SEASONAL AND DIEL CHANGES IN A SUBTROPICAL MANGROVE FISH ASSEMBLAGE

H.-J. Lin and K.-T. Shao

ABSTRACT

Fish were sampled by fyke nets for a year over diel cycles and a seasonal cycle in a subtropical mangrove creek of northern Taiwan. A total of 30 fish species belonging to 18 families were captured; Gobiidae and Mugilidae were the most diverse families. The fish assemblage was dominated by a small number of small-sized and commercially important species. Total fish number and biomass were highly variable and showed little seasonal differences. However, species richness and diversity were significantly higher in fall than in winter-spring. An ordination analysis demonstrated that monthly changes in species composition followed a gradual pattern and showed a clear seasonal cycle. A combination of water temperature and salinity best explained the monthly changes in species composition. Pearson correlations indicated that water temperature was positively correlated, and salinity was negatively correlated, with the species richness and diversity. There were no significant diel differences in total fish number and species richness. However, biomass and diversity were significantly higher at night than during the day. Classification and ordination analyses showed that there were distinct 'day' and 'night' assemblages in winter-spring and fall, but not in summer. Our results suggest that a seasonal cycle was more important than diel cycles in structuring temporal changes in the fish assemblage of a subtropical mangrove creek.

Mangroves are characteristic features of most tropical and subtropical estuaries. Comparisons of fish in mangrove swamps with other adjacent waters have revealed the role of mangroves as nursery and/or feeding grounds for juvenile fish (Robertson and Duke, 1987; Little et al., 1988; Chong et al., 1990; Morton, 1990; Laegdsgaard and Johnson, 1995). Of particular importance is that many species found in mangrove swamps are linked directly or indirectly to existing commercial fisheries. Despite the importance of mangrove swamps as fish habitats, large-scale destruction and modifications of mangroves have been increasingly reported worldwide.

The fish assemblages in mangrove habitats have long been recognized to be dynamic on a variety of temporal scales. Much attention has been paid to the seasonality of the fish assemblage. At present, the available seasonality data are almost exclusively from tropical mangrove habitats (e.g., Wright, 1986; Robertson and Duke, 1990; Rooker and Dennis, 1991; Laroche et al., 1997). Only recently has the seasonality of the fish assemblage in the mangrove-lined estuaries in subtropical Australia begun to be studied (Laegdsgaard and Johnson, 1995). Northern Taiwan is characterized by a subtropical climate and lies near the northern latitudinal limit for the geographical distribution of mangroves in the Indo-West Pacific. Little is known about the seasonality of the fish assemblage and its relationship with environmental variables in the mangroves of subtropical Taiwan.

Detailed information on the diel changes in the fish assemblage in mangrove habitats is scarce. Our knowledge of diel changes in fish activity as influenced by changing ambient illumination has mainly come from direct field observations of single species in clear waters. Studies on diel changes in fish assemblage are largely restricted to temperate coastal waters (e.g., Nash, 1986; Burrows et al., 1994; Gibson et al., 1996) or non-mangrove tropical or subtropical waters (e.g., Quinn and Kojis, 1987; Wright, 1989). Only a

few studies regarding the diel changes in the fish assemblage in mangrove habitats have been reported in a mangrove key off the coast of Puerto Rico (Rooker and Dennis, 1991) and a semiarid mangrove zone in Madagascar (Laroche et al., 1997). Their conclusions for the effects of diel cycle on the fish assemblage did not concur. Rooker and Dennis (1991) observed that all species present during the day showed marked reduction in numbers at night and thus suggested that there was no evidence for a diurnal-nocturnal change over of fish assemblage. On the other hand, Laroche et al. (1997) found that many fish species can be separated into a day or night group and concluded that diel effects were evident on the species composition of the fish assemblage. Many factors such as prey availability, predation avoidance, and abiotic circumstances have been suggested to determine the diel activity pattern of fishes (Wright, 1989; Burrows et al., 1994; Laroche et al., 1997). It is possible that differences in fish species composition and environmental factors contributed to their different conclusions.

Here, we report the results of a study designed to investigate the effects of seasonal and diel cycles on the fish assemblage in a subtropical mangrove creek. Specific objectives were: (1) to determine seasonal and diel patterns in the abundance, diversity, and species composition of the fish assemblage; (2) to determine which environmental factors correlate with the seasonal changes; and (3) to examine whether diel changes are affected by season.

MATERIALS AND METHODS

STUDY SITE.—The study site was situated in the mangrove swamp (ca 72 ha) in the estuary of the Tanshui River at Chuwei in northern Taiwan (25°10′N, 121°27′E; Fig. 1). This mangrove swamp has been designated a wildlife reserve site. The estuary of the Tanshui River is vegetated by the mangrove *Kandelia candel* (L.) Druce (2 to 5 m high). It is subjected to semidiurnal tides with a tidal range of 1 to 2 m. Fish were collected at the mouth of the main water drainage creek of the mangrove swamps. This creek is about 5 m wide with about 0.2 m deep water covering a thick layer of sandy-silt sediment at low tide. Data on water temperature, salinity, turbidity, and other environmental variables were obtained from the annual report of water quality of the Tanshui River (Environmental Protection Agency, 1997). Water temperature in the creek ranged from 15°C in February to 30°C in July (Fig. 2). The salinity of the overlying waters was variable and remained low, ranging from 7 to 12 Practical Salinity Units (PSU) at low tide. The salinity might reach 25 PSU at high tide (pers. observ.). Considerable changes in turbidity (5 to 20 Nephelometric Turbidity Units) in the water column were observed, but there were no clear seasonal patterns. Anoxia did not occur in the water column of the creek during the study period.

SAMPLING DESIGN.—Most of the fish swim into the mangrove creek with the flood tide. To characterize the seasonal changes, fish in the mangrove creek were collected monthly for a year between January and December 1996 using fyke nets. This fishing gear is a passive sampler designed to use tidal dynamics to collect nekton within small mangrove creeks. It is well suited to sample in mangrove environments (Rozas and Minello, 1997) and is composed of two fence nets (10 m long; 1.5 m high; mesh size: 15 mm) and a hoop-net (mesh size: 10 mm). On each sampling date, two fyke nets were set at the mouth of the tidal creek draining the mangrove forest at low tide and lifted 24 h later to collect fish. This resulted in integrating samples to incorporate day and night assemblages. One fyke net was set towards the estuary to catch fish on rising tide and the other towards the opposite side (the mangrove forest) to catch fish on the falling tide. The fyke nets were set during the last quarter moon phase of each month to reduce gear avoidance of fish by swimming over net walls at high tidal stages. Samples from the two fyke nets were combined for later analyses.
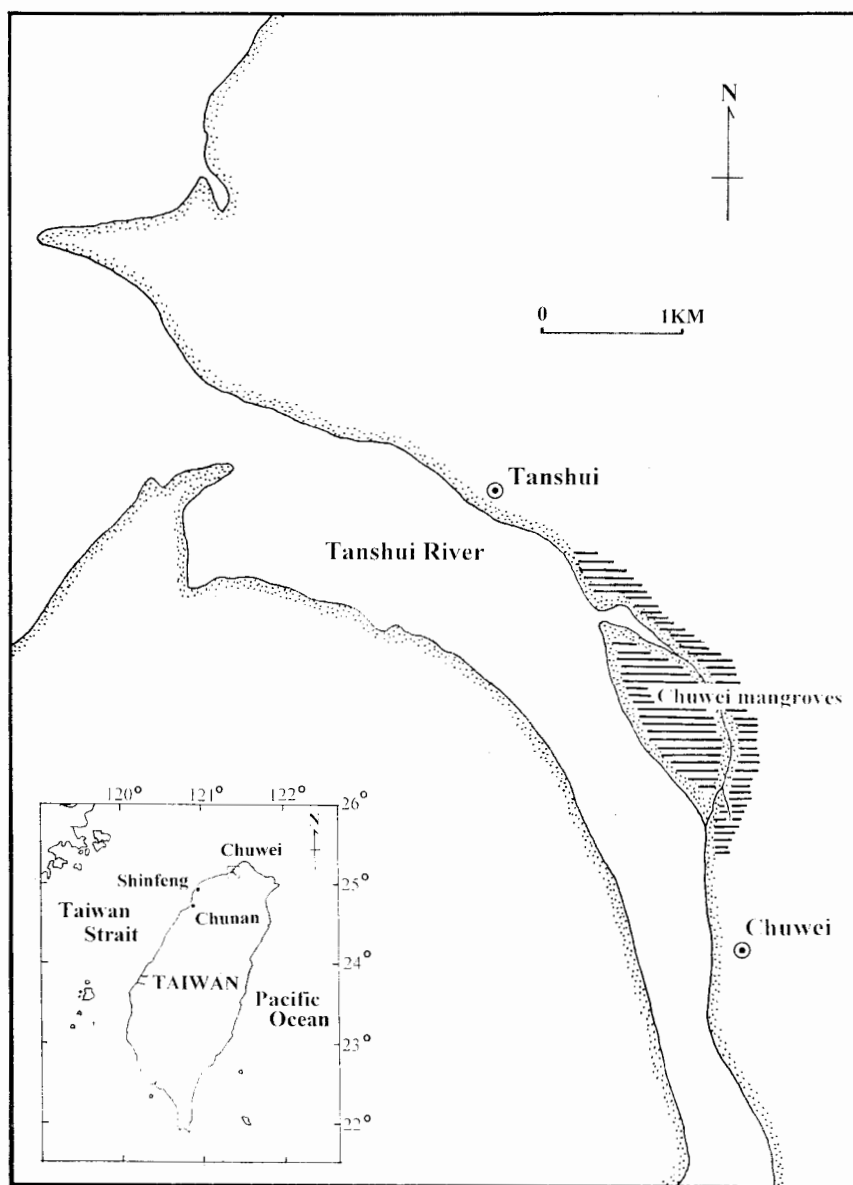
Figure 1. Study site in a mangrove creek at Chuwei in northern Taiwan.

To examine the diel changes and how they were affected by season, daytime and nighttime samples were separately collected by adjusting the setting time of the fyke nets at sunset when the tide was low in March (winter-spring), July (summer) and October (fall) of the year. Fish were then collected at each low water (at about 12-h intervals) on consecutive days over 4 to 7 d. Net samples were assumed to be independent of one another because the captured fish species and fish number did not decrease or increase over time. Fish moving into the creek with the flood tide during the night were collected at sunrise and designated as nighttime samples. Fish entering with the flood
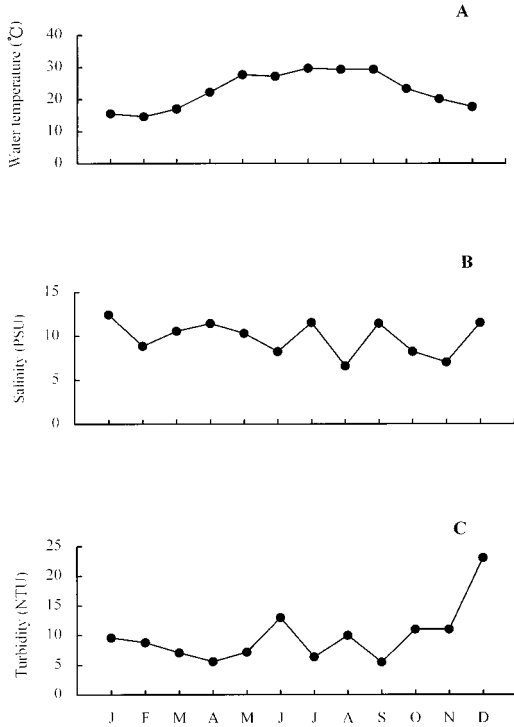
Figure 2. Water temperature (A), salinity (B), and turbidity (C) reported in the mangrove creek at Chuwei in 1996. Data were obtained from the annual report of water quality of the Tanshui River (Environmental Protection Agency, 1997).

tide during the day were collected at sunset and designated as daytime samples. All collected fish were brought back to the laboratory where they were identified, counted, and weighed.

DATA ANALYSIS.—Seasonal changes were determined by grouping the monthly samples into three seasons (winter-spring: December to March, summer: April to July, and fall: August to November) according to the results of the later classification and ordination analyses on the fish assemblage (see Fig. 5). A fixed ANOVA model (Sokal and Rohlf, 1981) was used to examine seasonal differences in total fish number, biomass, species richness, and diversity. Diel changes were examined by using a two-way ANOVA fixed model (Sokal and Rohlf, 1981) to determine whether total fish number, biomass, species richness, diversity, and numbers of the nine most common species differed significantly among months or between day and night. Before the analyses, all data on fish numbers and biomass were log-transformed ($\log_{10}(n+1)$) to conform to normality and homogeneity of variance assumptions. If the result of ANOVA indicated significant treatment effects at the 0.05 probability level, the Tukey-Kramer method was used to determine which means were significantly different (Sokal and Rholf, 1981).

The PRIMER package (Carr, 1997) was used to calculate the indices of Margalef's species richness and Shannon-Wiener diversity for the fish assemblage. Changes in species composition of the mangrove fish were studied using multivariate analyses in the PRIMER package. Each individual fish was considered as the basic functional component in the determination of species structure. Prior to multivariate analyses, fish numbers were log-transformed ($\log_{10}(n+1)$), and the Bray-Curtis similarity measure was used to produce a similarity matrix. The abundance of each species in terms of fish number captured on each date was classified by hierarchical agglomerative clustering using

the unweighted pair-group mean arithmetic linking method (UPGMA) and ordinated using the non-metric multidimensional scaling techniques (MDS). Stress values <0.2 indicated that a two-dimensional MDS plot gave a usable summary of sample relationships. The RELATE routine in the PRIMER package was applied to test if monthly changes in the species composition were related to a seasonal cycle, that is if the assemblage returned to the initial structure. This routine used a Monte Carlo permutation procedure to recompute the distribution of statistics derived from sample relationships under permutations for absence of cyclicity. Significance level was then determined by referring observed statistic to the permutation distribution (Clarke and Warwick, 1994). The BIOENV routine was used to examine which environmental variables best explained the observed seasonal pattern of the species composition. In order to avoid multicollinearity problems (Jongman et al., 1995), the environmental variables which had mutual correlations (0.95) were reduced to a single representative before the BIOENV analysis. This produced eight environmental factors for correlation: water temperature, dissolved oxygen, turbidity, salinity, river discharge, pH value, and the concentrations of NH_3 and BOD_5 in the water column. Analysis of similarities (ANOSIM) was used to determine whether temporal differences in the species composition were significant by referring the observed statistics derived from sample relationships to the distributions of statistics under permutations for absence of differences. Similarity of percentages (SIMPER) was employed to ascertain the species most responsible for the similarity within each month (most common species) and for the dissimilarities among months and between day and night (most discriminating species). For further details and algorithms of the PRIMER package see Clarke and Warwick (1994).

RESULTS

ICHTHYOFAUNA.—A total of 957 fish and 26 species belonging to 14 families were recorded in the monthly catches over one year (Table 1). Of the fish species, 73% were demersal species, 15% were reef-associated species and 12% were pelagic species. About 85% of the individuals were marine migrants from the sea, and the other 8% and 6% were estuarine and freshwater species, respectively. Most of the individuals (77%) were omnivores, 15% were benthic invertebrates feeders and 7% were planktivores.

Of the fish families collected, the Gobiidae (7 species) and Mugilidae (4 species) were the most diverse. The fish assemblage was dominated by a small number of commercially important species (*Liza macrolepis*, *Liza affinis*, *Oreochromis* hybrid, *Ambassis gymnocephalus*, *Acentrogobius viridipunctatus*, *Engraulis japonicus*, and *Eleotris acanthopomas*) whose abundance varied by month. Each represented >18% of the total numbers of the catches. Of these species, *L. macrolepis* was the most frequently caught species in the mangrove creek and was the only species captured throughout the year. The contribution of the four most numerous species averaged about 90% of the total numbers, but only 74% of the total biomasses (Table 2), indicating that fish of small size dominated the assemblage (standard length of 3 to 7 cm). The species composition by weight presented a slightly different picture because the total weight was often affected by the presence of a few relatively large individuals of *Oreochromis* hybrid (standard length of 10 to 14 cm) and *Anguilla japonica* (standard length of 44 to 70 cm). For example, *A. japonica* contributed only 1.2% of the total number of the catch in July, but contributed more than half (51%) of the total biomass.

SEASONAL CHANGES.—Considerable variations in fish number, biomass, species richness, and Shannon-Wiener diversity of the fish assemblage over time, but no clear patterns were observed (Fig. 3). Despite higher fish number and biomass per netting in March (Table 3), there were no significant seasonal differences (Fig. 4) due to the high

Table 1. Species composition of monthly catches by fyke nets in the mangrove creek at Chuwei as percentages of total fish number.

Family and species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Anguillidae												
Anguilla japonica							1.2	5.9				
Engraulidae												
Engraulis japonicus			23									
Centropomidae												
Ambassis gymnocephalus		2.3			7.3		1.2				34	22
Ambassis interruptus											0.8	
Teraponidae												
Terapon jarbua			7.0	5.1	1.8					2.6		
Carangidae												
Caranx ignobilis								5.9	4.0			
Caranx sexfasciatus									1.3			
Leiognathidae												
Leiognathus nuchalis									16	2.6		
Lutjanidae												
Lutjanus argentimaculatus										2.6	3.3	
Lutjanus russelli									1.3		4.1	
Gerreidae												
Gerres sp.					1.8							
Sparidae												
Acanthopagrus latus								5.9	1.3			
Scatophagidae												
Scatophagus argus							1.2			31	0.8	
Cichlidae												
Oreochromis hybrid	5.9	8.0	2.3	2.6				18	25	7.7	15	1.0
Gobiidae												
Acentrogobius viridipunctatus				5.1	1.8	8.5		29	2.7	7.7	1.6	
Bostrychus sinensis						0.8						
Butis melanostigma					1.8					2.6	1.6	1.0
Eleotris acanthopomas	2.0			5.1	1.8	11	1.2	18				
Eleotris melanosoma			0.8	2.6	1.8	1.7				2.6		0.5
Ophiocara porocephala	3.9			2.6		4.2	3.6					1.0
Taeniodes cirratus							1.2					
Mugilidae												
Liza affinis	5.9	52	1.6	7.7	42	7.6	11		27	2.6		2.5
Liza alata								5.9				
Liza macrolepis	61	40	84	46	40	66	80	12	21	33	37	71
Liza subviridis	22		2.3							5.1	1.6	1.0
Polynemidae												
Eleutheronema tetradactylum												0.5
Total number	51	25	128	39	55	118	84	17	75	39	122	204

Table 2. Species composition of catches by fyke nets in the mangrove creek at Chuwei as percentages of total weight.

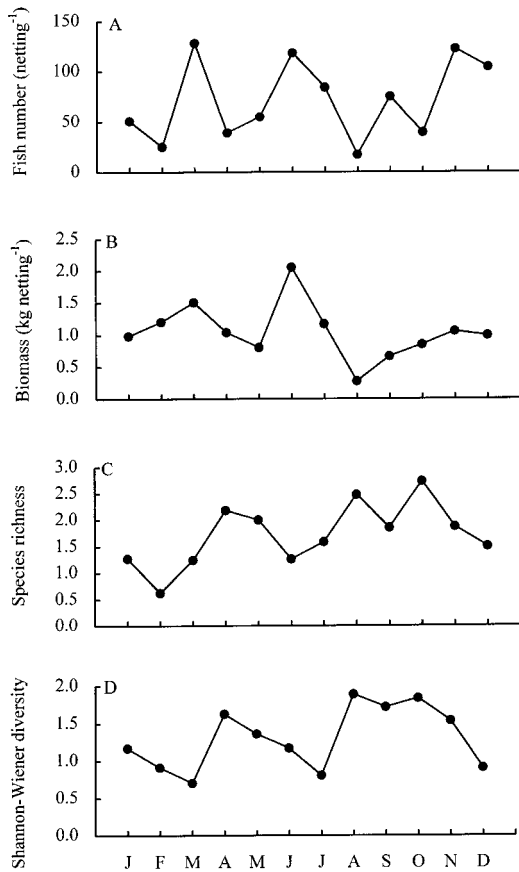| Family and species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Anguillidae												
Anguilla japonica							51	13				
Engraulidae												
Engraulis japonicus			7.6									
Centropomidae												
Ambassis gymnocephalus		0.2			0.1		0.1				6.1	5.3
Ambassis interruptus											0.1	
Teraponidae												
Terapon jarbua			1.2	4.0	0.1					5.5		
Carangidae												
Caranx ignobilis								1.8	3.8			
Caranx sexfasciatus									0.9			
Leiognathidae												
Leiognathus nuchalis									3.5	0.4		
Lutjanidae												
Lutjanus argentimaculatus										0.5	2.1	
Lutjanus russelli									1.2		2.9	
Gerreidae												
Gerres sp.					0.1							
Sparidae												
Acanthopagrus latus								1.5	0.3			
Scatophagidae												
Scatophagus argus							0.1			3.7	0.5	
Cichlidae												
Oreochromis hybrid	20	57	26	14				28	37	14	43	2.7
Gobiidae												
Acentrogobius viridipunctatus			3.4	1.2	8.6			22	3.8	3.8	4.4	
Bostrychus sinensis						3.6						
Butis melanostigma					1.0					0.9	1.0	0.8
Eleotris acanthopomas	0.8			3.8	1.6	12	0.9	12				
Eleotris melanosoma			0.9	1.3	2.5	1.1				1.1		0.3
Ophiocara porocephala	26			17		34	3.6					21
Taeniodies cirratus							5.7					
Mugilidae												
Liza affinis	8.7	28	0.9	6.8	47	3.3	1.8		23	1.3		7.8
Liza alata								5.1				
Liza macrolepis	36	15	58	42	46	37	36	18	27	30	33	48
Liza subviridis	7.7		12							40	6.5	7.1
Polynemidae												
Eleutheronema tetradactylum												7.3
Total weight (kg)	0.98	1.20	1.51	1.04	0.80	2.05	1.17	0.27	0.66	0.84	1.05	0.99

Figure 3. Monthly changes in fish number (A), biomass (B), species richness (C), and Shannon-Wiener diversity (D) of the fish assemblage in the mangrove creek at Chuwei in 1996.

variations (df = 2, 9; P = 0.73 and 0.11, respectively). However, species richness and diversity were significantly higher in fall than in winter-spring (df = 2, 9; P = 0.01 and 0.003, respectively). The diel samples also showed that species richness and diversity were higher in October (Table 3).

For the nine most common species (occurrence > 66% of the samples), the catches of *L. macrolepis*, *Oreochromis* hybrid, and *T. jarbua* in terms of fish number were higher in March (Table 3). But the catch of *A. viridipunctatus* was higher in July and October. The standard length of six species (*L. macrolepis*, *Oreochromis* hybrid, *L. affinis*, *L. subviridis*, *Scatophagus argus*, and *T. jarbua*) also showed a significant monthly effect (Table 4). The sizes of *L. macrolepis* and *T. jarbua* were smaller in March and July than in October. On the other hand, the sizes of *Oreochromis* hybrid, *L. affinis*, *L. subviridis*, and *S. argus* were larger in March and smaller in October or July.

Non-metric MDS ordination of the numbers of each fish species in each month separated the assemblage structures into fall (upper), winter-spring (middle) and summer (lower) groups (stress = 0.14) (Fig. 5). The results of the RELATE routine showed that monthly changes in the species composition followed a gradual pattern and showed a significant

Table 3. Two-way ANOVA (month × day-night) of fish number, biomass, species richness, and Shannon-Weiner diversity of all fish and of the nine most common species in terms of fish number recorded in the mangrove creek at Chuwei. Fish numbers were log-transformed ($\log_{10}(1+n)$) before analyses. The Tukey-Kramer method was used to determine which treatments are different (* significant at $P < 0.05$; ** highly significant at $P < 0.01$; NS not significant at $P > 0.05$).

	Month		Day-night		Month × Day-night		Separation
	F	P	F	P	F	P	
	(d.f. = 2,26)		(d.f. = 1,26)		(d.f. = 2,26)		
Fish number	9.55	**	1.03	NS	0.98	NS	Mar > Jul = Oct
Biomass	3.19	*	5.46	*	0.25	NS	Mar > Jul = Oct, Night > Day
Species richness	9.07	**	2.72	NS	1.04	NS	Oct > Jul = Mar
Shannon-Weiner diversity	12.10	**	8.37	**	3.38	*	Oct > Jul = Mar, Night > Day
Liza macrolepis	16.80	**	0.01	NS	1.38	*	Mar > Jul > Oct
Oreochromis hybrid	11.80	**	2.83	NS	0.81	NS	Mar = Oct > Jul
Liza affinis	1.29	NS	4.10	*	1.80	NS	Night > Day
Liza subviridis	2.46	NS	1.43	NS	0.08	NS	
Scatophagus argus	1.73	NS	0.26	NS	0.14	NS	
Acentrogobius viridipunctatus	3.42	*	0.67	NS	0.83	NS	Jul = Oct, Oct = Mar, Jul > Mar
Terapon jarbua	59.10	**	64.00	**	37.20	**	Mar > Oct = Jul, Night > Day
Ophiocara porocephala	0.62	NS	0.22	NS	0.20	NS	
Eleotris melanosoma	1.97	NS	0.06	NS	0.02	NS	

seasonal cycle at the 5% significance level in a permutation test for absence of cyclicity (sample statistic = 0.22; number of permutations = 5000; significance level = 0.013). Among the eight examined environmental variables, the BIOENV routine showed that the combination of water temperature and salinity best explained the seasonal pattern of the species composition in the mangrove creek. Pearson correlations indicated that water temperature correlated positively, and salinity negatively, with species richness and diversity of fish (Fig. 6). About 28 and 20% of the variation in species richness and diversity can be explained by variation in water temperature, respectively. The other 8% and 18% of the variance of species richness and diversity was due to variation in salinity.

ANOSIM demonstrated that the species structures were significantly different between March and October and between July and October at the 5% of significance level in a permutation test for absence of month effect (Table 5). But there was no significant difference in species structure between March and July. SIMPER showed that *L. macrolepis* were the most common species appearing in the samples from March and July (Table 6). In October, *Oreochromis* hybrid and *L. macrolepis* were the most representative species. SIMPER also revealed that the assemblages between July and October were the most dissimilar (71%), and *Oreochromis* hybrid was most responsible for this dissimilarity. *Oreochromis* hybrid also made the most substantial contribution to the dissimilarity between October and March. *T. jarbua* and *A. viridipunctatus* were the two major species responsible for the difference between March and July.

DIEL CHANGES.—In the study of diel changes, a total of 1154 individuals belonging to 25 species in 15 families were captured, 623 at night and 531 during the day (Table 7). Most of the species have been recorded in the monthly collection except four rare species. Six of the 25 species were present only at night: *Pisodonophis boro*, *Chanos chanos*, *Ambassis interruptus*, *Lateolabrax japonicus*, *Butis melanostigma*, and *Taeniodies cirratus*. *A. gymnocephalus* and *T. jarbua* were captured in extremely low numbers during the day. Four other species were completely absent at night: *Arius maculatus*, *Caranx ignobilis*,
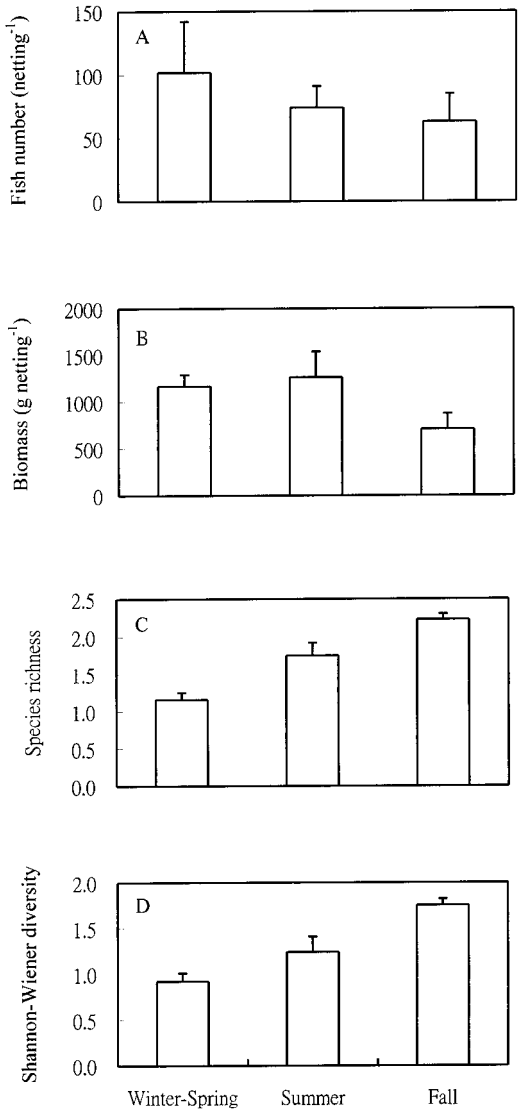
Figure 4. Mean values (±SE) of fish number (A), biomass (B), species richness (C), and Shannon-Wiener diversity (D) of the fish assemblage captured in the mangrove creek at Chuwei in winter-spring (from December to March), summer (from April to July), and fall (from August to December) 1996.

Leiognathus nuchalis, and *Pomadasys kaakan*. *E. acanthopomas* was captured in low numbers at night.

The differences in fish number, biomass, species richness, and Shannon-Wiener diversity between day and night were more evident in March and July than in October (Fig. 7). Overall, there was no significant diel effect on total fish number and species richness (Table 3). However, biomass was significantly higher at night than during the day. Diversity was significantly higher at night only in March and July.

Table 4. Two-way ANOVA (month × day-night) on the standard length of the nine most common species recorded in the mangrove creek at Chuwei. The Tukey-Kramer method was used to determine which treatments are different. (* significant at P < 0.05; ** highly significant at P < 0.01; NS not significant at P > 0.05)

	Month			Day-night			Month × Day-night		Separation
	F	P	d.f.	F	P	d.f.	F	P	
Liza macrolepis	16.4	**	2, 757	2.8	NS	1, 757	0.02	NS	Oct > Jul = Mar
Oreochromis hybrid	12.0	**	1, 43	0.7	NS	1, 43	1.1	NS	Mar > Oct
Liza affinis	32.5	**	2, 84	0.02	NS	1, 84	1.8	NS	Mar > Oct > Jul
Liza subviridis	5.8	*	2, 15	0.2	NS	1, 15	0.5	NS	Mar = Oct > Jul
Scatophagus argus	11.2	**	2, 16	10.7	**	1, 16	5.9	*	Mar > Oct > Jul, Night > Day
Acentrogobius viridipunctatus	1.5	NS	2, 21	0.1	NS	1, 21			
Terapon jarbua	7.5	**	2, 50	0.4	NS	1, 50			Oct > Mar = Jul
Ophiocara porocephala	2.2	NS	2, 3	3.4	NS	1, 3	0.7	NS	
Eleotris melanosoma	0.1	NS	1, 6	1.3	NS	1, 6	1.5	NS	

Significant diel differences in fish number were detected for two of the nine most common species (Table 3). Both numbers of *L. affinis* and *T. jarbua* were higher at night than during the day. Significant diel differences in fish size were detected for only one of the nine most common species. The size of *S. argus* was smaller during the day than at night in July (Table 4).

Classification of the numbers of each fish species from each sample separated the species structures into two major groups at a similarity level of 30%, one containing mainly samples from March and July (A) and the other comprising those taken from October (B)(Fig. 8). The former group then separated into two subgroups at the level of 45%. One contained samples captured during the day in March (Group C), and the sec-
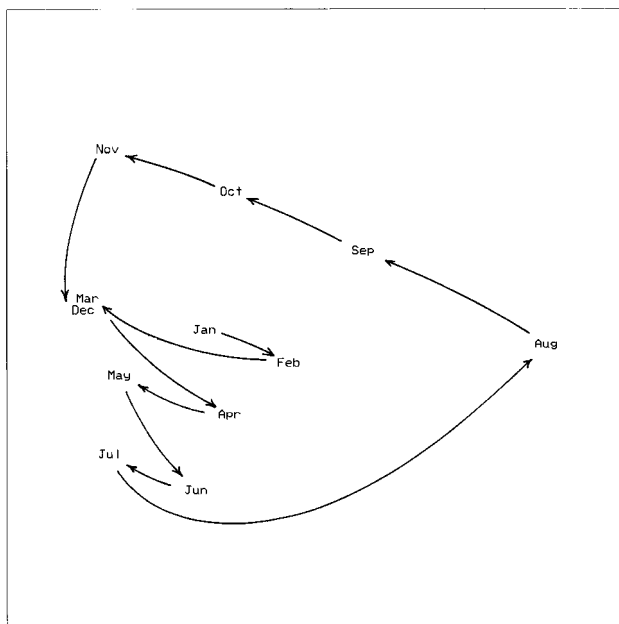

Figure 5. Non-metric MDS ordination of abundance data for each species of the fish assemblage captured in each month in the mangrove creek at Chuwei in 1996.
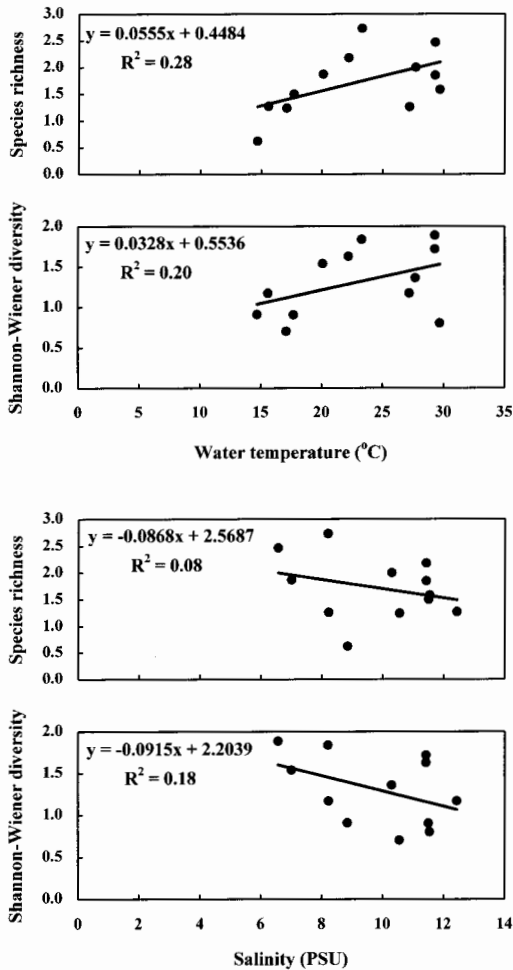
Figure 6 Pearson correlations between species richness and diversity of the fish assemblage and water temperature (upper) and salinity (lower) in the mangrove creek at Chuwei.

ond contained samples taken mainly from the same month but were captured at night (Group D). The daytime and nighttime samples captured in July were not well separated in the dendrogram and were scattered in the Groups C and D. Samples included in the latter group were captured in October. One subgroup comprised daytime samples (Group E) but the other contained nighttime samples (Group F).

The results of the non-metric MDS ordination paralleled those produced by the classification (stress = 0.20). The fish assemblage was primarily structured by the month of the year, and secondarily by day and night. Non-metric MDS showed that catches in October were distinct from those in March and July (Fig. 9). Daytime and nighttime catches were then well-separated in March and October, but not in July.

ANOSIM showed that overall assemblage structures were significantly different between day and night at the 5% significance level in a permutation test for absence of diel effect (Table 5). The species most responsible for the dissimilarity between day and night

Table 5. Two-way crossed ANOSIM (analysis of similarities) table. The effects of month and day-night on the fish assemblages captured in March, July, and August in the mangrove creek at Chuwei were tested by recomputing the distribution of statistics derived from sample relationships under permutations for absence of month and diel effects. Significance level was calculated by referring the observed statistic (sample relationship) to its permutation distribution (Clarke and Warwick, 1994).

Factor	Observed statistic	Permutations used	Significant statistics	Significance level
Month				
Global test	0.49	5,000	0	0.0%
Pairwise test				
Mar vs. Jul	0.26	5,000	116	2.3% (NS)
Mar vs. Oct	0.65	5,000	0	0.0%
Jul vs. Oct	0.62	5,000	0	0.0%
Day vs. Night	0.23	5,000	17	0.4%

Tests were significant at the level of 5% except where indicated by N.
The Bonferroni correction for the pairwise test (n=3) when α=0.05 is α'=0.05/3=0.017 or 1.7%.

Table 6. Percentage contributions (%) of the most abundant species (>10% of total fish number) to the average similarity within each month and the dissimilarities between months and between day and night catches captured in the mangrove creek at Chuwei.

	March	July	October
Average similarity within each month (%)	62	46	46
Species			
Liza macrolepis	71	70	30
Oreochromis hybrid	11		35
Terapon jarbua	9		
Acentrogobius viridipunctatus		12	
Liza affinis		8	
Lutjanus argentimaculatus			12
	Mar. vs Jul.	Jul. vs Oct.	Oct. vs Mar.
Average dissimilarity between months (%)	55	71	63
Species			
Terapon jarbua	12		
Acentrogobius viridipunctatus	12		
Oreochromis hybrid	11	17	13
Liza affinis	11		
Liza macrolepis		9	11
Leiognathus nuchalis		9	10
Lutjanus argentimaculatus		8	10
	Day vs Night	Day vs Night	Day vs Night
Average dissimilarity between day and night (%)	45	57	63
Species			
Terapon jarbua	31		
Oreochromis hybrid	14		13
Liza macrolepis	13	21	12
Liza affinis		18	
Acentrogobius viridipunctatus		12	
Leiognathus nuchalis			19

Table 7. Species composition of catches by fyke nets in the mangrove creek at Chuwei as percentages of total fish number (N) and weight (kg) (W) captured during the day and at night.

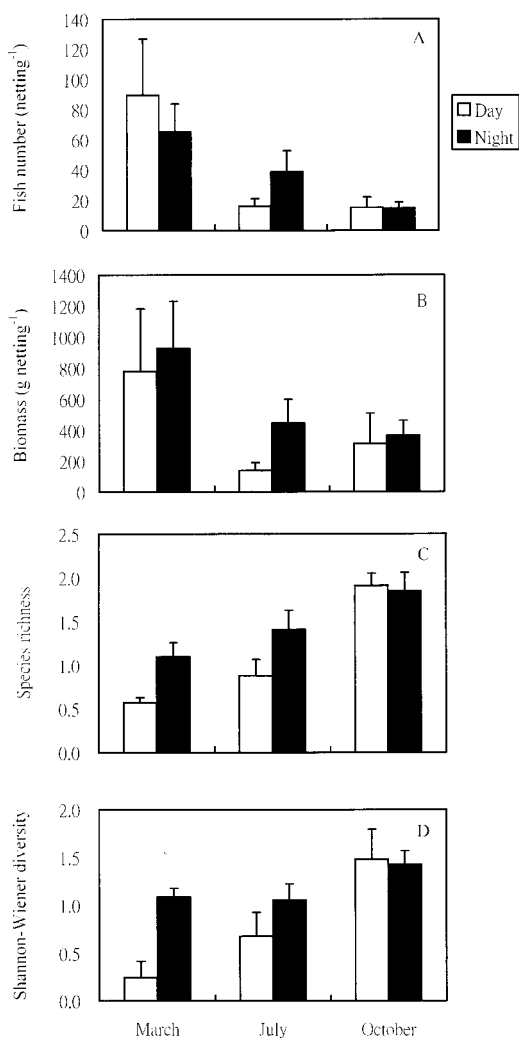| Family and species	March Day N	March Day W	March Night N	March Night W	July Day N	July Day W	July Night N	July Night W	October Day N	October Day W	October Night N	October Night W
Anguillidae												
Anguilla japonica							0.4	19	1.3	19		
Ophichthidae												
Pisodonophis boro							1.1	24				
Chanidae												
Chanos chanos							0.4	0.2				
Arridae												
Arius maculatus					1.0	0.7						
Centropomidae												
Ambassis gymnocephalus			3.1	0.2	1.0	<0.1	2.2	<0.1				
Ambassis interruptus							0.4	<0.1				
Percichthyidae												
Lateolabrax japonicus											1.1	15.2
Teraponidae												
Terapon jarbua	0.6	0.1	19	3.2			0.4	<0.1			2.3	2.2
Carangidae												
Caranx ignobilis									1.3	2.1		
Leiognathidae												
Leiognathus nuchalis									32	5.8		
Lutjanidae												
Lutjanus argentimaculatus							0.4	0.2	6.6	1.9	4.6	0.9
Haemulidae												
Pomadasys kaakan									5.3	0.8		
Scatophagidae												
Scatophagus argus	0.3	0.2	0.8	0.2	1.0	<0.1	0.4	0.1	4.0	0.6	16	1.7
Cichlidae												
Oreochromis hybrid	2.0	32	6.9	36					17	38	31	40
Gobiidae												
Acentrogobius viridipunctatus	0.3	0.9			7.2	12	4.0	6.0			5.7	3.4
Butis melanostigma											3.4	1.2
Eleotris acanthopomas					4.1	11	0.7	0.9				
Eleotris melanosoma					2.1	4.4	1.1	0.9	2.6	1.5	3.4	1.6
Glossogobius olivaceus	0.3	0.1	0.4	0.1								
Ophiocara porocephala			0.4	6.1	2.1	24	1.1	4.3	1.3	9.0	1.1	1.1
Taeniodies cirratus							0.4	2.1				
Mugilidae												
Liza affinis	0.6	1.8	2.3	2.4	8.3	0.7	26	4.5	1.3	0.2	4.6	1.5
Liza alata					1.0	1.1	1.1	0.5				
Liza macrolepis	95	52	64	31	71	46	59	36	26	19	24	15
Liza subviridis	1.1	13	3.8	21	1.0	0.7	1.1	0.7	1.3	2.7	3.4	16
Total	358	3.1	262	3.7	97	0.8	273	3.1	76	1.6	88	2.2
No. of samples	4		4		6		7		5		6	

Figure 7. Mean values ± SE) of fish number (A), biomass (B), species richness (C), and Shannon-Wiener diversity (D) of the fish assemblage captured during the day and at night in the mangrove creek at Chuwei in March (winter-spring), July (summer), and October (fall) 1996.

varied by month (Table 6). SIMPER showed that *T. jarbua* contributed most to the dissimilarity in March. *L. nuchalis* was a good species for discriminating between the species structures captured at night and during the day in October.

DISCUSSION

The primary ichthyofauna captured in this study is similar to that of other western Pacific mangrove creeks (Pinto, 1987; Chong et al., 1990; Blaber and Milton, 1990). Quantitative comparisons of the fish assemblage with those of other subtropical mangroves are seldom possible, since studies using the same sampling technique are few. The dominant species captured in the mangrove creek at Chuwei are similar to those recorded

Figure 8. Classification of abundance data for each species of the fish assemblage captured on each sampling date in the mangrove creek at Chuwei in 1996. MN: at night in March (early spring); MD: during the day in March (early spring); JN: at night in July (summer); JD: during the day in July (summer); ON: at night in October (fall); OD: during the day in October (fall).

by Kuo et al. (unpub.) for other adjacent mangrove creeks off Shinfeng and Chunan (Fig. 1) using the same sampling technique. All three subtropical mangrove creeks were dominated by a few species, including *L. macrolepis*, *L. affinis, A. viridipunctatus,* and *Oreochromis* hybrid. The number of fish species collected from Chuwei (30) in a year is comparable to the numbers recorded for the mangrove creeks off Shinfeng (29) and Chunan (21). The diversity indices of the fish assemblage captured in Chuwei averaged 1.24, which is also comparable to the mean values of Shinfeng (1.39) and Chunan (0.95). These diversity indices are lower than the range of 1.62–1.81 of the fish assemblages captured in the tropical mangrove creeks in southern Taiwan using the same sampling technique (Kuo et al., unpubl.). It appears that the fish assemblages in subtropical mangrove swamps are less diverse than in tropical mangrove habitats.

Laegdsgaard and Johnson (1995) found that fish abundance in subtropical Australia is greatest in summer and lowest in winter. In this study, no clear seasonal pattern for total fish number was observed (Fig. 3). A possible explanation is that the mangrove creek was dominated by well-known marine migrants from the sea. These marine migrants have similar life histories, but each has distinctive features, such as different spawning seasons. Furthermore, the distance of spawning site from coastal mangroves may be different. For example, Mugilidae and Teraponidae spawn in late winter, Lutjanidae spawns in summer, but Gerreidae breeds all year round (van der Elst, 1981; Wen, 1996; Blaber, 1997). Mugilidae, Teraponidae, Lutjanidae and Gerreidae breed offshore, but
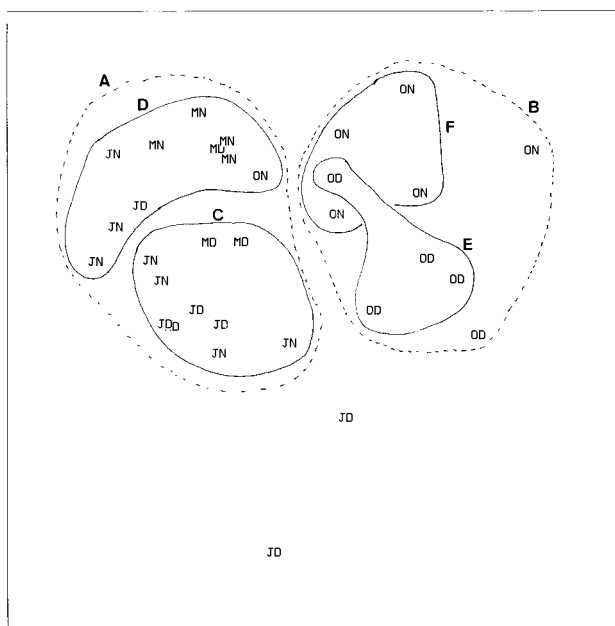
Figure 9. Non-metric MDS ordination of abundance data for each species of the fish assemblage captured on each occasion in the mangrove creek at Chuwei in 1996. MN: at night in March (early spring); MD: during the day in March (early spring); JN: at night in July (summer); JD: during the day in July (summer); ON: at night in October (fall); OD: during the day in October (fall).

Leiognathidae, Engraulidae and Sparidae spawn near or just outside estuaries (van der Elst, 1981; Blaber, 1997). Their juveniles thus occurred in the mangrove creek at different times of the year and the total fish number changed on an irregular basis. The influence of offshore processes on the density of mangrove nekton has been observed in studies on the dynamics of the banana prawn *Penaeus merguiensis* in northern Australia (Crocos and Kerr, 1983). This suggests that temperature may play an important role in determining the spawning behavior of the marine migrants. It is not surprising that water temperature is one of the most important factors affecting the structure of the fish assemblage in the subtropical mangrove creek. Wang et al. (1991) also reported that the occurrence of the fish eggs and larvae in the coastal waters off the estuary of the Tanshui River was related to water temperature.

Besides water temperature, we also found that salinity is important in structuring the fish assemblage in the subtropical mangrove creek. This finding is somewhat different from findings in other subtropical (Laegdsgaard and Johnson, 1995) and temperate (Bell et al., 1984) mangrove swamps. This may be because salinity in other subtropical (24 to 36 PSU) and temperate (30 to 38 PSU) mangrove swamps was much higher than in the mangrove creek at Chuwei (7 to 25 PSU). The variation in salinity was also greater in our subtropical creek than in other subtropical and temperate creeks. As a result, although a large proportion of the individuals in our creek were marine migrants and estuarine species which have a wide tolerance to salinity (Blaber, 1997), large numbers of exclusively freshwater species often occurred when salinity declined in response to rainfall and freshwater input. For example, large numbers of *Oreochromis* hybrid were often brought into the mangrove forests by river discharges between August and November when rainfall

was high and salinity reduced (generally <8 PSU). The contributions made by *Oreochromis* hybrid may reach 25% of the total number of the catch. Therefore, salinity explains part of the seasonal pattern of the subtropical fish assemblage. This may be one of the reasons why our seasonal pattern in fish abundance was different from that observed in other subtropical mangrove habitats with peaks in summer and lows in winter (Laegdsgaard and Johnson, 1995). In tropical mangrove habitats where low salinity may occur, salinity (Wright, 1986) or rainfall (Robertson and Duke, 1990; Rooker and Dennis, 1991) has been suggested as the most important variable affecting the seasonal patterns of fish abundance.

Our results show that day and night had an influence on activity patterns of some species moving into the mangrove creek. The diel activity patterns of many species captured as juveniles in this study, however, differed from those captured as adults in other habitats. For example, juveniles of *L. macrolepis* showed no diel change in abundance, which is inconsistent with the species captured as adults in other tropical mangrove creeks (Laroche et al., 1997). Juveniles of the well-known nocturnal species *L. argentimaculatus* also showed no diel change in abundance. Furthermore, *L. nuchalis* and *Pomadasys kaakan* were captured as juveniles in great numbers and exclusively during the day. Juveniles of *T. jarbua* were caught almost exclusively at night. Nevertheless, previous studies documented that adults of *Leiognathus equulus, Leiognathus brevirostris, Pomadasys stridens*, and *T. jarbua* showed no significant diel differences in abundance (Wright, 1989; Laroche et al., 1997).

The cause of the diel activity patterns of the mangrove fish assemblage is unclear. Rooker and Dennis (1991) suggested that the diel activity patterns are related to feeding strategy. The nocturnal feeding trend of some Mugilidae was observed in another tropical mangrove creek (Laroche et al. 1997). Therefore, increased foraging activity of *L. affinis* may be responsible for its significantly greater abundance at night in this study. On the other hand, Burrows et al. (1994) suggested that the nocturnal inshore movement of juveniles is possibly in response to predator avoidance. Wright (1989) suggested that fish avoid shallow water during the day because of increased predation risk from diurnal predators, particularly birds. In this study, however, no clear conclusion can be drawn because the mangrove fish varied in their activity patterns. Each activity pattern may have been determined by combined responses to prey availability, predation avoidance, and abiotic circumstances. Gibson et al. (1996) came to a similar conclusion for the diel changes of fish on a Scottish sandy beach.

Whether observed increases in biomass and diversity of fish caught at night were real or simply because net avoidance was lower at night has been a contentious issue (e.g. Nash, 1986; Wright, 1989; Gibson et al., 1996). Eight of the nine most common species showed no change in size in the catches between day and night (Table 4). In addition, the creek site was always shaded by mangrove trees, and the water in the creek was often turbid. Therefore, diel changes in biomass, diversity and species composition in the mangrove creek were unlikely to be a reflection of avoidance of the fyke nets in daylight. The lack of significant diel difference in total fish number and species richness also suggests that there was no difference in catch efficiency between day and night. The overall significantly greater biomass captured in the mangrove creek at night was mainly due to the contribution of relatively large individuals of *Lateolabrax japonicus* and some benthic burrowing species, such as *Pisodonophis boro* and *Taeniodies cirratus* (Table 7). These benthic burrowing species were generally buried in sediments during the day and exclusively captured at night when they were active.

Unlike other mangrove habitats (Rooker and Dennis, 1991) and a Scottish sandy beach (Gibson et al., 1996), this study showed that there were distinct "day" and "night" assemblages in the subtropical mangrove creek (Nash, 1986; Helfman, 1993). However, the existence of two distinct assemblages depended upon season, being more evident in fall and less evident in summer. In the catches during fall, four of 16 species were captured exclusively during the day and another four were captured exclusively at night. While *L. nuchalis* dominated the day assemblages, *Oreochromis* hybrid dominated the night assemblages. In summer, although seven of 18 species were captured exclusively at night, this difference in assemblage structure was slight because all nocturnal species were rare. As a result, the only difference between day and night assemblages in summer was mainly caused by the changing abundance of a few dominant species rather than by their presence or absence. This may be the reason for Rooker and Dennis (1991) and Gibson et al. (1996) to conclude that there were no distinct day and night assemblages simply according to their summer observations. Nevertheless, the diel changes in the assemblage structure in this study were relatively small when compared to the seasonal changes (Fig. 8). It is thus concluded that the structuring effect of a seasonal cycle was more important than diel cycles in determining the temporal patterns of changes in the fish assemblage of a subtropical mangrove creek.

Literature Cited

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

Blaber, S. J. M. 1997. Fish and fisheries of tropical estuaries. Chapman and Hall, London. 367 p.
—————— and D. A. Milton. 1990. Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. Mar. Biol. 105: 295–267.

Burrows, M. T., R. N. Gibson, L. Robb and C. A. Comely. 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. J. Exp. Mar. Biol. Ecol. 177: 251–268.

Carr, M. R. 1997. Primer user manual. Plymouth routines in multivariate ecological research. Plymouth Marine Laboratory. 36 p.

Chong, V. C., A. Ssaekumar, M. U. C. Leh and R. D. Cruz. 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. Estuar. Coast. Shelf Sci. 31: 703–722.

Clarke, K. R. and R. W. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory. 859 p.

Crocos, P. J. and J. D. Kerr. 1983. Maturation and spawning of the banana prawn *Penaeus merguiensis* de mau (Cruatacea: Penaeidae) in the Gulf of Carpeutaria. Australia. J. Exp. Mar. Biol. Ecol. 69: 37–59.

Gibson, R. N., L. Robb, M. T. Burrows and A. D. Ansell. 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 130: 1–17.

Helfman, G. S. 1993. Fish behavior by day, night and twilight. Pages 479–512 *in* T. J. Pitcher, ed., Behavior of teleost fishes, 2nd ed. Chapman and Hall, London.

Jongman, R. H. G., C. J. F. ter Braak and O. F. R. van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge Univ. Press, Cambridge. 299 p.

Laegdsgarrd, P. and C. R. Johnson. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser. 126: 67–81.

Laroche, J., E. Baran and N. B. Rasoanandrasana. 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. J. Fish Biol. 51: 3–20.

Little, M. C., P. J. Reay and S. J. Grove. 1988. The fish community of an East African mangrove creek. J. Fish Biol. 32: 792–747.

Morton, R. M. 1990. Community structure, density and standing crop of fishes in a subtropical australian mangrove area. Mar. Biol. 105: 385-394.

Nash, R. D. M. 1986. Diel fluctuations of a shallow water fish community in the inner Oslofjord, Norway. Mar. Ecol. 7: 219–232.

Pinto, L. 1987. Environmental factors influencing the occurrence of juvenile fish in the mangrove of Pagbilao, Philippines. Hydrobiologia 150: 283–301.

Quinn, N. J. and B. L. Kojis. 1987. The influence of diel cycle, tidal direction and trawl alignment on beam trawl catches in an equatorial estuary. Env. Biol. Fish. 19: 297–308.

Robertson, A. I. and N. C. Duck. 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.

_____ and _____. 1990. Mangrove fish communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and assemblage structure. Mar. Biol. 104: 369–379.

Rooker, J. R. and G. D. Dennis. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bull. Mar. Sci. 49: 684–698.

Rozas, L. P. and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20: 199–213.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. Freeman, San Francisco. 859 p.

van der Elst, R. 1981. A guide to the common sea fishes of southern Africa. C. Struik Publishers, Cape Town. 587 p.

Wang, Y. T., W. N. Tzeng and S. C. Lee. 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, Tawian (1984–1985). J. Fisher. Soc. Taiwan 18: 7–20.

Wen, D. J. 1996. The reproductive biology of *Chelon maerolepis* and *C. subviridis* in Kaohsiung River and its Harbor area, Taiwan. MS Thesis, Institute of Marine Resources, National Sun Yat-sen University, Kaohsiung. 98 p.

Wright, J. M. 1986. The ecology of fish occurring in shallow water creeks of a Nigerian mangrove swamp. J. Fish Biol. 29: 431–441.

_____. 1989. Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. Mar. Biol. 102: 135–142.

ADDRESSES: (H.-J.L.) *Department of Botany, National Chung Hsing University, Taichung 402, Taiwan, Republic of China;* (K.-T.S.) *Institute of Zoology, Academia Sinica, Taipei 115, Taiwan, Republic of China.* CORRESPONDING AUTHOR: (K-T.S.) *Institute of Zoology, Academia Sinica, Taipei 115, Taiwan, Republic of China. Tel: +886-2-27899545, Fax: +886-2-27883463, Email: <zoskt@gate.sinica.edu.tw>.*