Vital population statistics based on length frequency analysis of the exploited Japanese eel (*Anguilla japonica*) stock in the Kao-Ping River, southern Taiwan

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Summary

Vital statistics such as growth, mortality, and maturity parameters are crucial in understanding the population dynamics of a species. A total of 7 074 Japanese eels (*Anguilla japonica*) in the lower reach of the Kao-Ping River, southern Taiwan, were collected with eel tubes in 1998 ~ 2004 and shrimp nets in 2004 ~ 2007. Data from 2004 were excluded due to mixed gear information and escapement of cultured eels; in subsequent years escaped cultured eels were identified and excluded from analyses. The estimated asymptotic length in the von Bertalanffy growth function (84.5–110 cm) was smaller, while the Brody growth parameter (0.30–0.44 year⁻¹) was higher using electronic length frequency analysis (ELE-FAN) than when using Shepherd's length composition analysis (SLCA). The total instantaneous mortality rate (*Z*) was around 1 for periods 1998–2003 and 2 year⁻¹ for 2005–2007 using length-converted catch curves. The 95% confidence intervals of *Z* did not overlap for two of the periods, suggesting that the mortality rates were significantly higher during 2005–2007, possibly due to the introduction of shrimp nets. The maturity function differed significantly between sexes, indicating that females become silver eels at a larger size. The Japanese eels in the lower reach of the Kao-Ping River were likely heavily exploited, thus management and conservation actions are strongly recommended.

Introduction

The Japanese eel, *Anguilla japonica*, is a catadromous fish widely distributed in Taiwan, China, Japan, and Korea (Tesch, 2003). The eels spawn in the tropical Pacific Ocean west of the Mariana Islands (Tsukamoto, 1992, 2006). The leaf-like larva, leptocephali, are transported passively via the North Equatorial and Kuroshio currents and metamorphose to the glass eel stage over the continental shelf and further develop into pigmented elvers in the estuary (Cheng and Tzeng, 1996). The elvers then either migrate upstream to freshwater habitats or remain in brackish estuaries as yellow eels. After 4–10 years the yellow eels begin sexual maturation and become silver eels with enlarged eyes and darkened body color (Han et al., 2001, 2003; Tzeng et al., 2002). These silver eels then migrate to the spawning grounds in the ocean to spawn and die (Tesch, 2003).

Vital population statistics such as growth parameters, total, natural, and fishing mortality and length at maturity are crucial in understanding population dynamics and making fisheries assessments (Quinn and Deriso, 1999; Jennings et al., 2001). Japanese eel populations, along with those of other temperate eel species, have been declining to historically low

levels (Haro et al., 2000; Feunteun, 2002; Tatsukawa, 2003; Tseng et al., 2003; Dekker, 2004; Han and Tzeng, 2006). However, the availability of these statistics for Japanese eel stocks is limited relative to species such as the European eel *A. anguilla* (De Leo and Gatto, 1995; Svedäng, 1999; Dekker, 2004), American eel *A. rostrata* (Robitaille et al., 2003; Weeder and Uphoff, 2003), and Australian short-finned *A. reinhardtii* and long-finned *A. dieffenbachii* eels, and *A. australis* (Francis and Jellyman, 1999; Hoyle and Jellyman, 2002; Doole, 2005). Without appropriate vital population statistics, efficient and active management of *A. japonica* stocks may be difficult.

Traditional methods of studying the dynamics of exploited fish stocks were mostly based on age-structured data. However, use of computers and theoretical advantages of analytical methods based on length-frequency data led to their development during the 1980s (Jones, 1984; Gulland, 1987; Pauly, 1987; Pauly and Morgan, 1987) and widespread use in recent years (e.g. Özbilgin et al., 2004; García and Duarte, 2006; Velasco et al., 2007). Length-frequency data is easier to obtain than age-structured data, and correctly ageing fishes in tropical waters may be difficult due to reduced seasonal growth contrast (Campana, 2001) or problems in interpreting otolith growth increments (Morales-Nin and Panfili, 2005). Thus, length-frequency methods were used to overcome such difficulties.

The lower reach of the Kao-Ping River in Taiwan (Fig. 1) is one of the most important fishing grounds for elvers, juveniles, and adult Japanese eels. Fishermen use bamboo eel tubes to harvest the juvenile and adult eels (Chang and Tzeng, 1990; Tzeng and Chang, 2001). In Taiwan, although great numbers are reared in aquaculture ponds, eels harvested in the wild attain prices 3–4 times higher than for cultured eels (Chang and Tzeng, 1990). Considerable quantities of both juveniles and adults are also caught as by-catch in shrimp nets in the lower reach, possibly because the eels follow the shrimp into the nets. Moreover, shrimp nets are widely used by eel fishermen because they are highly efficient in catching juvenile and adult eels (Lin and Tzeng, 2008), which further increases fishing pressure on the local eel stocks. However, information on growth, mortality, and maturity is limited, especially for yellow and silver eels. Thus, the path to meaningful management and restoration of *A. japonica* in Taiwan remains uncertain.

The study objective was to estimate the vital population statistics and evaluate the state of exploitation of *A. japonica* stock in the lower reach of the Kao-Ping River based on the length frequency data from the eel catch, 1998–2007.

Fig. 1. Japanese eel *Anguilla japonica* sampling site, lower reaches of Kao-Ping River, southern Taiwan

Materials and methods

Study area

The Kao-Ping River is the second largest river in Taiwan with a length of 171 km and a drainage area of 3 256 km². Mean annual rainfall is 3 046 mm and characterized by a dry season in winter and spring (October ~ May) and a rainy season in summer and autumn (June ~ Sept.). The rainfall is mainly contributed by the monsoon in early summer and by irregular typhoons during late summer and autumn. As a result, the river water level fluctuates in the mid- and upper reaches but is relatively stable in the lower reach. In the region where fishermen harvest the eels and sand shrimp, salinity is 10 ~ 30 ppt and mean ($\pm$ SD) bottom temperature is $25.9 \pm 2.7^\circ\text{C}$ (Chen, 2005).

Sample collection and measurement

Monthly eel catch in numbers was recorded from one cooperative fisherman using eel tubes during 1998–2004 and from another two fishermen using shrimp traps in 2004–2007 (Table 1). Gear information in 2004 was mixed and unable to be distinguished clearly. Moreover, the local eel stock was greatly influenced in 2004 by escaped cultured eels due to Typhoon Mindulle in July 2004 (Chu et al., 2006), and which might have influenced the estimation of vital parameters. This appeared to be most significant in 2004, decreasing substantially in 2005 and nearly disappearing in early 2006 (Lin and Tzeng, 2008). Moreover, the escaped cultured eels could be distinguished from wild eels by their different body coloration (Chu et al., 2006). Thus, data were separated into two periods: 1998–2003 and 2005–2007; data from 2004 was excluded from the length-frequency analysis. Escaped cultured eels were also excluded from analyses in 2005 and 2006.

Captured eels were anesthetized immediately with ice, measured for total length (to nearest 1 mm) and total weight (g), then transferred to the laboratory and frozen (-20°C). After defrosting, sex was determined by gross inspection of the gonads, and the development stage (yellow or silver eels) was determined by the body color, enlarged eyes, and blackened pectoral fins (Han et al., 2003; Tesch, 2003).

Growth

Anguilla japonica males are reported to have a mean growth rate in length of $>90\%$ vs females in the Kao-Ping River (Tzeng et al., 2003), and 102% in the Pearl River (Tzeng et al., 2000). Thus, the difference between sexes is not as significant as for other temperate eel species, and it was felt to be adequate to pool length data for both sexes in order to increase the sample size for analysis. Eel growth was described by the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty [1 - e^{-K(t-t_0)}]$$

where L_t is the length at time t , L_∞ is the asymptotic length, K is the Brody growth coefficient, and t_0 is the initial condition parameter when the hypothetical length is zero (Quinn and Deriso, 1999).

The population maximum length, estimated following Formacion et al. (1992), was set as the preliminary value of the asymptotic length. In addition, the estimated population extreme length with 95% confidence intervals was also used to estimate L_∞ according to Froese and Binohlan (2000):

$$\log_{10}(L_\infty, \text{cm}) = 0.044 + 0.9841 \times \log_{10}(L_{\text{max}}, \text{cm})$$

Given the estimated maximum length as initial estimate of L_∞ , the preliminary value of K was obtained using monthly catches-at-length data with 5-cm intervals by length frequency analysis (FiSAT-ELEFAN) (Pauly, 1987) and Shepherd's length composition analysis (FiSAT-SLCA) (Shepherd, 1987), respectively. The response surface analyses of ELEFAN and SLCA were then used to search for the optimal combination of L_∞ and K (Gulland, 1987; Shepherd, 1987), in which the preliminary estimates of L_∞ and K were used as the inference points. These estimating procedures were completed using FiSAT software (Gayanilo et al., 1996). Growth performance index (ϕ') (Pauly and Munro, 1984) was calculated as:

$$\phi' = \log_e(K) + 2\log_e(L_\infty)$$

Mortality

Natural instantaneous mortality (M) was estimated using Pauly's (1980) empirical formula (Gayanilo et al., 1996):

$$\log_e(M) = -0.0066 - 0.279 \log_e(L_\infty) + 0.6543 \log_e(K) + 0.463 \log_e(T), \text{SD}(\log M) = 0.245$$

where L_∞ and K are VBGF parameters and T is the mean environment temperature, i.e. 25.9°C in this study.

Total instantaneous mortality (Z) was estimated using the length-converted catch curves developed from length frequency distributions (Pauly, 1990; Gayanilo et al., 1996), given the estimated value of VBGF parameters. The instantaneous fishing mortality (F): $F = Z - M$, the exploitation rate (E): $E = F \times Z^{-1}$ and the mean annual survival rate (S): $S = \exp(-Z)$.

Sexual maturity

The silver eels were sexually maturing in preparation for spawning in the ocean. The maturation process, represented by the silvering process, was assumed to depend on size rather than age (Vøllestad, 1992; Oliveira, 1999). It was further assumed that the corresponding parameters for the maturity equations were the same during the period from 1998 to 2006

Table 1
Monthly eel catch by cooperative fishermen 1998–2007 in lower reach of Kao-Ping River

	1998 ^T	1999 ^T	2000 ^T	2001 ^T	2002 ^T	2003 ^T	2004 ^{TS}	2005 ^{S*}	2006 ^{S*}	2007 ^S
January		18					51		205	545
February		40		55	16				155	640
March				95			15	154	84	411
April							54		61	
May	16	3		63		30	66		314	
June		11		6			156	76	309	
July		9				40	264	134	113	148
August		38	62		152		124	235		50
September		71	16	30		47	52		99	
October	22		18	34			214	76	159	
November							241	269	222	33
December			16				35	310	92	
Sum	38 (38)	190 (190)	112 (112)	283 (283)	168 (168)	117 (117)	1272 (1272)	1254 (1092)	1813 (588)	1827 (841)
F	23	110	81	196	117	94	519	682	401	560
M	4	24	11	28	28	9	689	206	39	9
U	11	56	20	59	23	14	74	204	148	272

*Escaped cultured eels were identified and excluded from the study.

Numbers in parentheses, number of eels sexed; Superscript T, eels caught by eel tubes; S, eels caught by shrimp nets; F, number of females; M, males; U, sexually undifferentiated eels. Individuals in 2004 were excluded due to mixed gear information and escaped cultured eels.

and between wild and escaped cultured eels in 2004 (Chu et al., 2006). They were also assumed to be the same between different types of gear. However, the silvering of *A. japonicus* was significantly different between sexes in that the silver females were generally larger and older (Han et al., 2003), thus the silvering process was fitted separately in females and males.

Let $\gamma(L_i)$ be the proportion of the silver eels in the length class L_i , then the silvering pattern was fitted by two models:

(1) Logistic model:

$$\gamma(L_i) = \frac{\exp(a + bL_i)}{[1 + \exp(a + bL_i)]},$$

where a , b are parameters

(2) De Leo and Gatto's (1995) model:

$$\gamma(L_i) = \frac{\gamma_{\max}}{[1 + \exp(\frac{\lambda - L_i}{\eta})]}$$

where $\gamma_{\max}$ is the asymptotic maturation rate, λ is the semi-saturation constant which corresponds to the length at which the maturation rate = $0.5 \times \gamma_{\max}$. η is a shape parameter which is inversely proportional to the slope of the curve at $L = \lambda$ (De Leo and Gatto, 1995). Note that the two models are identical when $\gamma_{\max} = 1$. The optimal values of the parameters of the two equations were found by minimizing the sum of squared error using the Microsoft EXCEL SOLVER routine.

After the parameters of above models were estimated, the length at 50% maturity (L_{m50}) was calculated as:

$$\hat{L}_{m50} = \begin{cases} -\frac{\hat{a}}{\hat{b}}, & \text{for logistic model} \\ \hat{\lambda} - \hat{\eta} * \log_e(2\hat{\gamma}_{\max} - 1), & \text{for De Leo \& Gatto's model} \end{cases}$$

The null hypothesis that females and males have the same silvering process was tested by the analysis of the residual sum of squares (ARSS, Chen et al., 1992; Kimura, 2000) using the F_c : $F_c = \frac{SSH/P(Q-1)}{SSR(H_a)/(n-QP)}$ where $SSH = SSR(H_0) - SSR(H_a)$ = the sum of squared residuals for the null hypothesis – that of the alternative hypothesis. P = the number of parameters in the model (P equals 2 for the logistic model and equals 3 for De Leo & Gatto's model), Q = the number of groups

compared (i.e. = 2 for comparisons between sexes), and n = total sample size. F_c for the logistic and De Leo & Gatto models was calculated and compared with a critical value $F_{crit} = F_{P(Q-1), n-QP, 1-0.5\alpha}$ (Kimura, 2000). Statistical significance level (α) was set at 0.05.

Results

Sample collection

A total of 7 074 eels were caught from 1998 to 2007, in which 4 601 eels were sexed and their developmental stages (yellow or silver) determined (Table 1). Annual catch increased from around 130 eels in 1998–2003 and to more than 700 individuals after 2004, which coincided with introduction of the shrimp net to this area. Prior to 2007 most eels were sexed, with females dominating the catch from 1998 to 2003. However, in 2004, males increased due to cultured eel escapement (Chu et al., 2006). Also, the catch record from shrimp nets included more months than those from eel tubes (Table 1), implying that the fishing season for eel tubes was shorter than for the shrimp nets.

Growth

A total of 908 eels caught in 1998–2003 and 4 894 eels in 2005–2007 were used for length-frequency analyses using FiSAT-ELEFAN and FiSAT-SCLA. Observed and predicted maximum length, optimal combination of VBGF parameters, L_{∞} and K and the growth performance index ϕ' are shown in Table 2. Observed and predicted maximum length was 78.50 and 87.95 cm from 1998 to 2003, and 87.50 and 89.94 cm from 2005 to 2007, respectively. Overlapping 95% CIs for predicted maximum lengths indicated a statistically insignificant difference between the two periods. The predicted L_{∞} from L_{max} was 89.39 cm (95% CI: 84.11–97.17 cm) and 94.43 cm (95% CI: 84.92–100.39 cm) for 1998–2003 and 2005–2007, respectively. VBGF parameters (L_{∞} , K and ϕ') were estimated by ELEFAN as 101.00 cm, 0.33 year⁻¹, and 8.12, and by SLCA as 84.50 cm, 0.38 year⁻¹, and 7.91 for eels from 1998 to 2003. For eels caught from 2005 to 2007, the corresponding values were 110.00 cm, 0.30 year⁻¹, and 8.20, and 94.00 cm,

Table 2

Observed and predicted maximum length (L_{max}), corresponding estimate of asymptotic length (L_{∞}) from L_{max} , estimates of VBGF growth parameters (L_{∞} and K), growth performance index (ϕ) by length frequency analysis (ELEFAN) and Shepherd's length composition analysis (SLCA) and corresponding estimates of instantaneous total mortality rate (Z), natural mortality rate (M), fishing mortality rate (F), exploitation rate (E), and annual survival rate (S) of Kao-Ping River Japanese eels, 1998–2007

Period	1998–2003		2005–2007	
N	908		4894	
L_{max} (cm)				
Observed (cm)	78.50		87.50	
Predicted (cm)	87.95 (81.52–94.39)		89.94 (82.31–97.57)	
L_{∞} from L_{max} (cm)	89.39 (84.11–97.17)		91.43 (84.92–100.39)	
Method	ELEFAN I		ELEFAN I	
	SLCA		SLCA	
Growth				
L_{∞} (cm)	101.00		110.00	
K (year ⁻¹)	0.33		0.30	
ϕ	8.12		8.20	
Mortality				
Z (year ⁻¹)	1.13 (0.89–1.36)		1.99 (1.76–2.28)	
M (year ⁻¹)	0.59		0.54	
F (year ⁻¹)	0.54		1.45	
E (%)	47.8		72.6	
S (%)	32.3 (25.7–41.1)		13.7 (10.3–17.4)	
	40.7 (35.7–45.8)		12.5 (10.4–14.7)	

N, number of eels caught. Numbers in parentheses, 95% confidence interval.

0.44 year⁻¹, and 8.26 (Table 2). L_{∞} estimate from ELEFAN was higher compared to SCLA and outside the 95% CI of L_{∞} from L_{max} , while the L_{∞} estimate from SCLA fell into this range. Thus, the K estimate from ELEFAN I was smaller than that from SCLA due to the negative correlation between L_{∞} and K . The estimates of ϕ were similar between periods and methods, except for the 1998–2003 period when the SLCA method gave the lowest value.

Mortality

Instantaneous total mortality rates Z , estimated from the length-converted catch curves based on growth parameters from ELEFAN and SLCA for eels caught from 1998 to 2003 were 1.13 year⁻¹ (95% CI: 0.99–1.36) and 0.90 (95% CI: 0.78–1.03), respectively. The confidence intervals include uncertainties in the catch curves only, assuming correct growth parameter values (Fig. 2a,b). For 2005–2007, Z values were estimated as 1.99 year⁻¹ (95% CI: 1.76–2.28) and 2.08 (95% CI: 1.92–2.26), respectively (Fig. 2c,d).

The annual natural mortality rates (M) from Pauly's empirical formula based on ELEFAN and SLCA growth parameters were 0.59 and 0.68 year⁻¹, respectively, in 1998–2003, and amounted to 0.54 and 0.74 year⁻¹ in 2005–2007. According to the 95% confidence interval of individual data in Pauly's regression these estimates of M are statistically uncertain by a factor of 3, when assuming correct growth parameters.

Instantaneous fishing mortality rates (F) were derived as 0.54 and 0.22 year⁻¹ in 1998–2003, and 1.45 and 1.34 year⁻¹ in 2005–2007. The exploitation rates (E) during 1998–2003 for Japanese eels were estimated as 47.8 and 24.4%, with annual survival rates (S) of 32.3 and 40.7%. After 2005, exploitation rates increased to 72.6 and 65.0% with S of 13.7 and 12.5%, suggesting that fishing pressure increased on the eels after the use of shrimp nets began (Table 2).

Maturity

The 4 601 eels sexed from 1998 to 2007 (Table 1) were used to calculate maturation rates (represented by the proportion of

silver eels) at a given size class. Females at about 40 cm TL started to become silver eels, this proportion increasing greatly from 50 to 70 cm TL (Fig. 3). All females larger than 80 cm were silver eels (Fig. 3a). Males began to silver at 35 cm TL, the proportions thereof increasing considerably with length so that all males larger than 70 cm were silver eels (Fig. 3b). Both the logistic and De Leo & Gatto models fitted the original data well and were indistinguishable (Fig. 3). The slope (b) of the logistic model was greater and the intercept (a) smaller in females (0.18 cm⁻¹ and –11.55) than for males (0.15 cm⁻¹ and –8.47). For the De Leo & Gatto model, γ_{max} was similar for both males and females (1.00), while λ was larger and η was smaller for females (64.54 and 5.59 cm) than for males (57.41 and 6.78 cm). The length at 50% maturity for females (64.54 cm) was larger than for males (57.41 cm) (Table 3). Moreover, according to the ARSS, the silvering process differed significantly between the sexes for both the logistic and De Leo & Gatto models ($F_c = 33.56$ for the logistic and 20.34 for the De Leo & Gatto model, both $P < 0.0001$).

Discussion

Length-frequency analysis methods

For adequate results on growth from length frequency analysis, a total of 1 500 or more individuals collected over at least 6 months with an apparent shift in modal length over time is advisable (Pauly, 1987), as is a sample size of at least 10 times the number of length classes (Gerritsen and McGrath, 2007). In 2005–2007 the sample sizes were for most months sufficiently large enough to satisfy the Gerritsen and McGrath (2007) rule of thumb (Table 2). The change in fishing gear used in 2004 was believed to substantially alter the catchability of the eel, thus the data were separated into two periods for estimation of growth parameters. However, the estimation of Z during 2005–2007 is likely biased due to apparent changes in mortality after 2004.

Due to the lower eel catch rate of the eel tubes, the sample size was low for 1998–2003, which may have influenced the estimation of growth parameters. But the temporal scale was still large, as eels were collected over a 24-month period, which

Fig. 2. Length-converted catch curves for data from (a) 1998–2003 using ELEFAN I; (b) 1998–2003 using SLCA; (c) 2005–2007 using ELEFAN I; and (d) 2005–2007 using SLCA

Fig. 3. Proportion of silver eels as a function of body length for (a) females and (b) males. Obs, observed in a given length class (squares on solid line); Logistic, predicted using logistic model (open circles on solid line); De Leo = predicted using the De Leo and Gatto (1995) model (asterisks on broken line)

might reduce the bias resulting from the small sample size in this period. Length class width (5 cm) was determined from a prior search of several possible widths (1–10 cm) to ensure distinct peaks in length distribution and clear changes in model length. However, the eel tube is more selective than the shrimp nets (Lin and Tzeng, 2008), perhaps making results from the

Table 3
Estimates of maturation parameters for the logistic and De Leo & Gatto models

Model	Parameters			
Logistic ^a	a	b (cm ⁻¹)	L_{50} (cm)	
F	-11.55	0.18	64.54	
M	-8.47	0.15	57.41	
Pooled	-9.77	0.16	63.11	
De Leo & Gato ^a	γ_{max}	λ (cm)	η (cm ⁻¹)	L_{50} (cm)
F	1.00	64.54	5.59	64.54
M	1.00	57.41	6.78	57.41
Pooled	1.00	63.10	6.46	63.11

*L*₅₀ = 50% length at maturity. F, females; M, males; and pooled sexes. ^asex-separate models differed significantly from pooled the model.

1998 to 2003 period inconclusive and inconsistent between the different methods of analysis. Conversely, shrimp nets were less selective and the number of eels caught per month was much larger (mostly above 160 individuals, except for 2 months). Consequently, the use of length-frequency data was believed appropriate to estimate the vital population statistics of *A. japonicus* for the 2005–2008 period.

Growth

Anguilla japonicus growth was assumed to follow a von Bertalanffy growth function, which has been verified by Lin and Tzeng (2009a). The optimal combination of *L*_∞ and *K* were estimated by ELEFAN and SLCA using response surface analysis because the estimates of *L*_∞ and *K* are highly correlated (Gulland, 1987; Shepherd, 1987). Both methods may be affected by differences in growth strategies, individual variability in growth, seasonal oscillations of growth, variation

in recruitment pattern, size-dependent selection, and the width of length classes (Isaac, 1990). The lower reach of the Kao-Ping River is tropical (Lin and Tzeng, 2009b), thus any seasonal oscillation in eel growth was assumed to negligible. Elvers recruit to the estuary regularly in winter from November to January and are not found after April (Tzeng, 1997). Thus, the recruitment season of the Japanese eel in Taiwan is considered to be stable, making the use the length-frequency data possible (Pauly, 1984).

L_{∞} estimated by ELEFAN was not included by the 95% CI of L_{∞} from L_{max} , implying that L_{∞} from ELEFAN might be overestimated in this study. However, the uncertainty of growth parameters cannot be fully examined in this study. The variances of estimation of growth parameters were not given by FiSAT, thus statistical comparisons could not be conducted. It is still necessary to estimate the growth of *A. japonicus* using other data, e.g. lengths-at-age derived from annulus in the calcified structures that would enable comparisons of growth between sexes, time period and different data sources (Morales-Nin, 1989).

The values of L_{∞} and K for Japanese eel vary considerably among different regions. In this study, L_{∞} was estimated between 84.5 and 112 cm when stages (i.e. yellow and silver eels) and sexes were pooled, while it was 98.2 cm for yellow eels from the Quilu River in southern China (Guan et al., 1994), and 55.7 cm for male and 77.5 cm for female silver eels from the Pearl River in southern China (Tzeng et al., 2000). Estimated L_{∞} values fell within the upper range of published values, while K was higher ($0.29 \sim 0.45 \text{ year}^{-1}$) than in other studies (0.07 year^{-1} in Guan et al., 1994 and 0.21 year^{-1} for males and 0.14 year^{-1} for females in Tzeng et al., 2000). For Kao-Ping River eels the fishing pressure may be very high, perhaps reducing the intra-specific competition for food and suitable habitats and thus possibly enhancing individual growth rates. However, the relevance of this or other factors requires confirmation.

Mortality

Japanese eels in the Kao-Ping River probably faced a heavier fishing pressure after the introduction of shrimp nets. The 95% CI of Z for 1998–2003 did not overlap with that for 2005–2007

with growth parameters derived from both ELEFAN and SLCA, suggesting a significant increase in Z in 2005–2007. This may be contributed by the introduction of shrimp nets, which are less-selective than eel tubes and have been widely used by eel fishermen (Lin and Tzeng, 2008). In addition, F and E for *A. japonicus* were generally higher with a lower S than for other fished eel species (Table 4). Thus, the Japanese eel stock in the lower reach of the Kao-Ping River may suffer higher fishing pressure than do the eels in other regions.

Hoyle and Jellyman (2002) predicted a reduction in spawner per recruit of 48% for female *A. australis* and 96.5% for female *A. dieffenbachii* under an annual E of 10%. Consequently, the impact of an annual exploitation rate larger than 60% in 2007 on the spawning biomass of the local Japanese eel stock might be severe. To enhance elver production, not only the harvest of elvers but also the biomass of eels in the river and escapement of silver eels to the spawning stock should be managed. Moreover, because of the time lag between a decrease in stock size and decrease in recruitment (7–14 years for *A. anguilla*; Feunteun, 2002) due to the catadromous nature of eels, where they spend about 1 year as migrating leptocephali and several years in freshwater or brackish waters, a precautionary approach (Russell and Potter, 2003) should be applied.

However, the estimates of Z in this study still have a large uncertainty. Because Z was estimated from a length-converted catch curve, the input of different growth parameters would obviously alter the shape of the converted catch curve and thus the estimates of Z (Isaac, 1990). Also, M was derived from Pauly's empirical formula rather than estimated directly from the population (e.g. mark-recapture experiment), and is correspondingly sensitive to the uncertainties in the growth parameters. Thus, the obtained high M compared to other eel species (Table 4) is at least in part due to high values of the growth parameters. Moreover, the estimation of Z was still under the influence of eel tubes for some years after the introduction of shrimp nets. The catch curves in 2005–2007 (Fig. 2c,d) appear to have a sudden drop after the relative age of 2.5 years, implying a sudden increase in Z for older individuals. Studies to estimate mortality rates independent of these growth parameters are required to further evaluate the current exploitation rate of eels in the Kao-Ping River.

Table 4
Comparison of mean annual natural mortality (M), fishing mortality (F), total mortality (Z), exploitation (E), and annual survival rate (S) among other eel species

Species	Locality	M (year ⁻¹)	F (year ⁻¹)	Z (year ⁻¹)	E (%)	S (%)	Note	References
<i>A. anguilla</i>	Valli di Conacchio Lagoon, Italy					30–90	30% for age 1 to age 2, 90% for other ages	De Leo and Gatto, 1995
<i>A. anguilla</i>	West coast, Sweden	0.23	0.31	0.54	57	58		Svedäng, 1999
<i>A. anguilla</i>	IJsselmeer Lake, Netherlands		0.14 to > 2				F increases with length	Dekker, 2000
<i>A. australis</i>	New Zealand	0.038			10		E increases with length	Hoyle and Jellyman, 2002
<i>A. dieffenbachii</i>	New Zealand	0.036			10		E increases with length	Hoyle and Jellyman, 2002
<i>A. rostrata</i>	Chesapeake Bay, US	0.25	0.27	0.52	52	59		Weeder and Uphoff, 2003
<i>A. rostrata</i>	St Lawrence River, Canada				19–24			Caron et al., 2003
<i>A. japonica</i>	Kao-Ping River, Taiwan	0.53–0.74	0.22–1.49	0.90–2.08	24–74	12–41		This study

Maturity

The maturity of Japanese eels, as represented by the silvering process, was assumed to be a function of size alone. This assumption seemed reasonable because the silvering of the eels was found to be dependent on size, not on age, for eel species such as *A. anguilla* (Vøllestad, 1992; De Leo and Gatto, 1995; Bevacqua et al., 2006), *A. rostrata* (Oliveira, 1999), *A. australis*, *A. dieffenbachii* (Jellyman, 2001; Hoyle and Jellyman, 2002), and *A. japonica* (Lin and Tzeng, unpubl. data). The silvering process was significantly different between female and male Japanese eels and the observed larger size of females at 50% maturity (Table 3) is consistent with the published data for this species (Tzeng et al., 2002, 2003; Han et al., 2003). Sex-dimorphism in silver eels is common in *A. anguilla*, *A. rostrata*, *A. australis* and *A. dieffenbachia* (Poole and Reynold, 1996; Oliveira, 1999; Jellyman, 2001; Tzeng et al., 2003), perhaps related to sex-dependent life history strategies (Helfman et al., 1987).

In the logistic model, it is assumed that all individuals (i.e. 100%) become silver eels at some older age or larger length class. The De Leo & Gatto model is more plastic because of addition of γ_{max} , the asymptotic probability of being silver eels, which can adjust the upper level of the silvering curve. Given that this study is the first to describe the maturation of *A. japonica*, no comparative published data are available for this species. For *A. Anguilla*, γ_{max} appeared to be more variable for females compared to males, being 0.12 ± 0.03 for females in the Valli di Comacchio Lagoon in Italy (De Leo and Gatto, 1995) and $0.60-1$ in southern France (Bevacqua et al., 2006). For males in the two regions, γ_{max} generally approached 1. For *A. japonica* in Kao Ping River in southern Taiwan, γ_{max} was 1 for both sexes in this study, suggesting that for *A. anguilla* and *A. japonica*, nearly all males tend to silver upon reaching some critical size, while for females the tendencies to become silver eels vary among regions and species. In other words, the conditions for females to become silver eels seem to be more plastic than for males.

Conclusion

Due to restrictions in the data set of the first time period and to the change in fishing method, the data on growth and mortality remain uncertain and require confirmation. In the absence of large environmental fluctuations, natural mortality rates were likely similar throughout the study period. The estimated decrease in survival rate, though uncertain in detail, was probably realistic due to the use of new fishing gear types that increased the fishing mortality and exploitation rate considerably.

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