower than the required threshold of the fish. The positive correlation between fish egg and larval abundance, as well as the depth and location of the station, suggested that most fish larvae and juveniles in the nearshore waters of the Tanshui River originated from offshore.

Discussion and conclusion

Species composition and their origin

A total of 1387 individuals, representing 43 families and 93 species, was captured in the nearshore waters of the Tanshui River during the period from April to June 1991 (Table 1). The larval fish community is comparable with the fish fauna existing in other tropical mangrove estuarine ecosystems (Blaber et al. 1985, Robertson and Duke 1990). *Liza macrolepis*, *Ambassis gymnocephalus*, *Terapon jarbua*, Mullidae and Gobiidae are most dominant and frequently occur in the estuary. They are estuarine-dependent marine and estuarine species (Deegan 1989) and their retention in the estuary was longer than for the other species. The remaining marine species, e.g., Myctophidae, *Coryphaena hippurus*, and *Scomber japonicus*, occurred in low numbers and their larvae occasionally drifted with the tidal current into the estuary (Table 1). No freshwater species was found in the present study (Table 1), probably due to the salinity (Fig. 2). Freshwater eel, *Anguilla japonica*, elvers are abundant at nighttime in the study area during upstream migration in winter; however, they were not caught during the investigated period because the sampling was conducted during daylight.

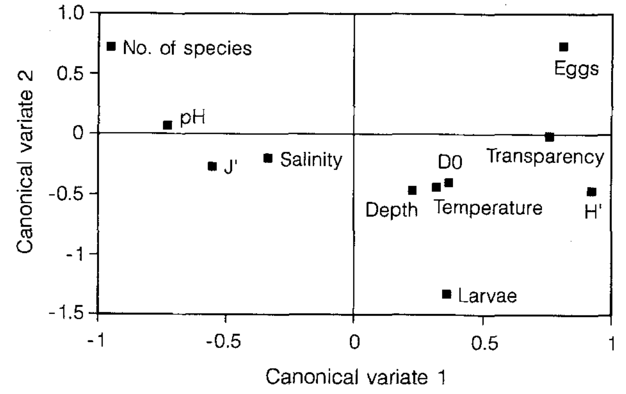

Fig. 8. Ordination of the biotic and abiotic factors by first two canonical variates. J′: Pielou's evenness index; H′: Shannon-Weaver's species diversity index

Fish larvae and juveniles in the estuary were classified into permanent residents, long- and short-term temporary residents and rare species according to their number and duration in the estuary (Bell et al. 1984). Most of the fish captured seemed to be temporary residents or rare species, because the number of individuals of most species was fewer than four per sample (Table 1). Most fish larvae and juveniles in the nearshore waters of the Tanshui River were spawned in adjacent marine waters, their eggs and larvae passively drifting with the current into the study area, where they stayed through the early stages of their life history. On the other hand, Gobiidae are estuarine spawning and may remain in the estuary throughout their life cycle. There are three major migration patterns by which fish use estuarine systems for reproduction and juvenile feeding (Deegan and Thompson 1985), viz.: (1) saltwater spawning, followed by immigration of the larvae into an estuary; (2) estuarine spawning, in which the larvae remain, for the most part, within an estuary; (3) freshwater spawning, followed by the downstream drift or swimming of larvae and juvenile fish into an estuary.

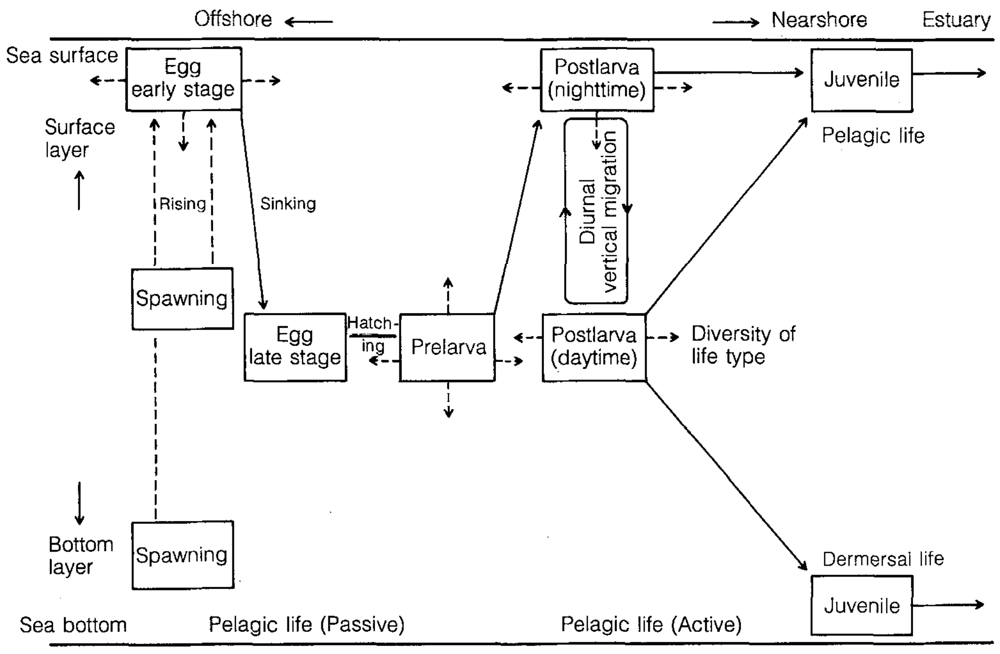

Fig. 9. Schematic diagram showing onshore movement of fish larvae and juveniles in relation to their ontogenetical behavioral changes and life-type (redrawn from Tanaka 1976)

To classify the species listed in Table 1 into the different migratory patterns, detailed information about the life history of the fish was necessary. This information was very limited except for some commercially important species, e.g. *Scomber japonicus*, *Anguilla japonica* and *Terapon jarbua* (Miu et al. 1990).

Larvae fish abundance in relation to estuarine transport and behavioral ontogeny

Transportation of fish larvae from offshore into the nearshore waters and further into estuarine nursery areas is influenced both by physical processes, as well as the fishes' activity and behavior (Tanaka 1976, 1985, 1990, Weinstein et al. 1980, Boehlert and Mundy 1988, Drake and Arias 1991a, b). This process of transportation is important in determining the occurrence and abundance of fish eggs and larvae in the nearshore waters. Many studies indicate that the buoyancy of fish eggs changes during early developmental stages (Russell 1976, Coombs 1981, Tanaka 1981, Coombs et al. 1985, Tanaka 1990). Pelagic fish eggs passively drift with the current into the estuary. Upon reaching the yolk-sac stage, their specific weight increases and thus the larvae sink to subsurface layers, so that the yolk-sac larvae are not accessible to surface sampling. This behavior could prevent the larvae from being transported away from suitable habitats. When the larvae develop to the postflexion stage, their gas bladder is completely formed and they can perform diel vertical movement and active migration. Then, the larvae can adjust their buoyancy to allow selective tidal stream transport, using currents to move into an estuary (Kuwahara and Suzuki 1984, Boehlert and Mundy 1988). After the juvenile stage, the fish differentiated into pelagic and benthic forms. Benthic forms settle down and do not drift with the tidal current (Fig. 9). Therefore, most benthic species beyond the juvenile stage were not caught by surface sampling, and the number of benthic species, e.g. *Terapon jarbua*, Mullidae, Apogonidae, Nemipteridae, Gobiidae, and Callionymidae, gradually decreased with increasing developmental stages (Table 1). In contrast, the pelagic forms, e.g. *Ambassis gymnocephalus* and *Liza macrolepis*, which are estuarine-dependent pelagic species, were abundant and stayed longer in the nearshore waters (Table 1). These facts indicated that ontogenetically behavioral change associated with developmental stage may play an important role in determining the abundance of the fish larvae in the nearshore waters (Fig. 5).

Distribution and abundance of fish larvae in relation to abiotic factors

The physico-chemical characteristics of the water in the studied area were significantly different in each of the five surveys (Figs. 2, 3). This indicates that the estuarine environment is very dynamic. The shallower area of the studied habitat was influenced by freshwater, lowering its salinity (Fig. 2). The abundance and species composition of fish larvae and juveniles also changed with the physicochemical conditions (Table 2). At the shallow water stations, the fish community was dominated by benthic species, e.g. Callionymidae, Blenniidae, and Gobiidae. In contrast, the deep-water stations of the study area were dominated by nearshore pelagic species, e.g. *Ambassis gymnocephalus*, *Liza macrolepis*, *Coryphaena hippurus*, *Formio niger*, *Scomber japonicus*, *Stephanolepis cirrhifer*, Carangidae, and Engraulidae, as well as mesopelagic fish, Myctophidae (Fig. 6).

The extent of onshore migration of fish is dependent on their tolerance to extremes of environmental variables (Kinne 1964, De Veen 1978, Whitfield et al. 1981, Claridge and Potter 1983, Tongiorgi et al. 1986, Boehlert and Mundy 1988, Tosi et al. 1988). The abundances of dominant species, *Liza macrolepis* and *Ambassis gymnocephalus*, were negatively correlated with salinity (Table 2), indicating that low salinity may act as a cue to guide these fish larvae and juveniles to inshore nursery grounds (Hughes 1969, Young and Carpenter 1977). However, this phenomenon may be different between species. Some species can not tolerate wide salinity ranges in the estuary and emigrate during later life stages. Thus, they appeared in low numbers and at very early stages of their life cycle (Table 1).

In conclusion, the community structure of fish larvae and juveniles in this estuarine area was very complex but consisted mainly of estuarine-dependent marine species. Their larvae drifted with the current into the estuary shortly after hatching. Not only physical factors, but also the development and ontogenetic behavior of the fish, played an important role in their transportation into the estuary.

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Literature cited

Bell, J. D. (1980). Aspects of the ecology of fourteen economically important fish species in Botany Bay, New South Wales, with special emphasis on habitat utilization and a discussion of the effects of man-induced habitat changes. M. Sc. Thesis, Macquarie University, New South Wales, Australia

Bell, J. D., Polard, D. A., Burchmore, J. J., Pease, B. C., Middleton, M. J. (1984). Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Aust. J. mar. Freshw. Res. 35: 33–46

Blaber, S. J. M., Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. 17: 143–162

Blaber, S. J. M., Milton, D. A. (1990). Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. Mar. Biol. 105: 259–267

Blaber, S. J. M., Whitfield, A. K. (1977a). The feeding ecology of juvenile Mugilidae in southeast African estuaries. Biol. J. Linn. Soc. 9: 227–284

Blaber, S. J. M., Whitfield, A. K. (1977b). The biology of the burrowing goby *Croilia mossambica* Smith (Teleostei: Gobiidae). Envir. Biol. Fish. 1: 197–204

Blaber, S. J. M., Young, J. W., Dunning, M. C. (1985). Community structure and zoogeographic affinities of the coastal fishes of the Dampier Region of North-western Australia. Aust. J. mar. Freshw. Res. 36: 247–266

Boehlert, G. W., Mundy, B. C. (1988). Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3: 51–67

Brander, K., Thompson, A. B. (1989). Diel differences in avoidance of three vertical profile sampling gears by herring larvae. J. Plankton Res. 11(4): 775–784

Chou, C. H., Bi, C. C. (1990). Dynamic distribution of nutrients and variation of environmental factors in Tamshui estuary ecosystem. Proc. natn. Sci. Coun., Taiwan, Republic of China (B: Life Sciences) 14(3): 131–141

Chou, C. H., Chang, F. C., Hwang, Y. S. (1987). Ecological research of mangrove forests: a review. In: Chou, C. H., Peng, C. I., Chaw, S. M. (eds.) Plant resources and conservation in Taiwan. Society for Wildlife and Nature, Republic of China, p. 23–48

Claridge, P. N., Potter, I. C. (1983). Movements, abundance, age composition and growth of bass, *Dicentrarchus labrax*, in the Severn River estuary and inner Bristol Channel. J. mar. biol. Ass. U. K. 63: 871–879

Clutter, R. I., Anruku, M. (1968). Avoidance of samplers in zooplankton sampling. Monogr. oceanogr. Methodol. (UNESCO) 2: 57–76

Coombs, S. H. (1981). A density-gradient column for determining the specific gravity of fish eggs, with special reference to eggs of mackerel *Scomber scombrus*. Mar. Biol. 63: 101–106

Coombs, S. H., Fosh, C. A., Keen, M. A. (1985). The buoyancy and vertical distributions of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). J. mar. biol. Ass. U.K. 65: 461–474

Deegan, L. A. (1989). Nekton, the free-swimming consumers. In: Day, J. W., Hall, C. A. S., Kemp, W. M., Yáñez-Arancibia, A. (eds.) Estuarine ecology. Wiley-Interscience, New York, p. 377–437

Deegan, L. A., Thompson, B. A. (1985). The ecology of fish communities in the Mississippi River deltaic plain. In: Yáñez-Arancibia, A. (ed.) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Editorial Universitaria, UNAM-PUAL-ICML, Mexico, D.F., p. 35–56

De Veen, J. F. (1978). On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. Neth. J. Sea Res. 12: 115–147

Dillon, W. R., Goldstein, M. (1984). Multivariate analysis – methods and applications. Wiley-Interscience, New York

Drake, P., Arias, A. M. (1991a). Ichthyoplankton of a shallow coastal inlet in south-west Spain: factors contributing to colonization and retention. Estuar. cstl. Shelf Sci. 32: 347–364

Drake, P., Arias, A. M. (1991b). Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S. W. Spain). J. Fish Biol. 39: 245–263

Haedrich, R. L., Haedrich, S. O. (1974). A seasonal survey of the fishes in the Mystic River, a polluted estuary in downtown Boston, Massachusetts. Estuar. cstl mar. Sci. 2: 59–73

Holliday, F. G. T. (1971). Salinity: fishes. In: Kinne, O. (ed.) Marine ecology, Vol. 2. Wiley-Interscience, Sydney, p. 997–1033

Hughes, D. A. (1969). Responses of salinity change as a tidal transport mechanism of the pink shrimp *Penaeus duroarum*. Biol. Bull. mar. biol. Lab., Woods Hole 153: 505–526

Kendall, A. W., Jr., Ahlstrom, E. H., Moser, H. G. (1984). Early life history stages of fishes and their characters. In: Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W. Jr., Richardson, S. L. (eds.) Ontogeny and systematics of fishes. Spec. Publ. No. 1. Am. Soc. Ichthyol. Herpetol. Allen Press Inc., Lawrence, Kansas, p. 11–22

Kimoto, S. (1976). Studying methods of community structure of animals – I. Deversity and species composition. Kyau-ritu Press, Tokyo (in Japanese)

Kinne, O. (1964). The effects of temperature and salinity on marine and brackish water animals – II. Salinity and temperature salinity combinations. Oceanogr. mar. Biol. A. Rev. 2: 281–339

Kuwahara, A., Suzuki, S. (1984). Diurnal changes in vertical distributions of anchovy eggs and larvae in the western Wakasa Bay. Bull. Jap. Soc. scient. Fish. 50: 1285–1292

Lee, C. W., Chu, T. Y. (1965). A general survey of Tanshui River and its tributary estuaries. Rep. Inst. Fish. Biol. Taipei 2(1): 34–45

Leis, J. M. (1986). Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Mar. Biol. 90: 505–516

Loneragan, N. R., Potter, I. C., Lenanton, R. C. J., Caputi, N. (1986). Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. Mar. Biol. 94: 631–641

McErlean, A. J., O'Connor, S. G., Mihursky, J. A., Gibson, C. I. (1973). Abundance, diversity and seasonal patterns of estuarine fish populations. Estuar. cstl Shelf Sci. 1: 19–36

Miu, T. C., Lee, S. C., Tzeng, W. N. (1990). Reproductive biology of *Terapon jarbua* from the estuary of Tanshui River. J. Fish. Soc. Taiwan 17(1): 9–20

Mountford, M. D. (1962). An index of similarity and its application to classificatory problem. In: Murphy, P. W. (ed.) Progress in soil zoology. Butterworths, London, p. 43–50

Mukai, T. (1987). Effects of micro-scale *in situ* environmental gradients concerning water qualities on the structure of the phytoplankton community in a coastal embayment. Estuar. cstl Shelf Sci. 25: 447–458

Nakai, Z. (1962). Apparatus for collecting macroplankton in the spawning survey of iwashi (sardine, anchovy and round herring) and others. Bull. Tokai reg. Fish. Res. Lab. 9: 221–237

Omori, M., Hamner, W. M. (1982). Patchy distribution of zooplankton: behavior, population assessment and sampling problems. Mar. Biol. 72: 193–200

Pielou, E. C. (1966). The measurement of diversity in different types of biological collections. J. theor. Biol. 13: 131–144

Powell, A. B., Hoss, D. E., Hettler, W. F., David, S. P., Wanger, S. (1989). Abundance and distribution of ichthyoplankton in Florida Bay and adjacent waters. Bull. mar. Sci. 44: 35–48

Quinn, N. J. (1980). Analysis of temporal changes in fish assemblages in Serpentine Creek, Queensland. Envir. Biol. Fish. 5: 117–133

Robertson, A. I., Duke, N. C. (1987). Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar. Biol. 96: 193–205

Robertson, A. I., Duke, N. C. (1990). Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Mar. Biol. 104: 369–379

Russell, F. S. (1976). The eggs and planktonic stages of British marine fishes. Academic Press, London

Sebatès, A. (1990). Changes in the heterogeneity of mesoscale distribution patterns of larval fish associated with a shallow coastal haline front. Estuar. cstl shelf Sci. 30: 131–140

Siegel, S. (1956). Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Smith, P. E., Richardson, S. L. (1977). Standard techniques for pelagic fish egg and larva surveys. F.A.O. Fish. tech. Pap. 175: 1–100

Tanaka, K. (1976). Ecological consideration on meeting and parting of fish eggs and larvae. Bull. Jap. Soc. Fish. Oceanogr. 28: 79–89 (in Japanese)

Tanaka, M. (1981). Feeding and survival in marine fish larvae – V. Vertical distribution and migration of eggs and larvae. Aquabiology, Tokyo 16: 379–386 (in Japanese)

Tanaka, M. (1985). Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream *Pagrus major* to a nursery ground. Trans. Am. Fish. Soc. 114: 471–477

Tanaka, Y. (1990). Change in the egg buoyancy of Japanese anchovy, *Engraulis japonicus* during embryonic development. Nippon Suisan Gakk. 56: 165

Tongiorgi, P., Tosi, L., Balsamo, M. (1986). Thermal preferences in upstream migrating glass-eels of *Anguilla anguilla* (L.). J. Fish Biol. 28: 501–510

Tosi, L., Sala, L., Sola, C., Spampanato, A., Tongiorgi, P. (1988). Experimental analysis of the thermal and salinity preferences of glass-eels, *Anguilla anguilla* (L.), before and during the upstream migration. J. Fish Biol. 33: 721–733

Tzeng, W. N., Wang, Y. T. (1992). Structure, composition and seasonal dynamics of larval and juvenile fish community in the mangrove estuary of Tanshui River, Taiwan. Mar. Biol. 113: 481–490

Wang, Y. T., Tzeng, W. N., Lee, S. C. (1991). A preliminary study on species composition and seasonal abundance of fish eggs and larvae from the coastal waters adjacent to the Tanshui River estuary, Taiwan, J. Fish. Soc. Taiwan 18(1): 7–20

Weinstein, M. P. (1979). Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. U.S. 77: 339–357

Weinstein, M. P., Weiss, S. L., Hodson, R. G., Gerry, L. R. (1980). Retention of three taxa of postlarval fishes in an intensely flushed tidal estuary. Fish. Bull. U.S. 78: 419–435

Whitfield, A. K., Blaber, S. J. M., Cyrus, D. P. (1981). Salinity ranges of some southern African fish species occurring in estuaries. S. Afr. J. Zool. 16: 151–155

Yáñez-Arancibia, A., Linares, F. A., Day, J. W. Jr. (1980). Fish community structure and function in Terminos Lagoon, a tropical estuary in the southern Gulf of Mexico. In: Kennedy, V. S. (ed.) Estuarine perspecitves. Academic Press, New York, p. 465–482

Young, P. C., Carpenter, S. M. (1977). Recruitment of postlarval penaeid prawns to nursery areas in Moreton Bay, Queensland. Aust. J. mar. Freshwat. Res. 28: 745–773

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