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Immigration Timing and Activity Rhythms of the Eel, *Anguilla japonica*, Elvers in the Estuary of Northern Taiwan, with Emphasis on Environmental Influences*

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Abstract

To predict the timing for success in harvesting the elvers of *Anguilla japonica*, the biological characteristics, upstream behaviour and migration period were studied on the basis of elver samples and commercial catch data collected from the rivers and coastal waters in northern Taiwan during the fishing seasons from 1980 to 1984. In addition, the influences of environmental factors on elver recruitment were also discussed. The results obtained are as follows:

(1) Seasonal decline in size was found for the elvers both from rivers and coastal waters. It is considered to be related to the temporal change in pigmentation stage of the elvers.

(2) The maximal catch of the elvers in the coastal waters seems to be correlated with the temperature. The maximum catch often occurred on the date or several days after when daily seawater temperature reached the lowest in the winter season. The minimum water temperature was recorded at 15–16°C.

(3) Instantaneous maximal catch occurred at the time when the salinity increased to plateau and the instantaneous rate of seawater influx reached maximum. Upstream of elvers also became most active during this period at night.

(4) The biological rhythm of elver-activity was found to follow the lunar cycle in the coastal waters. The peak catches appeared only once a month around the time of newmoon. In contrary, a semilunar rhythm of the elvers in the rivers was observed; two peak catches occurred in each lunar cycle, one around fullmoon, the other around newmoon. The semilunar rhythm in the rivers was further corresponding to spring tide. However, moon light seemed play some role in superimposing the tidal effect by inhibiting the elver activity in the coastal waters during full moon period.

1. Introduction

Elvers are herein referred to the juvenile of the freshwater eel, *Anguilla japonica*, from the end of metamorphosis in the leptocephalus which are drifted toward coastal waters and concentrated on estuary and move upstream (BERTIN, 1956; TESCH, 1977). There are four kinds of anguillid elvers in Taiwan (TZENG, 1982a, 1983; TZENG and TABETA, 1983). Among them, that of *Anguilla japonica* is the predominate and commercially important aquaculture fish. Since the eel culture industry has been developed in Taiwan since 1965, the supply of elvers have been insufficient to meet the need for eel farming. Increasing the elver catch has become an important fisheries policy in Taiwan.

Because elvers are nocturnal and always carried along by tidal current and they take advantage of the flood tide to get further upstream (DEELDER, 1952, 1958, 1960; CREUTZBERG, 1961), fishing are always carried out at night during their upstream migration. In foreign countries, most of the elvers are harvested from inner river. Due to the increasing demand of the elvers for eel farming, the fishing grounds in Taiwan extended from inner river to coastal waters. It has been reported that recruitment of elvers into freshwater is in two distinct phases characterized by behavioural differences: an initial invasion from the sea, and an upstream

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migration (JELLYMAN, 1977). After initial invasion into freshwater from the sea, upstream migration of elvers is delayed in estuarine or tidal area where they undergo certain physical and behavioural transitions (DEELDER, 1958; JELLYMAN, 1979; TZENG, 1984). Understanding the biological characteristics and upstream behaviours are essential in predicting the timing of fishing success. As such, there have been researches regarding the cyclic fluctuation of elver catch in relation to tidal cycle (MENZIES, 1936; LOWE, 1951; MATSUI, 1952; DEELDER, 1952; MEYER and KÜHL, 1953; JELLYMAN, 1979) and to moonphase (DEELDER, 1952; HIGASHI and SAKURAI, 1975; JELLYMAN, 1979) done elsewhere. However, little has been done along these lines in Taiwan (TZENG, 1982b).

The purpose of this paper is to elucidate the migration period and upstream behaviour of the elvers in order to predict the timing for fishing success. The daily catch data of elvers from Shuang River and estuarine waters as well as the neighboring rivers were collected and their relation to environmental factors, especially water temperature, tidal cycle and moonphases were analysed. Furthermore, biological characteristics of the elvers during upstream migration were also investigated.

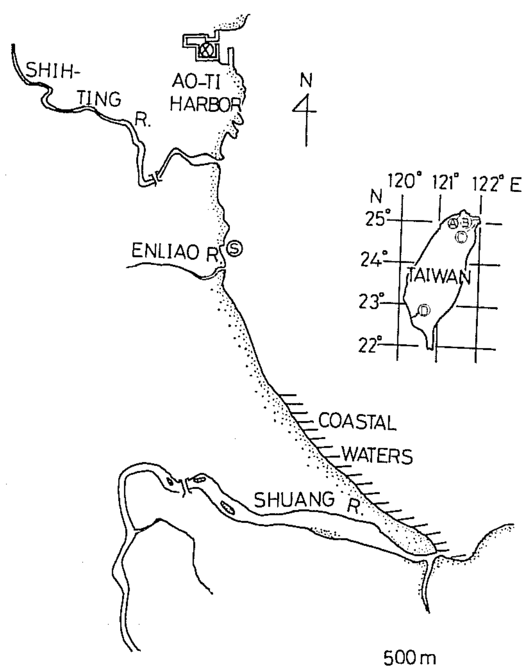

Fig. 1. Map showing the rivers and the coastal waters from which elvers were collected. A: Gong-Shy-Tyan River, B: Shih-Ting River, C: Shuang River, D: Tungkang River. And the stations where surface seawater temperature (circled S) and tidal level (circled X) were measured.

2. Materials and methods

(1) Measurement of specimen

Elvers were sampled from Shih-Ting River, Gong-Shy-Tyan River, Shuang River and the coastal waters off Shuang River (Fig. 1) during November–March of 1980–1984. First, the elvers were fixed in 10 % formalin solution as soon as they were caught to avoid stage pigmentation advancing due to stocking. Then, the species of the elvers were identified, morphometric characters and pigmentation stages were recorded. Methodology of species identification and morphometric measurements were presented in the previous studies (TZENG, 1982a, 1983; TZENG and TABETA, 1983). Determination of the developmental stages of the elvers was following the methods described by STRUBBERG (1913) and BERTIN (1956).

(2) Acquisition and processing of commercial catch data

Fishing gears for harvesting elvers varied with fishing site, i.e. using lamp and dip net in inner river, set net at river mouth and hand trawling net in coastal waters. Fishermen were asked to fill in questionnaires which include the items of fishing date, fishing time, fishing site, fishing method, elver species and catch. The fishermen classified these elvers into white- and black-types according to the pigmentation on the tail. The white-type which belongs to the elvers of *A. japonica* is sold for eel culture, whereas the black-type which includes the elvers of *A. marmorata*, *A. celebesensis* and *A. bicolor pacifica* has not been cultured in Taiwan. Only the catch data of the white-type were used in this study.

The questionnaires were distributed to the fishermen who caught elvers in the Shih-Ting River, Shuang River and the coastal waters off Shuang River (Fig. 1) during the fishing season of 1980-1984 (November-March). Only five fishermen had been investigated in the first two years. However in the third and fourth years, the number of fishermen involved increased considerably to 70 covering 80 % of all the fishermen in those areas. As a consequence, detailed analysis were focused on the catch data of the latter two years. Because fishing methods varied with fishing sites, catch per unit effort (CPUE) in the coastal waters and inner rivers were calculated separately and the fluctuation of CPUE in relation to the environmental factors, i.e. seawater temperature and tidal condition as well as moon phase were also analyzed.

The environmental data used in this study were adopted from the Monthly Hydrometeorologic Reports which were investigated by the power resources survey team of the Taiwan Power Company at Enliao coast for sea water temperature and at Aoti harbour for tidal level, which were not far from the fishing grounds of elvers (Fig. 1). Water temperature was measured four times a day during the first two years (1980-1982). The temperature read at 17:00, which was close to the time of fishing operation was used in the first two years. In the following two years, water temperature was measured by automatic instrument and hourly temperature was read. Daily maximal, minimal and average temperatures were used together in this period to see short-term variation in a day.

(3) **Field investigation of short-term fluctuation in elver catch**

To understand the upstream timing in relation to tidal influx, elvers were caught continually at night by dip net at river mouth of Gong-Shy-Tyan River during January 28, 29 and February 13, 15, 1984. Meanwhile, water temperature and salinity were measured by Oceanographic Salinity and Temperature measuring bridge (Model MC 5/2). Temperature and salinity on the bottom of the fishing site were read every 10 minutes. Maximal and minimal water levels were also read in every 10 minutes by using graduated pole. According to the changes of water level in 10 minutes interval, instantaneous influx rate of sea water were estimated as follows:

$$\Delta h = \frac{h_i - h_{(i-1)}}{t_i - t_{(i-1)}}$$

where Δh is instantaneous influx rate of sea water in t-time, and h_i and $h_{(i-1)}$ are tidal levels in time t_i and $t_{(i-1)}$. Δh was used as an index of the magnitude of tidal influx.

3. Results

(1) Biological characteristics of elvers

(a) Length frequency distribution

The samples of elvers collected from Shih-Ting and Shuang Rivers and the coastal waters off Shuang River during the periods of 1980-1981 and 1982-1983 were comparatively complete in time series. So, the seasonal variations of the body length of elvers were discussed on the basis

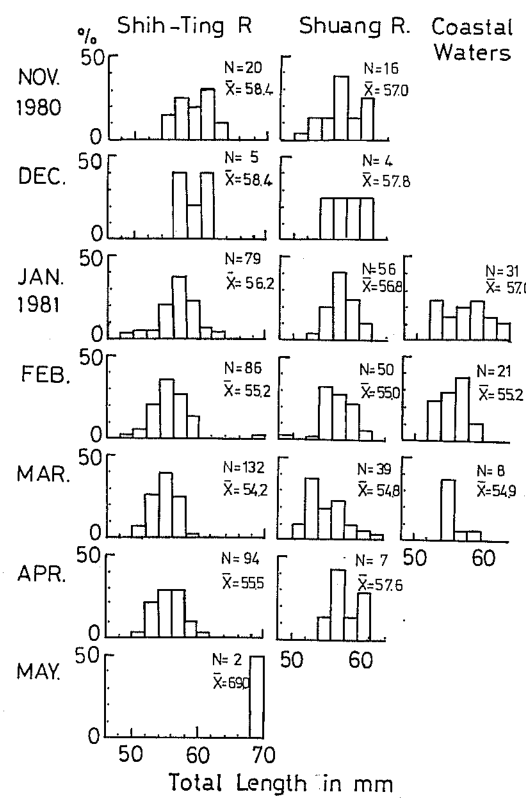

Fig. 2. Monthly length-frequency distribution of anguillid eel (*A. japonica*) elvers caught from Shih-Ting River, Shuang River and its coastal waters in 1980-1981. N: sample size, $\overline{X}$: mean total length in mm.

of these samples.

Seasonal decline in body length was found in elvers both from river and coastal waters. For the elvers collected from Shih-Ting River, mean total length was 58.4 mm in November and December 1980; it decreased gradually and reduced to 54.2 mm in March 1981. After the end of fishing season in April, mean length significantly increased. Similar tendency in the seasonal change of mean total length was also found in the elvers collected from Shuang River and its coastal waters (Fig. 2). Change in mean total length for the elvers collected from Shuang River and its coastal waters also showed similar phenomenon in the other fishing period, 1982–1983. Mean total lengths were 56.9 mm for the elvers collected from coastal waters and 57.7 mm for those from river in December, 1982. They decreased to 55.9 mm and 55.8 mm respectively in January, then increased in February and March 1983 (Fig. 3).

From the result mentioned above, it indicated that elvers which recruited into the estuary during early fishing season were larger than those in the mid fishing season. They got bigger due to growth at the end of the fishing season.

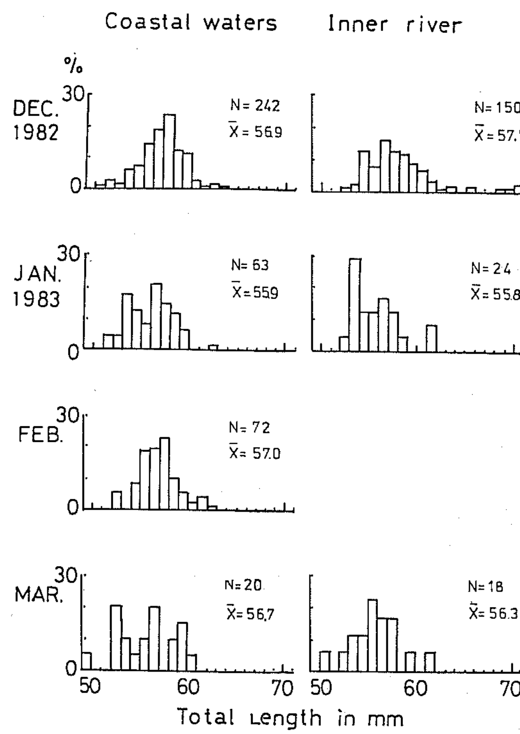

Fig. 3. Monthly length-frequency distribution of anguillid eel (*A. japonica*) elvers caught from Shuang River and its coastal waters in 1982–1983. N: sample size, $\overline{X}$: mean total length in mm.

Table 1. Monthly changes in composition of pigmentation stages for the anguillid eel (*A. japonica*) elvers caught from Shuang River, river mouth and its coastal waters during the fishing seasons of 1981–1982, 1982–1983 and 1984.

Locality	Month	Sample Times	Sample Size	Stage Composition (%)							
				VA	VB	VIA_1	VIA_2	VIA_3	VIA_4	VIB	Yellow eel
Coastal Waters	Dec. 1981	2	668	98.4	1.6						
	Jan. 1982	2	87	81.6	18.4						
	Dec. 1982	4	244	94.7	5.3						
	Jan. 1983	3	64	90.6	9.4						
	Feb. 1983	1	72	86.1	11.1	2.8					
	Mar. 1983	1	20	20.0	25.0	55.0					
	Jan. 1984	1	30	90.0	10.0						
	Subtotal	14	1185	93.7	5.2	1.1					
River Mouth	Dec. 1982	3	142	92.3	7.7						
	Jan. 1984	2	181	75.7	16.6	7.2	0.6				
	Feb. 1984	2	347	80.7	14.7	4.3	0.3				
	Subtotal	7	670	81.8	13.7	4.2	0.3				
Inner River	Dec. 1981	2	128	8.6	51.6	21.8	10.1	7.0	0.8		
	Jan. 1982	3	205	6.3	29.2	40.9	22.5	0.9			
	Dec. 1982	3	184	33.7	32.6	16.3	4.3	4.9	4.3	2.2	1.6
	Jan. 1983	1	24	25.0	50.0	25.0					
	Mar. 1983	1	19	5.3	21.1	73.7					
	Jan. 1984	1	23	73.9	26.1						
	Subtotal	11	583	18.9	35.7	27.7	11.5	3.4	1.5	0.7	0.5

Except those collected in December 1982, the mean total length and the mode of length frequency distribution for the elvers collected from coastal waters in the same month were larger than those from rivers (Figs. 2 & 3). The reverse was true for those collected in December 1982. This may be due to the situation that the samples were mixed with old elvers which had grown up in the river. In generally, the body length of elvers reduced during their upstream migration. However, the differences were sometimes too small to be detected.

(b) Pigmentation stage

A high percentage of elvers collected from coastal waters and rivers during early fishing season was at an early stage of the pigmentation stage composition. As fishing season progressed, the percentage of early stages decreased slightly and the percentage of advanced stage relatively increased. It can be seen from Table 1 that the percentage of elvers at the early VA stage occupied 98.4 % for the elvers collected from coastal waters in December 1981. VA then decreased to 81.6 % and elvers at VB, an advanced pigmentation stage, increased relatively in January 1982. Similar tendency was also found in the fishing period of 1982–1983; VA occupied 94.7 % of the elver sample in December 1982, then decreased to 90.6 % in the following month (January 1983) and decreased continuously to 86.1 % in February and to 20.0 % in March. These phenomena may be due to the mixed ratio of old recruited elvers increased during the later fishing season. These can be seen from the recaptured data for the elvers released in the coastal waters off Shuang River; the stages of elvers became more advanced for those elvers stayed longer in the coastal waters (Tables 2–5).

Table 2. Daily change in composition of pigmentation stages of the recaptured elvers released on Dec. 17, 1982 at the coastal waters off Shuang River.

Locality	Lapse of Time (day)	Recapture (No.)	Stage Composition %						
			VA	VB	VIA_1	VIA_2	VIA_3	VIA_4	VIB
Coastal Waters	0	204		74.5	24.0	1.5			
	1	86	2.3	62.8	33.7	1.2			
	2	10		50.0	50.0				
	3	3		100.0					
	6	2				50.0	50.0		
	9	2			50.0		50.0		
	14	1				100.0			
	Subtotal	308	0.6	69.5	27.3	1.9	0.6		
River Mouth	0	190		80.0	18.4	1.1	0.5		
	1	1		100.0					
	2	1		100.0					
	Subtotal	192		80.2	18.2	1.0	0.5		
Inner River	2	1			100.0				
	3	8	37.5	37.5	25.0				
	4	1		100.0					
	5	10		30.0	60.0	10.0			
	7	3		66.7		33.3			
	8	1			100.0				
	11	2		50.0	50.0				
	12	9		11.1	11.1	22.2	33.3	22.2	
	13	1				100.0			
	15	5		20.0	60.0	20.0			
	16	5		20.0		80.0			
	17	11			18.2	44.4	5.6		
	Subtotal	57	5.3	22.8	29.8	31.6	7.0	3.5	

Table 3. Daily change in composition of pigmentation stages of the recaptured elvers released on Jan. 12, 1983 at the coastal waters off Shuang River.

Locality	Lapse of Time (day)	Recapture (No.)	Stage Composition %						
			VA	VB	VIA_1	VIA_2	VIA_3	VIA_4	VIB
Coastal Waters	0	110		89.1	10.9				
	1	32		87.5	12.5				
	2	7		71.4	28.6				
	3	68		35.3	60.3	2.9	1.5		
	4	41	2.4	24.4	75.6				
	5	9		11.1	88.9				
	6	1			100.0				
	7	19		10.5	73.7	5.3	10.5		
	8	7		14.3	57.1	14.3	14.3		
	13	2				100.0			
	14	1						100.0	
	Subtotal	297	0.3	56.9	39.1	2.0	1.3	3.4	
River Mouth	0	177	0.6	76.8	22.6				
	Subtotal	177	0.6	76.8	22.6				
Inner River	0	34	2.9	76.5	20.6				
	1	29	6.9	75.9	17.2				
	2	6		50.0	50.0				
	3	18		44.4	55.5				
	4	6		16.7	66.7	16.7			
	5	11			90.9	9.1			
	6	9		22.2	77.7				
	7	2			50.0	50.0			
	11	2			50.0		50.0		
	17	3			33.3	66.6			
	19	5			80.0	20.0			
	20	1				100.0			
	Subtotal	126	2.3	49.2	42.0	5.6	0.8		

Table 4. Daily change in composition of pigmentation stages of the recaptured elvers released on Feb. 12, 1983 at the coastal waters off Shuang River.

Locality	Lapse of Time (day)	Recapture (No.)	Stage Composition %						
			VA	VB	VIA_1	VIA_2	VIA_3	VIA_4	VIB
Coastal Waters	0	443	1.4	52.7	45.9	0.2			
	1	21	4.8	38.1	57.1				
	2	21		28.6	71.4				
	3	54	1.9	27.8	68.5	1.9			
	4	16			93.8				6.3
	5	8			87.5	12.5			
	7	20			80.0	20.0			
	9	1			100.0				
	Subtotal	583	1.4	44.9	52.5	1.2			0.2
Inner River	5	5			100.0				
	6	5			100.0				
	Subtotal	10			100.0				

Table 5. Daily change in composition of pigmentation stages of the recaptured elvers released on Mar. 19, 1983 at the coastal waters off Shuang River.

Locality	Lapse of Time (day)	Racapture (No.)	Stage Composition %						
			VA	VB	VIA_1	VIA_2	VIA_3	VIA_4	VIB
Coastal	0	64		21.9	71.9	6.3			
Waters	1	4		25.0	75.0				
	Subtotal	68		22.1	72.1	5.9			
River	0	51		25.5	74.5				
Mouth	1	6	16.7		66.7	16.7			
	Subtotal	57	1.8	22.8	73.7	1.8			
Inner	3	1			100.0				
River	Subtotal	1			100.0				

The stages of elvers became more advanced after upstream movement. It can be understood by comparing the stage composition of the elvers collected in the coastal waters, river mouth and inner river (Table 1). The percentage of VA in the coastal waters was 93.7 %, but decreased to 81.8 % at river mouth and to 18.9 % in the inner river. The stages of the majority of elvers in the inner river were VB and VIA_1. In addition, seasonal advancement in the stage of elvers was also found in the inner river; percentage of VA decreased from 8.6 % in December 1981, to 6.3 % in January 1982. Similarly, percentage of VA in the following fishing period changed from 33.7 % to 25.0 %, then to 5.3 % from December 1982 to March 1983 (Table 1).

(c) Reduction of body length and the change of pigmentation stage

To clarify the relationship between body length and pigmentation stage of the elvers, the mean length for each pigmentation stage was computed by areas and the fishing period of different years. The curves of length-stage relationship were shown in Fig. 4. It is clear that mean length of elvers in the inner river decreased as pigmentation stage advanced from VA to VIA_3. It showed a sharp growth after stage VIA_3 in each of the fishing periods of different years. Similar tendency was also found in elvers from coastal waters; total length decreased as stages changed from VA to VB. However, this relationship was not clear for the elvers beyond stage VB. This may be due to the fact that elvers in advanced stage generally went into the river and very few of them in advanced stages still stayed in the coastal waters.

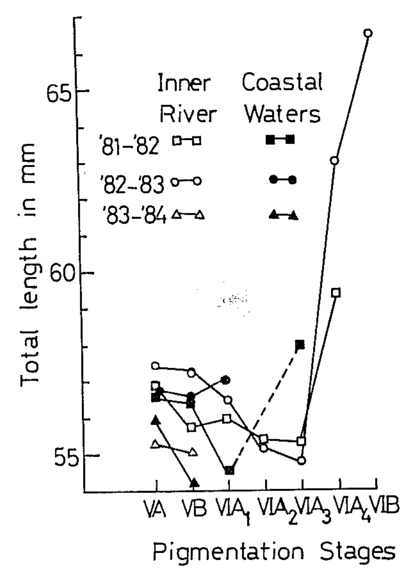

Fig. 4. Relation between length change and pigmentation in the elvers from Shuang River and its coastal waters during 1981-1984. Pigmentation stages follow that of STRUBBERG (1913).

(2) Seasonal arrival of elvers and sea water temperature

The timing of recruitment of elvers in relation to the fluctuation of sea surface temperature was analyzed on the basis of commercial catch data of elvers caught in the coastal waters off Shuang

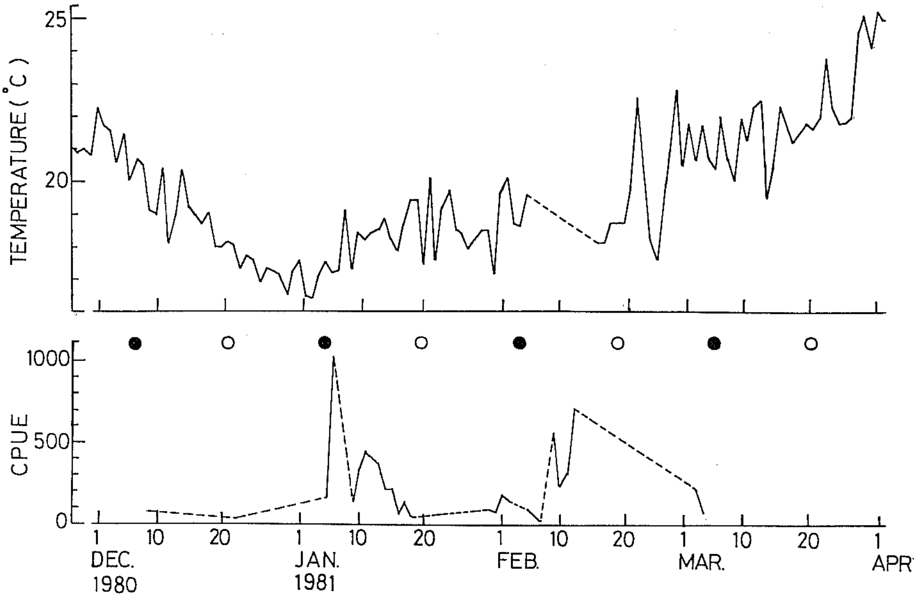

Fig. 5. Relation of surface seawater temperature and lunar phases to daily catch of anguillid eel (*A. japonica*) elvers caught in the coastal waters off Shuang River during December 1980–March 1981. Surface seawater temperature was measured at 5:00 P.M.

River and the sea surface temperature measured in the neighboring Enliao Coast during the winter season, 1980–1984.

As shown in Fig. 5, there were two significant peaks of daily CPUE during the fishing period of 1980–1981; one on January 5 and the other on February 12. The former peak was higher. In general, sea water temperature showed marked day-to-day fluctuation, but seasonal trend was also clear. Temperature dropped from December reaching a lowest value around January, then increased gradually after February. The day of lowest temperature, about 16.4°C, was found on January 2, 1981. It is obvious that these timings of peak catch and lowermost water temperature corresponded well each other. In other words, it is expected to catch more elvers around the period when water temperature drops to the lowermost in the winter season. Besides, the occurrence of peak catch seems to be a cyclic change; it is considered to be related to the moon phase (see below).

Similar trend was also found in the following fishing period, 1981–1982 (Fig. 6). Three significant peaks appeared in the daily change of

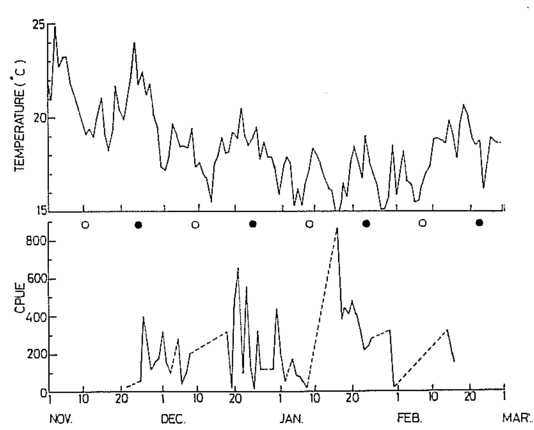

Fig. 6. Relation of surface seawater temperature and lunar phases to daily catch of anguillid eel (*A. japonica*) elvers caught in the coastal waters off Shuang River during November 1981–February 1982. Surface seawater temperature was measured at 5:00 P.M.

CPUE on November 26, December 21, 1981 and January 16, 1982 respectively; the height of peak CPUE increased one after the other. But the daily changes of temperature in the correspond-

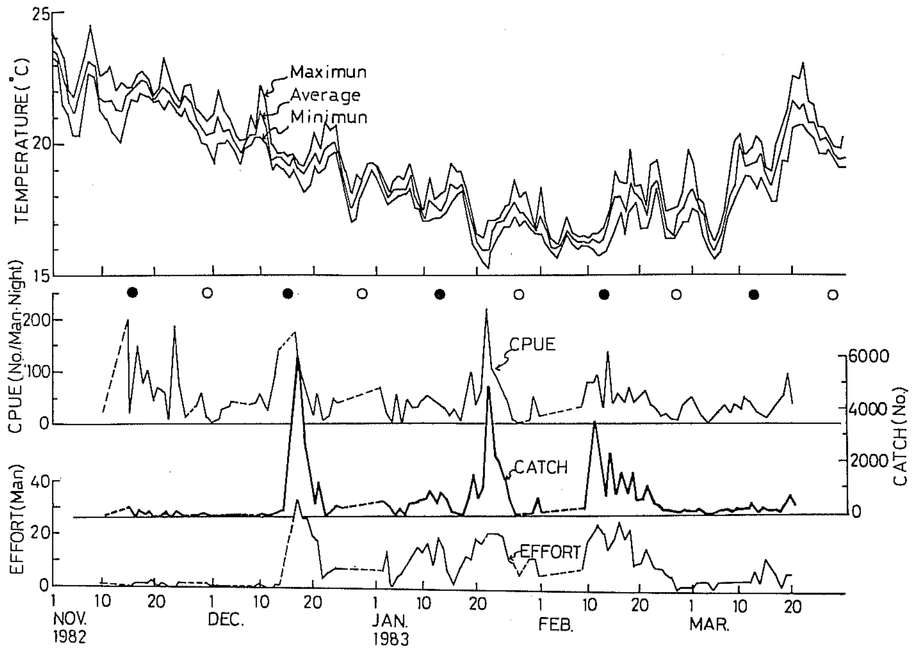

Fig. 7. Relation of surface seawater temperature and lunar phases to daily catch of anguillid eel (*A. japonica*) elvers caught in the coastal waters off Shuang River during November 1982–March 1983. Surface seawater temperature was expressed in maximum, minimum and average.

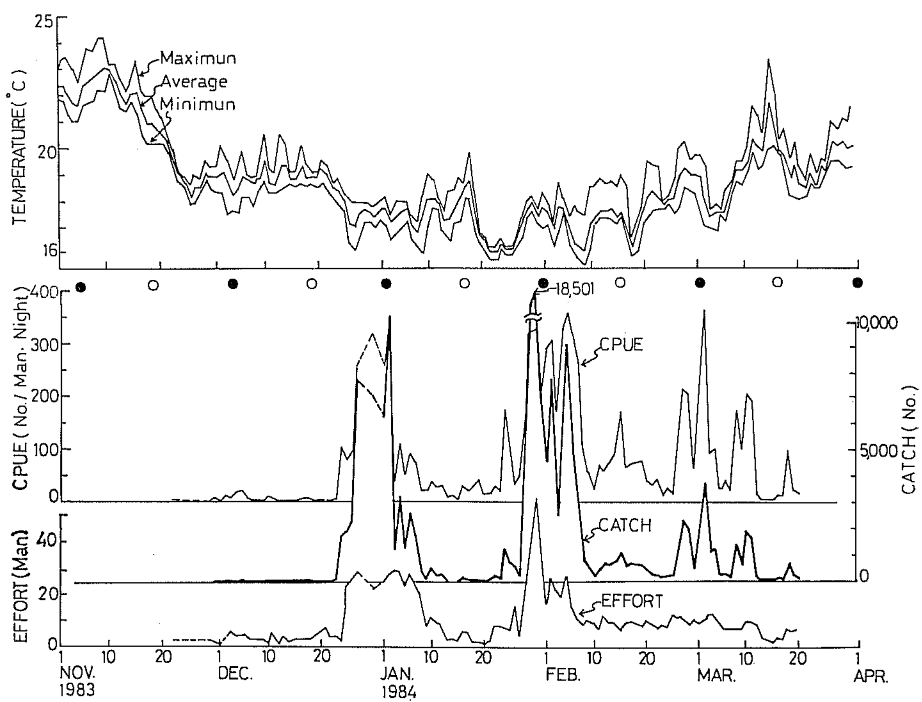

Fig. 8. Relation of surface seawater temperature and lunar phases to daily catch of anguillid eel (*A. japonica*) elvers caught in the coastal waters off Shuang River during November 1983–March 1984. Surface seawater temperature was expressed in maximum, minimum and average.

ing period showed a significant decreasing tendency. The timings of maximal peak catch and lowermost temperature, about 15°C, were occurred in the same day on January 16, 1982. After that day, water temperature showed an increasing tendency and CPUE significantly dropped.

In the third fishing period, 1982–1983 (Fig. 7) the daily changes of water temperature were expressed by maximal, minimal and average values. The range of variation of water temperature in a day was very large. According to the daily changes of minimal temperature, the lowermost temperature was about 15.3°C which was found around January 22, 1982. The day was also corresponding to the maximal peak of CPUE.

In the fourth fishing period from 1983–1984 (Fig. 8) the peak catch was found on three occasions, i.e. December 27–January 2, January 28–February 7 and February 27–March 1, respectively. It is clear that the good fishing condition in each period of peak catch lasted a few days, which was never found in the previous three fishing seasons mentioned above. Especially, in the second occasion, January 28–February 7, the peak catch even lasted for 10 days and their CPUE also maintained in a relatively high level. The second peak catch was found in the period between two lowermost temperature days, i.e. 15.8°C on January 23 and 15.7°C on February 9, respectively. The temperature level on January 23, seemed to be lower than that on Feb. 9 because the temperature maintained in a stable lower level and lasted a few days in all of the daily maximal, minimal and average values in contrast to a sharp minimum on February 9. However, the timing of peak catch seemed to be slightly delayed from the day of lowermost temperature level. The time lag may be due to the effect of moonphase which is considered more important in influencing the fluctuation of elver catch (also see below).

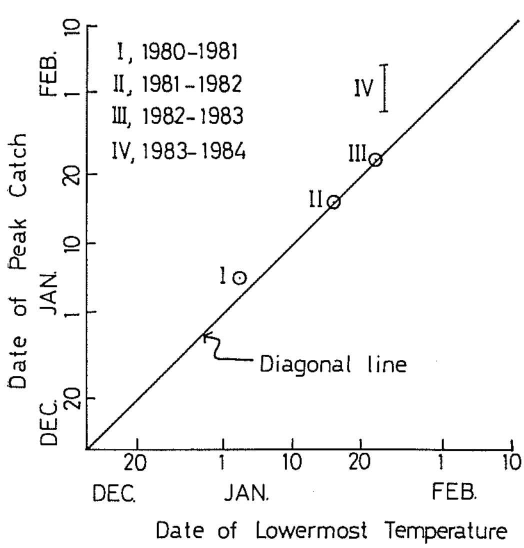

Fig. 9. The relationship between the timing of occurrence of lowermost surface seawater temperature and that of peak catch of elvers in the coastal waters off Shuang River in northeastern Taiwan during the fishing seasons of 1980–1981 to 1983–1984.

Based on the results mentioned above, it is indicated that maximal peak catch of elvers seems to be approximately occurred around the period when water temperature dropped to lowermost level in the winter season. The peak catch of the elvers in the coastal waters seemed correlated with the temperature. The relationship between the date of lowest temperature and the date of peak catch were plotted together for the four fishing seasons (Fig. 9). As shown in the figure, it is indicated that the peak catch often occurred on the date or several days after that when daily seawater temperature reached the lowest in the winter season. The lowermost temperatures were observed to be about 15–16°C. Therefore, it is possible to forecast the timing of peak catch of elvers if the fluctuation of water temperature can be predicted.

(3) **Upstream behaviour**

To understand the upstream behaviour of elvers in relation to influx of seawater, number of elvers were counted and tidal level and salinity were measured in every 10 minutes from low to high tide at the river mouth of Gong-Shy-Tyan River in the northwestern coast of Taiwan during the nights of January 28 & 29, and February 13 & 15, 1984. Cumulative catch (C) gradually increased as tidal level (h) continued to elevate (Figs. 10–13). Cumulative catch reached an asymptote as tidal level began to

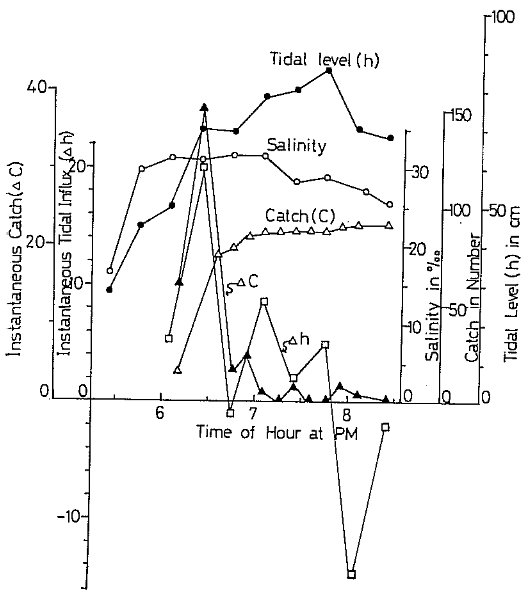

Fig. 10. Time series of salinity (S ‰), tidal level (h), instantaneous tidal influx ($\Delta h = h_{t+10} - h_t$), cumulative catch ($C_t$) and instantaneous catch ($\Delta C = C_{t+10} - C_t$) of elvers in the river mouth of Gong-Shy-Tyan River on January 28, 1984.

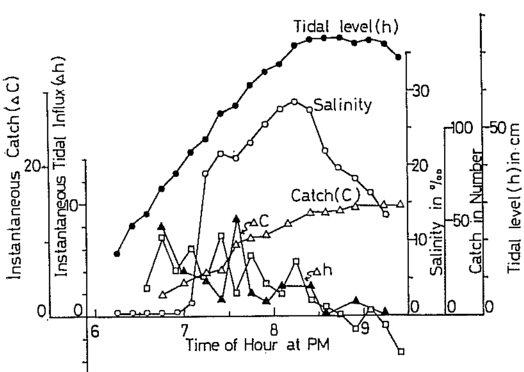

Fig. 11. Time series of salinity (S ‰), tidal level (h), instantaneous tidal influx ($\Delta h = h_{t+10} - h_t$), cumulative catch ($C_t$) and instantaneous catch ($\Delta C = C_{t+10} - C_t$) of elvers in the river mouth of Gong-Shy-Tyan River on January 29, 1984.

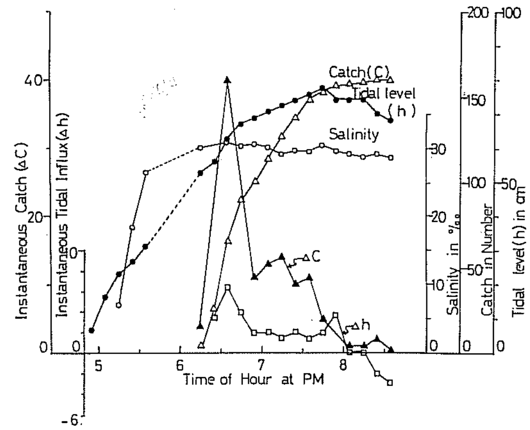

Fig. 12. Time series of salinity (S ‰), tidal level (h), instantaneous tidal influx ($\Delta h = h_{t+10} - h_t$), cumulative catch ($C_t$) and instantaneous catch ($\Delta C = C_{t+10} - C_t$) of elvers in the river mouth of Gong-Shy-Tyan River on February 13, 1984.

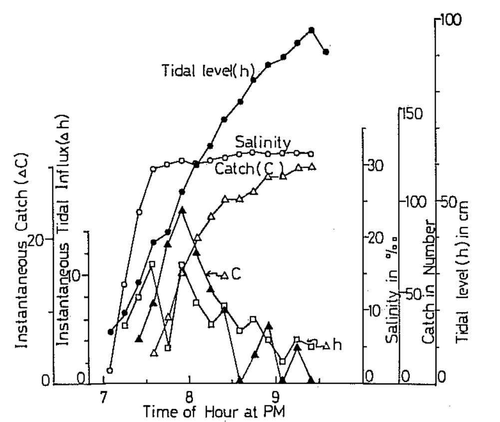

Fig. 13. Time series of salinity (S ‰), tidal level (h), instantaneous tidal influx ($\Delta h = h_{t+10} - h_t$), cumulative catch ($C_t$) and instantaneous catch ($\Delta C = C_{t+10} - C_t$) of elvers in the river mouth of Gong-Shy-Tyan River on February 15, 1984.

drop. Because the elevation of tidal level indicated the influx of sea water, the immigration of elvers seems to be drifted by flood tide. Besides, in order to understand the timing of peak catch of elver during upstream movement, instantaneous catch (ΔC) and instantaneous influx of sea water (Δh) were computed in every 10 minutes and the temporal changes of these parameters were also plotted in Figs. 10–13. It is clear that maximal instantaneous catch appeared during the hour when maximal instantaneous influx of sea water occurred, e.g. on January 28, 1984 both maximal ΔC and maximal Δh appeared at 6:30 P.M., after 6:30 P.M. both ΔC

and Δh dropped together (Fig. 10). On January 29, although both maximal ΔC and Δh was not clearly seen, both ΔC and Δh showed a same tendency in fluctuation (Fig. 11). During February 13 & 15, the changes were also very similar to that on January 28; the timing of appearance of maximal ΔC and maximal Δh was corresponding. On February 13 they took place at 6:35 P.M., and at 7:55 P.M. on February 15 (Figs. 12 & 13).

Changes in salinity were also an index for influx of sea water, salinity increased with the elevation of tidal level. After abrupt increase, salinity quickly reached a plateau state, and stopped to increase even if the tidal level continued to rise. Except the observation on January 29, both the beginning hour when elvers were more available and the hour of maximal instantaneous catch were all located in the hours after salinity had reached the plateau state (Figs. 10–13). The salinity at the plateau state was about 30–31‰ which was considered to be that of the water mass in the coasts where the elvers burried themselves in the bottom before upstream movement. It is clear that elvers may be carried upstream by the movement of the water mass during flood tide. The larger the volume of sea water inflows, the more the elvers are available. As mentioned above, cumulative

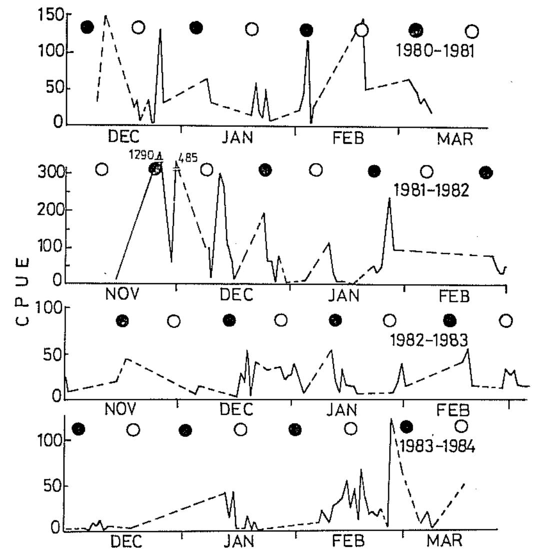

Fig. 14. Semilunar cyclic changes of the catch per unit effort of anguillid eel elvers (CPUE; elvers/man/night) caught in the Shuang River during the fishing season of 1980–1984. Solid circles, new moon; open circles, full moon.

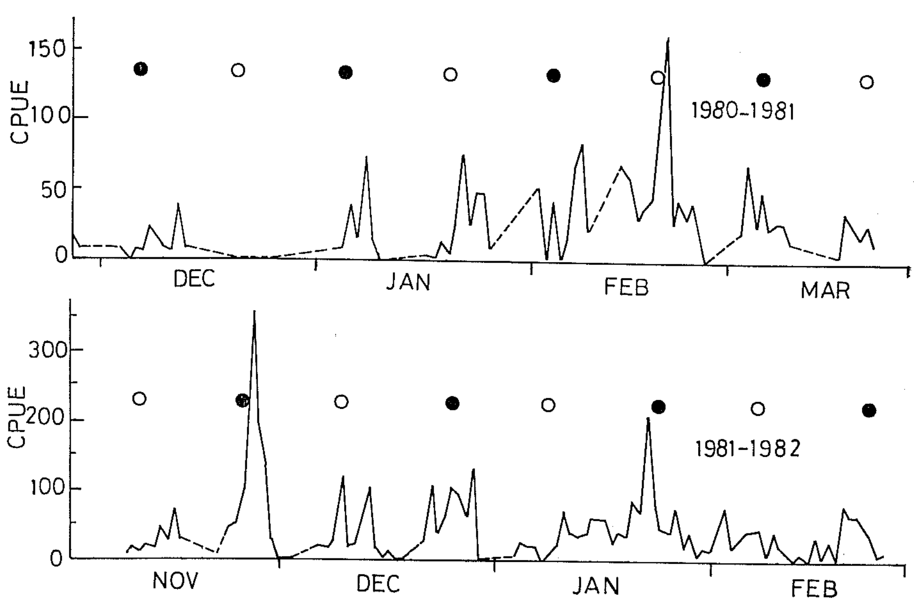

Fig. 15. Semilunar cyclic changes of the catch per unit effort of anguillid eel elvers (CPUE; elvers/man/night) caught in the Shih-Ting River during the fishing season of 1980–1982. Solid circles, new moon; open circles, full moon.

catch in January 29 was less abundant than the other three observations and the instantaneous peak catch was also not obvious. The reason may be due to the reduction in influx of sea water because salinity was lower than that in the other three observations.

Based on the above mentioned results, it is clear that upstream movement of elvers became most active during the hour when salinity reached a plateau state and when instantaneous influx of sea water reached the maximal speed.

(4) **Biological rhythms of the elvers and the zeitgeber**

(a) Semilunar rhythms of elvers-activity in the river

The daily CPUE were plotted with moon phases for the elvers caught in the Shuang River during the fishing periods of 1980–1984. All of the peaks of CPUE occurred in a semilunar interval, i.e. two peaks appeared in each month. The appearances of the CPUE peaks were almost found in the 2nd–3rd day after new and full mooons. Few or no elvers were caught and even fishing operations were ceased during the days of wane and wax moons (Fig. 14). These phenomena were also found in the Shih-Ting River located north of Shuang River during the fishing periods in 1980–1981 and 1981–1982 (Fig. 15) and in the Tungkang River, in southwestern Taiwan, during the fishing period in 1981–1982 (Fig. 16). Similarly, it was also reported in the rivers elsewhere (JELLYMAN, 1979). It is assumed that the elvers have a circasyzygic activity rhythm in the rivers.

As mentioned above, upstream migration of the elvers was depended on the influx of sea

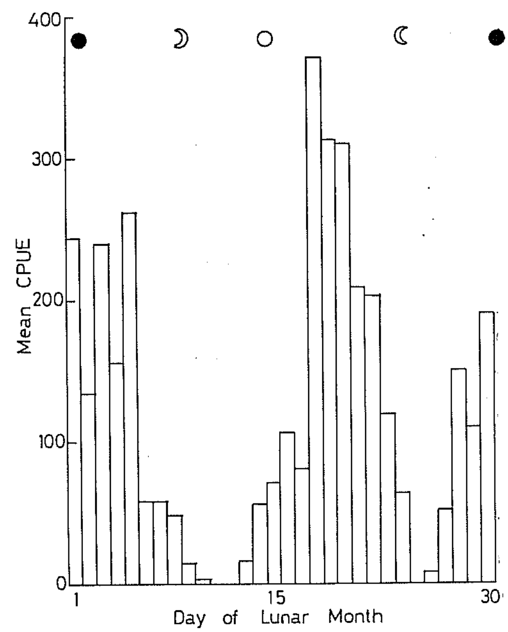

Fig. 16. Relationship between mean CPUE (elvers/man/night) and moon phases for the anguillid eel (*A. japonica*) elvers caught in the Tungkang River during the fishing season of 1981–1982.

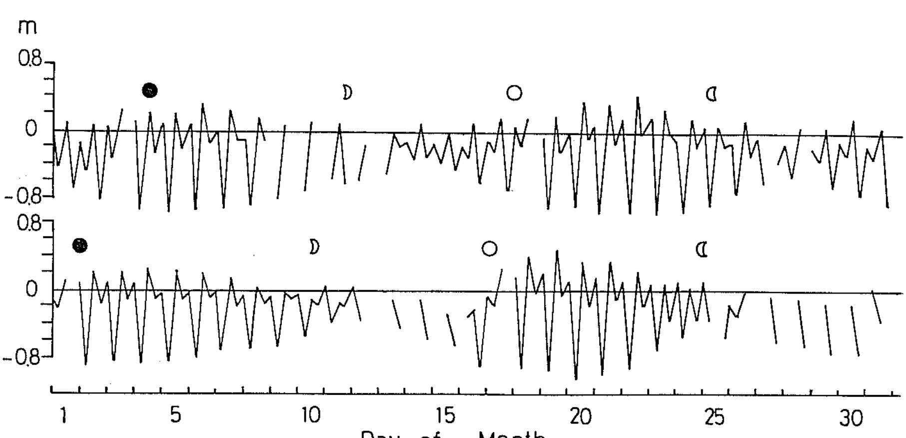

Fig. 17. Phases of the moon and the tidal curves at Aoti harbour in December 1983 (upper diagram) and January 1984 (lower diagram). Two high water and two low water were plotted in a day.

water which was expressed by elevation of tidal level as shown in previous description (Figs. 10–13). The change in tidal level at Aoti harbour, located near the fishing ground of the elvers, was shown in Fig. 17. The tidal patterns for December 1983 and January 1984 were very similar. They belonged to a semidiurnal tide and diurnal inequality. High high water level occurred at night time. Tidal range was about 1.5 meter during spring tide and only 0.05 meter during neap tide. Age of tide was about 2–3 days, i.e. the time lag of spring tide behind new and full moons. Therefore, it is expected that the influx of sea water in the fishing ground of the Shuang River changes along with the tidal cycles, and consequently influences the upstream movement of the elvers.

The average of daily night high water at Aoti harbour and the percentage of daily elver catch in the Shuang River were computed through out the fishing seasons of 1982–1983 and 1983–1984. The computed values were plotted over the period of a lunar month (Figs. 18 & 19, upper and middle panels). The fluctuation of the percentage of elver catch corresponded with the tidal level. In general, tidal level was higher in the spring tide during full moon than that during new moon. The changes of the daily elver catch curve were similar; the percentage catch was higher during full moon than that during new moon. The maximal percentage catch occurred about 2–3 days after full moon which corresponded very well with the age of tide. It is obvious that the upstream movement activity of elvers in the river was highly related to the tidal condition.

(b) Lunar rhythm of elvers-activity in coastal waters

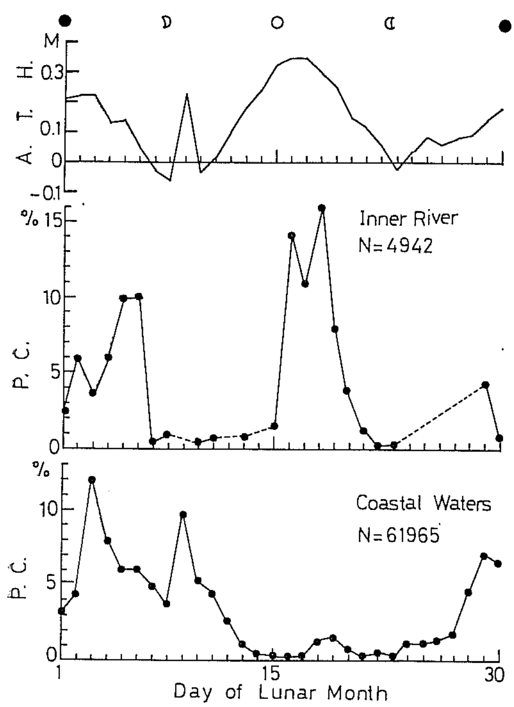

Fig. 18. Percentage catch (P.C.) of elvers in the Shuang River and its coastal waters (data from Figs. 14 and 7) and average tidal height (A.T.H.) of night high water expressed over the period of a lunar month (new moon occurs in day 1st) during the fishing season from November 1, 1982 to March 31, 1983. N: sample size in number.

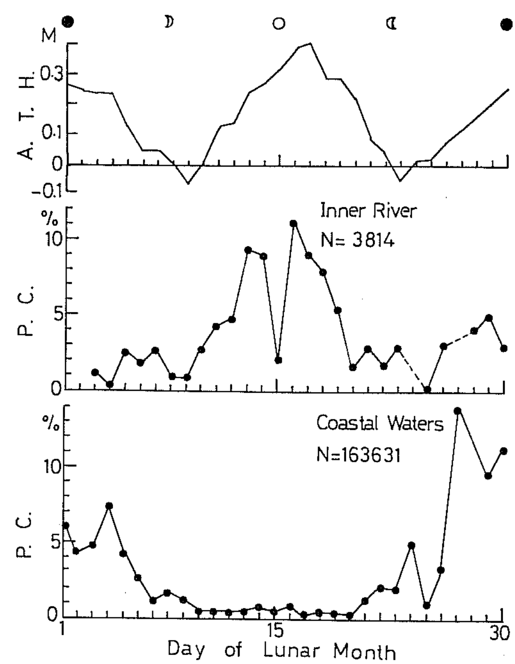

Fig. 19. Percentage catch (P.C.) of elvers in the Shuang River and its coastal waters (data from Figs. 14 and 8) and average tidal height (A.T.H.) of night high water expressed over the period of a lunar month (new moon occurs in day 1st) during the fishing season from November 1, 1983 to March 31, 1984. N: sample size in number.

The daily CPUE of the elvers caught from the coastal waters and the moon phases were shown over four fishing periods during 1980-1984 (Figs. 5-8). The periodicity of elver activity in the coastal waters was clearly different from that in the river. All of the peak catch and active fishing operation occurred around the period of new moon. Few elvers were caught and fishing operation became inactive during the period of full moon. In other words, the peak catch of elvers occurred only once per month in the coastal waters. The percentage of daily elver catch were computed and arranged in a lunar day for the fishing periods in 1982-1983 and 1983-1984. Its relation to the tidal cycle was shown in the lower panels of Figs. 18 & 19. It is obvious that the percentage catch increased as the tidal level began to rise from last quarter of the moon phases and reached its climax during new moon and began to decrease from the first quarter of the moon phases when the tidal level fell gradually. However, the percentage catch didn't rise again until the 3rd quarter of the moon phases even tidal level rised to the maximal value during full moon. The peak which appeared in the river during the period around full moon was vanished in coastal waters. Therefore, it is assumed that moonlight superimposed on the tidal effect to influence the activity of elvers in the coastal waters. The activity of elver was inhibited during the period of full moon.

4. Discussion

Seasonal declines in size of elvers are noted in this study and elsewhere (Japan: MATSUI, 1952; Europe: STRUBBERG, 1923; WIMPENNY, 1929; MENZIES, 1936; and New Zealand: JELLYMAN, 1979). Most of these authors believed STRUBBERG's (1923) conclusion that rapidly growing larvae moved faster than the smaller ones, so that the elvers first arriving might be the largest. But, JELLYMAN (1977) considered that leptocephali of the European eel migrated by passive current transport (e.g. DEELDER, 1970), and thus the time when the elvers arrived to the coast depended on the vectors of surface currents (HARDEN JONES, 1968). Accordingly, the swimming ability of leptocephali is probably of little consequence in explaining the seasonal decline in size. However, seasonal decline in size may be due to the reduction of body size with increasing pigmentation. For instance, percentage of stage VA occupied 94.7% of the sample in December 1982, but decreased to 90.6% in January 1983 for the elvers collected in the coastal waters, i.e. pigmentation stages increased with time (Table 1). On the contrary, average size decreased from 56.9 mm in December 1982 to 55.9 mm in January 1983 (Fig. 3). This negative correlation is also shown in Fig. 4. Besides, the pigmentation stages will become more advance when elver stays longer in the coastal waters (Tables 2-5). Accordingly, it is suggested that the seasonal decline in size may be caused by the mixed ratio of old recruited elvers which have advanced pigmentation stage increases in the later fishing season.

The distribution of *A. japonica* was reviewed by TESCH (1977); it was suggested that the spawning grounds lied to the south of Japan between 20° and 28°N and between the islands of Lutschu and Bonin, between 125° and 140°E. The larvae are probably carried by the North Equatorial current into the Kuroshio current, a strongly flowing stream which is directed northwards by continental shelf. Thus the distribution of the Japanese eel ranges from 18°N in the south to 42°N in the north (TESCH, 1977; Fig. 48). The surveyed area in the present study lies at the southern limit of the distribution of the eel. The continental shelf represents a clear dividing line between larvae and elvers which have undergone metamorphosis (SCHMIDT, 1909). Therefore, the distribution center of the elvers, which is possibly the original supply area in the present study area, is considered to be located in the waters of China Coastal current in the north of Taiwan. This current will be strengthened by the northeasterly wind in winter time and it moves southward from northern China along the coast of China (CHU, 1963). So, it is expected to catch more elvers when this current comes down to the coast of Taiwan. And because the current originates from north, seawater temperature in the coastal waters will decrease when the current comes down. Therefore, it can be explained why the peak CPUE of the elver always takes place when the surface seawater temperature becomes lowermost in the winter time (Figs. 5–8). However, the relationship between elver catch and the temperature was opposite in the northern limit of the distribution of the elvers, e.g. in Japan, the higher the water temperature, the more the elver was available (DOI, 1972).

The monthly lunar cycle is known to act as a biological clock for many of the recurring cycle found in nature (MCDOWALL, 1969). A biological rhythm may be defined as showing lunar or semilunar rhythm if the maxima and minima of the rhythmical process appear once or twice respectively in every lunar month. Many cases have been found in field studies, both by occasional observations and by statistical analysis of repeated observations (FOX, 1923; KORRINGA, 1947; CASPERS, 1951). A long-term examination over 4 years of elver catches in Taiwan reveales that the activity of elvers in the coastal waters is in a lunar rhythm, but in a semilunar rhythm in the rivers. Generally, elvers take advantage of tidal movements to go further upstream in the rivers (CREUTZBERG, 1961); the increased amplitude of spring tide initiates the migration of elvers and upstream migration reaching a peak generally 2–3 days after new and full moons which coincides with the age of tide (Figs. 18–19). Therefore, semilunar rhythm of the elvers in the rivers is considered to be synchronous with tidal cycle. Many researchers including MENZIES (1936), LOWE (1951), MATSUI (1952) and JELLYMAN (1979) also found that the tidal cycle was significant to migration periodicity. Sometimes, the relationship might not be clear when tidal amplitude was small (DEELDER, 1952; MEYER and KÜHL, 1953; JELLYMAN, 1977).

However, tidal cycle alone may not be the sole factor determing the apparent lunar periodicity of elver activity in the coastal waters. The peak catch takes place only once, which appears in new moon and is absent in full moon (Figs. 5–8, 18–19). It is clear that except for tidal cycle, moonlight seems to play an important role in influencing the periodic migration of elvers in the coastal waters. According to the observation made on the coast of Rügen: "In pound net systems made up of several chambers the seaward facing chambers in deeper waters caught more eels during the full moon than did chambers in shallow waters; when the moon was not so bright, the opposite was often found to be the case" (NOLTE, 1938). Therefore, it can be considered that moonlight is a zeitgeber to inhibit the elver activity in the coastal waters. Consequently, the catch of elvers in the coastal waters become smaller during full moon.

Acknowledgements

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台湾北部の河口域におけるシラスウナギの来遊するタイミング・活動周期ならびに同調因子に関する研究

曽　萬　年*

要旨: 河口域におけるシラスウナギ資源の有効利用や漁況予測をするため，1980年から1984年まで台湾北部の河川と沿岸から採集されたシラスウナギ標本や収集された漁獲統計をもとに，その生物的特徴や漁獲量変動の周期性について解析が行われ，また来遊するタイミング・溯河生態および生物リズムに関連する環境因子がモニターされた。得られた結果は次の通りである。(1) 来遊群の平均体長は季節的に小さくなるが，これは発育段階が進むことによって引き起こされることと思われる。(2) 沿岸に来遊するシラスウナギのピーク漁獲量の現われる日は水温と関係があり，いずれも最低水温の出現時と一致している。最低水温は 15°～16°C の間である。(3) 夜間の上げ潮時の最大瞬間漁獲量は塩分上昇後の横ばい期或は海水の瞬間流入速度の極大期に現われる。この事実から見ると，この時期にシラスウナギの溯河活動が一番活発であると思われる。(4) 沿岸におけるシラスウナギの漁獲量のピークは月一回で，その生物リズムはサーカルナ・リズム(月周期リズム)と思われる。いずれも新月のあたりに現われる。一方，河川内におけるシラスウナギの漁獲量には月２回のピークがあり，その生物リズムはサーカシジジック・リズム（半月周期リズム）と思われ，それぞれ新月と満月に現われる。河川内におけるシラスウナギの生物リズムは大潮のサイクルに同調すると思われる。しかし，沿岸におけるシラスウナギの生物リズムは月光にも影響されるようで，満月時には活動力が押さえられると思われる。

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