

國立臺灣大學生命科學院漁業科學研究所

博士論文

Institute of Fisheries Science

College of Life Science

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National Taiwan University

Doctor Thesis

高屏溪日本鰻族群動態及永續利用：YPR 和 SPR 模式的

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Population dynamics and sustainable use of Japanese eel
(*Anguilla japonica*) in Kao-Ping River: application of
YPR and SPR models



林裕嘉

15

Yu-Jia Lin

指導教授：曾萬年 博士

Advisor: Wann-Nian Tzeng, Ph.D.

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中華民國 98 年 1 月

Jan., 2009



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Chinese abstract

日本鰻(*Anguilla japonica*) 為一高度經濟價值的物種。由於過度捕撈，鰻魚族群量急劇下降，因此急切需要管理及保育。本研究藉由估計成長參數、死亡率以及成熟參數來探討南台灣高屏溪下游鰻魚族群之族群動態，且利用單位加入生產量及加入親魚量模式估計過漁的風險，進而評估當地鰻魚資源的永續利用。並將估計參數時所產生的誤差，利用蒙地卡羅法納入兩模式中考量。經過已知年齡之養殖鰻，以及野生鰻的耳石邊緣成長率的驗證，確認年輪形成之年週期性，顯示可以利用耳石來估計當地鰻魚的年齡及逆算年齡形成時的體長。經由資訊理論的判定，范氏成長方程式(von Bertalanffy growth model)為最符合推套用逆算體長之成長方程式。當利用標誌放流法估計死亡率時，發現死亡率估值會受到標誌鰻的來源(野生或養殖)或是標示方式(微晶片或剪鰭)所影響。當用銀鰻來代表鰻魚之成熟並估計族群的成熟曲線時，發現成熟曲線有顯著的雌雄差異，顯示了鰻魚在銀化上之兩性差異。

雌雄成長性過漁的風險相對為小，其風險在 1 到 40 % 左右。然而加入性過漁的風險相對較高，在 24 到 98 % 之間。漁獲死亡率降低時，成長性及加入性過漁的風險也隨之降低。當漁業受到最小捕獲體長的管制時，最小捕獲體長越大，成長性過漁之風險明顯地減少，然而加入性過漁的風險只有些許的降低。當漁業受到最大捕獲體長的管制時，將最大捕獲體長向下調整時越小，成長性過漁的風險只有些許的降低，但加入性過漁的風險有顯著的降低，顯示限制最大捕獲體長可以有效地保護產卵親魚量。在現今的捕撈水準下，發生成長性過漁的風險相對較低，但加入性過漁的風險卻相當有可能，甚至可能已經發生。為了永續利用鰻魚資源及提供足夠的產卵親魚量，本研究建議將現有之漁獲死亡率下降 40%，或是執行不小於 500 公厘之最小捕獲體長及不大於 850 公厘的最大捕獲體長管制。

25 **關鍵字:** 日本鰻、生命參數估計、單位生產量模式、成長性及加入性過漁。

English abstract

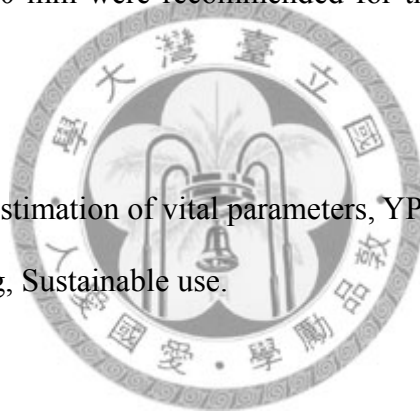
Japanese eel (*Anguilla japonica*) is a highly-priced commercial fish in Asia. Due to heavy exploitation, the Japanese eel population declined drastically and thus conservation and management of the eel population are urgently needed. In this study
5 the population dynamics of the eel population in the lower reaches of Kao-Ping River in the southern Taiwan were examined by estimating its growth, mortality rate and maturation parameters. The sustainable use of the eel population was evaluated by assessing the risks of growth and recruitment overfishing using yield per recruit (YPR) and spawner per recruit (SPR) models. Uncertainties in parameter estimation were
10 incorporated into the models by Monte Carlo simulation.

In order to obtain accurate age estimates, otolith annuli were validated by known-age cultured eels and otolith marginal increment ratio of the wild eels. Then the back-calculated lengths-at-age from otolith were used to estimate the growth parameters in von Bertalanffy growth model, which best fitted the lengths-at-age data according to
15 information theory. Mortality rates estimated from mark-recapture data were found different between eel origins and marks. The maturation curves, described by the silvering of the eels, were found to be different between females and males, indicating a sexual dimorphism in the silvering of the eels.

Analysis of YPR model indicated that the risks of growth overfishing (GOF),
20 defined as probabilities that current fishing level were larger than F_{max} at which the YPR was at its maximum, ranged 1 to 5 % for both sexes. A more conservative risks of GOF, defined as the probabilities that current fishing mortality exceed $F_{0.1}$ at which the increase in YPR was 10 % of that when the eels were not exploited ($F = 0$), were from 30 to 40 %. Two risks of recruitment overfishing (ROF), defined as the probabilities that
25 the SPR under current fishing mortality was less than 40 and 50 % of that when $F = 0$,

were relatively higher, 23.9 to 84.8 % and 67.0 to 97.6 %. When the minimum legal sizes increased, the risks of GOF decreased considerably but the decreases in risk of ROF were less apparent. When the maximum legal sizes decreased, the risks of GOF decreased a bit but the risks ROF were effectively reduced due to better protection of larger spawners. The risks of GOF for the eel fisheries in the study area were low to considerable, while the risks of ROF were substantially higher. To sustain the eel resources, especially for supplying sufficient amount of glass eels for eel culture, control of fishing mortality rate, and exploitation rate, e.g. a 40 % reduction, and the enforcement of minimum legal sizes of not smaller than 500 mm or a maximum legal sizes of not larger than 850 mm were recommended for the eel fisheries in the lower reaches of Kao-Ping River

Keywords: Japanese eel, Estimation of vital parameters, YPR and SPR models, Growth and recruitment overfishing, Sustainable use.



1. Introduction

1.1. Background information

1.1.1. Life history of the Japanese eel

Japanese eel (*Anguilla japonica*) is a catadromous fish, spawning in seawater but
5 growing in freshwater habitats. It is widely distributed in Taiwan, mainland China,
Japan, and Korea (Tesch, 2003). The spawning ground of the eel is probably located in
the seamounts of the tropical Pacific Ocean west of the Mariana Islands (Tsukamoto,
2006). After hatching the leaf-like larvae, leptocephali, are passively transported by the
North Equatorial and Kuroshio currents, and metamorphose to glass eels over the
10 continental shelves of the above-mentioned countries. After the metamorphosis, the
glass eels further develop into pigmented elvers in estuaries (Cheng & Tzeng, 1996).
Like other anguillids, the Japanese eel is found to be facultatively catadromous, i.e. the
elvers do not obligatorily migrate upstream to freshwater habitats, but some of them
stay in brackish estuaries and seawaters as yellow eels (Tzeng et al., 1997; Tsukamoto
15 & Arai, 2001; Tzeng et al., 2002). After 4 to 10 years of growth, the yellow eels begin
sexual maturation and become silver eels with darken body, reduced digestive tract and
enlarged eyes (Han et al., 2000; Han et al., 2003). They migrate downstream to the
ocean for spawning. The Japanese eel is semelparous; they die after spawning (Tesch,
2003).

20 The genetic structure of Japanese eel was found weakly differentiated (Tseng et al.,
2006) or panmictic (Sang et al., 1994; Ishikawa et al., 2001; Liao, 2007) among the
distribution range of Japanese eel, probably due to its catadromous life history that
enables both larvae and spawners to have the chance to be mixed during their migration
(Kettle & Haines, 2006).

25

1.1.2. Population status of the Japanese eel

The population of Japanese eel was found to decline dramatically since 1970s, similar to the cases of European eel *A. anguilla* and American eel *A. rostrata* (Tatsukawa, 2003; Dekker, 2003). In Japan, commercial catches of glass eels decreased greatly that in 2000 they reduced to about 20 % of the 1970 level, lower than the biological safeguard limit (Dekker, 2003). A similar declining trend was found for the annual landings of adult eels (yellow and silver eels) in Japan, mainland China and Korea; it was 765 tons in 2000, being only about 35 % of that in 1984 (2,125 tons) (Fig. 1, Ringuet et al., 2002).

In Taiwan, the Japanese eel is the most dominant species among four known eel species, including *A. japonica*, *A. marmorata*, *A. bicolor pacifica* and *A. celebesensis*. It makes up 89.8 % of total catch of all eel species from the wild (Tzeng & Chang, 2001). The Japanese eel is also the only species that is commercially cultured in Taiwan (Liao, 2001). To enhance the spawning population, the hormone-injected female eels had been released in the coastal waters in southern Taiwan by Fisheries Research Institute since 1967 (Liao et al., 1994). However, the contribution of the releasing to the eel population is unclear. The catches of the glass eels from the wild in Taiwan did not demonstrate a decreasing trend as that in Japan, but showed great fluctuation among years (Tzeng, 1997; 1998; 2006). According to the official statistics from Fisheries Agency, Council of Agriculture, Taiwan, the temporal changes of the annual catches of glass eels also fluctuated between 10 million to 100 million during 1993 to 2007 (Fig. 2).

Moreover, we were not optimistic about the status of the eel population in Taiwan because of high exploitation pressure on the elvers in Taiwan to meet the demand for eel culture. For example, the exploitation rate on the elvers in the coastal waters off Shuang-chi River ranged between 44 and 75 % and could be higher if the catches of elvers in the river were included (Tzeng, 1984). Even the elvers were under high

exploitation pressure, its catch in Taiwan was still insufficient to meet the domestic cultural demands, possibly only for 10 % (Tzeng, 1984). Moreover, a clear negative relationship between catches of glass eels and adult (yellow and silver) eels was found (Tzeng & Chang, 2001), indicating that the exploitation on the glass eels might further
5 impact the adult population in the river. The increasing demand for glass eels in recent years possibly made the exploitation pressure even higher, drastically affecting the adult eel population (Tzeng, 1997).

Some studies with indirect indicators also implied that the eel population in Taiwan was probably at a low level. Tseng et al. (2003) found that the decreased genetic
10 polymorphism in microsatellite DNA of the eel probably resulted in lowered population stability. Meanwhile, females were found being dominant in area with low population density and vice versa for the males, and thus, Han & Tzeng (2006) suggested that the population size of the yellow and silver eels in the lower reach of Kao-Ping River was probably small. The overfishing of glass eels and habitat degradation were probably the
15 principal causes of its low population density.

1.2. Eel fishery in Kao-Ping River

Kao-Ping River is a relatively less polluted river in Taiwan and its lower reach is one of the most important fishing grounds for elvers, juveniles, and adult Japanese eels,
20 where the fishermen traditionally use bamboo eel tubes to harvest the juveniles and adults (Chang & Tzeng, 1990; Tzeng & Chang, 2001). Japanese eel tends to live in the lower reach of the Kao-Ping River, while the marbled eel *A. marmorata* are dominant in the middle and upper reaches (Tzeng & Chang, 2001; Shiao et al., 2003). This has been confirmed by local fishermen that the Japanese eels are rare in the middle and upper
25 reaches. Therefore, the lower reach of Kao-Ping River is an important as a suitable habitat for the Japanese eel and a fishing ground for the eel fishery (Tzeng & Chang,

2001).

The market price of yellow and silver eels from the wild was 3 to 4 times higher than that from aquaculture, consequently driving fishermen to catch eels from the wild (Chang & Tzeng, 1990). A shrimp fishery, targeted mainly on sand shrimps (*Metapenaeus* spp.) is also operating in the lower reach of the river. Besides small trawlers working in the river mouth, fishermen have recently (about in 2003) introduced a new shrimp nets for the fishery hereafter. Both juvenile and adult eels have been found in considerable amounts in the shrimp nets as by-catch, resulting from that the eels may chase the shrimps into the nets and are trapped inside. Because the shrimp nets are easily to operate with and high efficiencies for catching both shrimps, yellow and silver eels, the shrimp nets have been widely used lower reach since 2004, virtually replaced the traditional bamboo eel tubes. But the effects of shrimp nets on the eels, such as the eel size vulnerability and the gear efficiency were still unclear (Lin & Tzeng, 2008a). Moreover, the eel fishery in the lower reach of Kao-Ping River was neither regulated by the authority, such as the development of fishing right, total allowable catches, fishing seasons, licenses of the fishermen and constrains in legal size of the eel, nor official statistics about the eel fishery, such as the landings, fishing effort and catch at size data, were collected. The assessment of the eel fishery was greatly needed, but the degree of availability of the information would strongly determine the assessing approaches (Gabriel & Mace, 1999).

1.3. Assessment of the eel fishery in the lower reach of Kao-Ping River

The declining trend of the overall eel population size and the population status in Taiwan is described in 1.1.2. Its assessment and management were urgently needed (Dekker, 2003; Stone, 2003). Compared to other anguillids such as *A. anguilla*, *A. rostrata*, *A. diffebachii* and *A. australis* (De Leo & Gatto 1995; Hoyle & Jellyman,

2002; Chisnall & Martin., 2003; Dekker, 2003; Weeder & Uphoff, 2003), the studies on the population dynamics and the fishery of the Japanese eel were surprisingly few. The lack of multi-regional and international integrated data may be one of the reasons to prevent the assessment of the Japanese eel in large geological scales (Dekker, 1999).

5 The wide distribution of eel population might also make some common fishery assessment models inapplicable. For example, the assumption of population at equilibrium state might be hardly satisfied in different geographical regions at the same time. A common spawner-recruitment relationship applying to all regions was probably unreasonable, either.

10 However, it is still practical to evaluate the eel fishery on a local population with small geographic range, as cases widely used for other eel species (Dekker, 2000; Hoyle & Jellyman, 2002; Benjamin et al., 2003; Weeder & Uphoff, 2003). A single set of parameters seemed more appropriate and reasonable to describe the small-scaled population and it is also easier to meet the assumptions necessary for fishery models.

15 Moreover, a case study approach is regarded as the first step toward a large-scaled study because once the methodology and the models for the assessment are established, they were able to be applied to other regions and thus, enable the multi-regional studies become possible in the future.

The lower reach of Kao-Ping River in the southern Taiwan is one of the most

20 important fishing grounds for the glass eels, elvers, yellow and silver eels with relatively long time series of catch data from 1998 to 2007. The local eel population in this region has been well studied (Cheng & Tzeng, 1996; Han et al., 2000; Tzeng & Chang, 2001; Tzeng et al., 2002; Shiao et al., 2003; Han et al., 2003; Lin & Tzeng, 2008*a,b*), and some basic information on the population dynamics was available. Two

25 mark-recapture experiments for the yellow eels were conducted in 2005 and 2006 that could provide supplemental information other than catch data. Consequently, the lower

reach of Kao-Ping River seemed a suitable place as a case study for the population dynamics and sustainable use of the Japanese eel.

1.4. Information about the eel population dynamics

5 Information about the vital parameters of the eels, such as age and length at recruitment, age and length at maturity, growth rate, fishing and natural mortality rates and maturity parameters, was essential to understand the eel population dynamics as well as for successful management and assessment of the eel fishery. For eels in the lower reach of Kao-Ping River, it usually takes the leptocephali about 160 days to drift
10 from the spawning ground, to metamorphose to glass eels, and pigmented elvers with a mean size of 56.5 mm and to arrive at the mouth of Kao-Ping River (Cheng & Tzeng, 1996). Most of the yellow eels (86 %) spend their life in the brackish, implying that their movement is probably restricted in the lower reach (Tzeng et al., 2002; Tzeng et al., 2003). The yellow eels spend at an average of 6.4 years for females and 5.8 years for
15 males to become sexually matured silver eels (Han et al., 2000). Female and male silver eels also differ in mean (\pm SD) sizes (622 ± 74 and 545 ± 72 mm for females and males, Han et al., 2000) and habitat preferences that 54 % of males prefer freshwater, while 16% for the females (Han & Tzeng, 2007). However, other crucial parameters in the population dynamics, such as growth parameters, total, natural and fishing mortality
20 rates and maturation curve in relation to eel length remained unclear.

1.4.1. Growth parameters from otolith annuli readings

1.4.1.1. Validation of otolith annuli

Accurate and precise age estimation is important for understanding the fish life
25 history and population dynamics. Estimation of vital parameters, such as growth rate, mortality rate, and time at maturity, depends on accurate age determination (Quinn &

Deriso, 1999). Among the hard structures used for age estimation, otolith is generally considered to be the best for estimating the age of many teleost fishes (Campana & Thorrold, 2001). However, annulus formation in otoliths requires validation before it is used to for estimating age of fish (Beamish & McFarlane, 1983; Campana, 2001).

5 Annulus formation in otoliths has been validated in some *Anguilla* species in temperate zones (Berg, 1985; Oliveira, 1996; Graynoth, 1999; Pease et al., 2003) but not for the Japanese eel, particularly from tropical zones (Guan et al., 1994). It has been hypothesized that otolith annuli of Japanese eels in Kao-Ping River of the southern Taiwan are deposited annually, similar to those of other anguillids (e.g. in Han et al.,
10 2000; Tzeng et al., 2000; 2002; 2003). However, the annual deposition rhythm in otoliths of tropical fishes has been considered problematic because of less seasonal variation in water temperature and relatively stable growth. This may cause controversy in the age and growth estimation for tropical fishes (Morales-Nin, 1989; Morales-Nin & Panfili, 2005). Moreover, the supernumerary (false or incomplete) growth increments
15 are found in eel species (Berg, 1985; Vøllestad, 1985; Michaud et al., 1988; Svedäng et al., 1998; Graynoth, 1999; Pease et al., 2003), and further stress importance of the annulus validation for the Japanese eel.

1.4.1.2. Selection of the best growth model fitting the data

20 After the validation of otolith annuli, the fish growth curve describing the mean fish growth was estimated from annuli readings. Fish growth is one of the most important processes determining population dynamics that many formulae and models are proposed to describe and estimate the mean individual growth. In theory, individual growth is often considered as the net result of two opposing processes, anabolism and
25 catabolism (von Bertalanffy, 1938). Different possible interactions of the two processes and various relationships between growth rate and size or age either from empirical

observations or theoretical calculation are assumed in different growth models. Different growth models are represented by differential equations and the corresponding solutions are used for modelling fish growth (Schnute & Richards, 1990; Quinn & Deriso, 1999; Katsanevakis, 2006; Katsanevakis & Maravelias, 2008).

5 The von Bertalanffy growth model is probably the most popular in describing the growth of fish. However, use of this model without considering other alternatives could introduce additional sources of uncertainty into the modelling, i.e. model errors resulting from selection of an inappropriate model (Schnute & Richards, 2001), affecting a subsequent stock assessment (Patterson et al., 2001). Moreover, ignoring
10 alternative models might result in inaccurate parameter estimates, underestimated standard errors, and overly optimistic confidence intervals for the parameters (Buckland et al., 1997; Burnham & Anderson, 2002; Johnson & Omland, 2004). In addition, if the objectives include the examination of whether the growth parameters differ among population subgroups, the underestimated standard errors could cause an incorrect
15 statistical differentiation of the parameters (Katsanevakis & Maravelias, 2008).

The von Bertalanffy growth model has been fitted in numerous studies of the Japanese eel (e.g. Guan et al., 1994; Tzeng et al. 2000; 2003, Kotake et al., 2005; Lin & Tzeng, 2008b), but it is still unclear whether the von Bertalanffy growth model was the best model fitting the data, and alternative growth models have been little used and may
20 have provided a better fit. Meanwhile, Japanese eels display sexual dimorphism in growth (Han et al., 2000; Tzeng et al., 2000; 2003; Kotake et al., 2005), implying that sex should be incorporated in modelling of the eel growth. Differences in growth between sexes may be reflected by different values for growth parameters (Rabaoui et al., 2007) and by different forms of growth models (Coelho & Erzini, 2007).
25 Consequently, the use of von Bertalanffy growth model for the Japanese eel *a priori* in most studies may introduce additional uncertainty in model selection, affecting the

assessment and evaluation of the eel population dynamics.

1.4.2. Fishing and natural mortality rates from mark-recapture experiment

Fishing and natural mortality rates are also the essential parameters in assessment
5 and management of a fishery. Among the numerous approaches to estimate fishing and
natural mortality rates, mark-recapture experiment is a powerful tool and has been
widely used for animals of different taxonomic groups (Seber, 1982; Lebreton et al.,
1992; Schwarz & Seber, 1999). Besides estimation, variability occurring from natural
causes, such as trap response, individual and temporal variations (Schwarz & Seber,
10 1999; Lebteton et al., 1992; Pledger, 2000; Pledger et al., 2003) and different
experimental designs may confound the estimation of the parameters based on
mark-recapture experiments, resulting in erroneous conclusion (Lebreton et al., 1992;
Schwarz & Seber, 2002).

Designs of mark-recapture experiments vary among studies to meet specific
15 objectives or to cope with different practical limitations (Seber & Schwarz, 2002), and
thus, they inevitably introduce additional sources of variability into the data and
consequently the estimation of mortality rates. First possible source of variability is the
difference in release sites. In a mark-recapture experiment in a river, marked fish are
commonly released directly in the region where the fish are caught (*e.g.* Laffaille et al.,
20 2005; Thibault et al., 2007). Also, they may be released slightly upstream of the fishing
ground to enhance their dispersion via river current, to study the downstream migration
(*e.g.* Caron et al., 2003), or the homing behaviour of the fish (Crook, 2004).

A second source of variability is the difference in fish origins. In general the fish
released are previously collected from the experimental region, but fish from rearing
25 ponds may also be used either to increase the number of fish released or to evaluate
differences in behaviour and survival of the reared fish in the wild environment

(Saloniemi et al., 2004). A third source of variability is a difference in the marks used. Various kinds of marks and tags have been developed and applied to a wide range of fish species (McFarlane et al., 1990). Some tags, such as passive integrated transponder (PIT) tag, coded wire tag (CWT), microchip and data storage tag, may store information such as individual identity and records of environmental variables that other tag options cannot (e.g. fin clipping), but the number of these tags used was constrained by their expensive prices and large sizes. One possible way to balance this trade-off is to mark a certain number of fish using informative tags (PIT, CWT or microchips) and the rest by the more economic fin clipping (Hammer & Blankenship, 2001; Labonne & Gaudin, 2005) but the consequent effects on the results of mark-recapture experiments are little known in anguillids (Briand et al., 2005).

To estimate fishing and natural mortality rates for the Japanese eel, two mark-recapture experiments were conducted in the lower reach of Kao-Ping River in 2005 and 2006. However, the two experiments had different release sites (1 km upstream from the fishing ground in 2005 to enhance the dispersion of the eels and in the fishing ground in 2006 for comparison), eel origins (captured and cultured), and marks applied (microchips or fin clippings). The variability in these aspects might lead to different recapture rates and subsequent bias in the estimation of the population parameters (Lebreton et al., 1992; Pledger et al., 2003; Zabel, 2005).

1.4.3. Maturation curve

Estimation of maturation curve is important in fishery management because it plays a key role in determining the spawning biomass and enables us to establish the spawner-recruit relationship and calculation of spawner per recruit (Quinn & Deriso, 1999). The maturation process of fish is influenced by many factors, but usually the age and size are the most critical one (Roff, 2002). After the growth for several years as

yellow eels, they experienced second metamorphosis to become silver eels with enlarged eyes, darkened pectoral fins, degenerated digestive tracts, and silvered or darkened belly, which are thought to be the pre-adaptation to the marine environments for spawning migration (Han et al., 2000; Tesch, 2003).

5 As the silver eels start their spawning migration into the sea, silvering is considered as the maturation in this study. The silvering of the anguillids has been known to depend mainly on size, rather than on age for many anguillids species, such as *A. anguilla* (Vøllestad, 1992), *A. rostrata* (Oliveira, 1999), *A. australis*, *A. dieffenbachii* (Jellyman, 2001), and *A. japonica* (Lin & Tzeng, *unpublished data*). In other words, eels tended to
10 become silvering when it reaches a certain length, not to a specific age. Therefore, the silvering curve related to length was used in modelling the silvering process in this study.

1.5. Evaluation of the eel fishery

15 1.5.1. Application of YPR and SPR models

It is clear that the eel fishery in Kao-Ping River needs to be evaluated. However, the lack of information on total yields, number of fishermen and gears used, and the uncertainty about the spawner-recruit relationships of the Japanese eel makes it impossible to estimate maximum sustainable yield (MSY) and corresponding fishing
20 mortality (F_{MSY}). Therefore, it is recommended to assess the fishery from life-history parameters that use per-recruit models, such as the yield per recruit (YPR) and spawner per recruit (SPR) models to elucidate whether the local population of the Japanese eel was under overfishing (Clark, 1991; Gabriel & Mace, 1999). Per-recruit models were used to examine the trade-off between capturing a large number of fish early in their life
25 span vs. capturing a smaller number of larger fish later in their life for one cohort or year-class of fish, in which the selection curve of the fishing gear is assumed to be

knife-edge (King, 1995; Quinn & Deriso, 1999). If the assumption of steady state of the fisheries is added, which indicates that the total yield in any one year from all age classes (all pseudo-cohorts) is the same as that from a single cohort over its whole life span, per-recruit models can be used for all age classes (King, 1995).

5 To assess the current state of the fishery, biological reference points are given to compare current exploitation pressure (fishing mortality rate or time at first capture) and maximum or sustainable level. Commonly used reference points suggesting the maximum yield or the most efficient use of the fishery include F_{max} , the fishing mortality at which yield per recruit is at its maximum, and $F_{0.1}$, the fishing mortality at
10 which the increase of yield per recruit is only 0.1 of the increase of yield per recruit when fishing mortality is zero (King, 1995). F_{max} and $F_{0.1}$ are regarded as limiting reference point (LRPs), rather than target reference points (TRPs) that F_{max} and $F_{0.1}$ are boundaries to constrain harvesting within safe biological limits within which the eel population can produce MSY (UN Straddling Stock Agreement, 1995). However, the
15 two LRPs derived from YPR model only reflects the mortality and weight at age in the catches and are only indicators of growth overfishing (Gabriel & Mace, 1999). To understand whether the recruitment overfishing occurred in the eel population, the situation that the fish stocks can not produce enough offspring to replace themselves (Sissenwine & Shepherd, 1987), spawner per recruit model is used. The spawner per
20 recruit related to unfished level ($\%SPR$) is an important indicator for the recruitment overfishing that it may occur when it is below 30 to 50 %, depending on the degree of compensation and species-specific life history characteristics (Sissenwine & Shepherd, 1987; Clark, 1991; Goodyear, 1993; Mace & Sissenwine, 1993; Mace, 1994; Gabriel & Mace, 1999).

25 Per-recruit models are usually used to suggest the changes in yield (or spawner) of fish resulted from the changing in fishing effort (or age at first capture). They have also

been used to assess other anguillids such as *A. anguilla* (Dekker, 2000), *A. rostrata* (Weeder & Uphoff, 2003), *A. australis* and *A. dieffenbachii* (Hoyle & Jellyman, 2002). They are relatively simple and easy to implement for fisheries with moderate information (Restrepo 1999), which is capable to be used for the assessment of the eel fishery in Kao-Ping River.

1.5.2. Risks of growth and recruitment overfishing

To sustainable use of the eel resource, it is important to prevent the occurrence of both growth and recruitment overfishing. The yellow and silver eels are traditionally exploited by fishermen using bamboo eel tubes and also by the shrimp nets introduced around 2003. The eels caught by the shrimp nets are smaller in size as compared to those by the eel tubes (Lin & Tzeng, 2008a), but the influences of the newly-introduced shrimp nets on the local population are still unclear. Consequently, the smaller eels vulnerable to the shrimp nets and the increasing use of the shrimp nets might lead to growth overfishing, in which the fishing pressure (fishing mortality rates) is so high that too many individuals are harvested with the sizes smaller than the optimum size (Haddon, 2001; Jennings et al., 2001), which can be detected when current fishing mortality rate (F_{cur}) is larger than F_{max} or $F_{0.1}$.

Meanwhile, the Japanese eels are mainly harvested as elvers (Liao, 2001; Ringuet et al., 2002) and therefore the sustainable use of the glass eels has to be included in the management of the elver fishery (Tzeng & Chang, 2001), as well as the maintenance of sufficient amount of spawner biomass. The exploitation pressure of the elvers was fairly high (Tzeng, 1984), but the impacts of eel (yellow and silver eel) fisheries on the spawner biomass, namely the biomass of silver eels, is still unclear. It is also unknown whether the current fishing level would result in recruitment overfishing, in which the

fish stock is harvested so hard that the spawner abundance is below the level at which the successive generation can replace each other (Haddon, 2001; Jennings et al., 2001), ex. below the 30 to 50 % of the unfished spawner per recruit (Sissenwine & Shepherd, 1987; Hoyle & Jellyman, 2002). Keeping sufficient amount of large spawners (silver eel) is also the major objective of the management anguillids to make the use of the eel resource sustainable, (ICES, 2005; McCarthy et al., 2008).

1.5.3. Incorporation of the uncertainty and sensitivity analysis

Consideration of uncertainty and possible sources of error has become an important part of the fishery management. Incorporation of uncertainty into the assessment models is usually required in recent decision-making process in regard to the assessment of current status of the fishery resource, as well as for short-, medium- and long-term forecasts (Patternson et al., 2001). When the fishery was modelled and examined, four kinds of uncertainty or error are identified, namely the measurement error, process error, model selection error, and operation error (Chen & Paloheimo 1998; Schnute & Richards, 2001). In modelling the fish growth, von Bertalanffy growth model is often applied without consideration of other alternative models, which might add the model selection error, resulting in inaccurate parameter estimates, underestimated standard errors, and overly optimistic confidence intervals for the parameters (Buckland *et al.*, 1997; Burnham & Anderson, 2002; Johnson & Omland, 2004; Katsanevakis & Maravelias, 2008). For estimating the vital parameters, the uncertainty in parameter estimation inevitably arises as a kind of measurement error. The uncertainty not only affects the estimation of the model parameter, i.e. current fishing mortality rate, but also influences the estimation of the biological reference points. Treating assessment as exact and ignoring the possible sources of uncertainty can lead to incorrect conclusion on the stock (Chen & Wilson, 2002; Grabowski & Chen, 2004).

1.6. Objectives

(1) Evaluation of the effects of the shrimp trap fishery on the Japanese eel population in the lower reach of Kao-Ping River. Temporal changes in size and sex compositions of the catch, as well as the catch per unit effort (CPUE) were examined to reveal possible effects.

(2) Estimation of the vital parameters, such as length-weight relationship, growth parameters, fishing, natural and total instantaneous mortality rates, and maturation (silvering) curve in relation to length of the eels. To exclude the model selection error in selecting growth models, five candidate models, namely von Bertalanffy, generalized von Bertalanffy, Gompertz, logistic, and power growth models, were used. The one fitting the observed data the best was selected in this study.

(3) Evaluation of the risks of both growth and recruitment overfishing for the eel population by YPR and SPR models. Monte Carlo simulation was conducted to simulate how the uncertainty in parameter estimation affects the estimates of key biological reference points, F_{max} and $F_{0.1}$ and %SPR. The effects of some feasible management acts, minimum and maximum legal size, on the YPR or SPR were also simulated. A sensitivity analysis was conducted to elucidate the degree and magnitude of the effects of error on parameter estimation on F_{max} , $F_{0.1}$ and %SPR and the risk of growth or recruitment overfishing. Suggestions and recommendations were proposed accordingly.

2. Materials and Methods

2.1. Characteristics of the study area.

The Kao-Ping River is the largest river in southern Taiwan with a length of approximately 171 km and the drainage area of 3256 km² (Fig. 3). The annual precipitation in the area is not uniformly distributed; it is characterized by the dry season during October to March and the rainy season during April to September, resulting in a high fluctuation of water level (Shiao et al., 2003). The low water levels during the dry season may restrict the movement of the eels between middle and lower reaches. Meanwhile, a great amount of sewage has been discharged in the middle reach and numerous obstructions are constructed between the middle and lower reaches of the river. Consequently, the connectivity between middle and lower reaches was probably poor.

The elvers are harvested by fyke nets in the river mouth during the upstream migration in winter from November to February, but the fishing activities for elvers peaked mainly during late December to January. Yellow and silver eels are presently harvested by fishermen using shrimp nets, introduced initially for sand shrimps in 2003. However, due to its high efficiency in catching both juvenile and adult eels, the shrimp nets have become the most popular fishing gear for catching eels. In the study area, both eel tubes and shrimp nets were deployed in a restricted area of the lower reach with a salinity of 10 ~ 32 ‰ (Fig. 3). The mean annual bottom water temperature at the river mouth was around 25.9°C and fluctuated around 21°C in winter (December to March) and to ~23-24°C in spring (March to May). It was highest (~ 28°C) in midsummer (July), relatively stable at 25 ~ 26°C in late summer and autumn (August to November), and then decreased in winter (Fig. 4, redraw from Chen et al., 2007).

2.2. Sampling design

2.2.1. Collection of wild eels

Wild Japanese eels were collected by cooperative fishermen in 1998 to 2007 and the
5 catch data were summarized and maintained by previous fellows in our laboratory (i.e.
Chang, C.W., Cheng, J.H., Han, Y.S., Shiao, J.C... etc.). Most of the eels were caught by
eel tubes during 1998 to 2005, but by shrimp nets during 2005 to 2007 (Lin & Tzeng,
2008a). The hit of Typhoon Mindulle in July, 2004 caused a large amount of cultured
eels escaping into the sampling site, resulting in substantial changes in sex ratios of the
10 catch in 2004 and 2005 (Chu et al., 2006; Lin & Tzeng, 2008a). Therefore, the catch
data of the eels in 2004 and 2005 were excluded from validation of the otolith annuli
and estimation of the growth parameters to prevent possible bias due to the cultured eels.
The total length and weight of each eel were measured to nearest 1 mm and 0.1g,
respectively. The determination of sex was based on gross inspection of the gonads,
15 while the developmental stages (yellow or silver eels) were determined by the body
color, enlarged eyes, and blackened pectoral fins (Han et al., 2000), which were further
confirmed by Dr. Han, Y.S.

2.2.2. Collection of cultured eels

20 Cultured eels were non-selectively collected for validation of otolith annuli and
mark-recapture experiment from eel culturing ponds in Donggang Town (22N° 28',
120E° 26', Fig. 3). For validation of otolith annuli, the cultured eels used had been
reared from elvers since the winter of 2004 to 2005, and were at approximately 2 years
old after the elver stage. They were reared in 1.5 m deep water outdoor ponds. The
25 change in water temperature in the ponds was closely related to that in air temperature
because no temperature controls were applied in the ponds. The mean seasonal air

temperature in Donggang Town during 2005 to 2007 ranged from 18.5 ~ 20 °C in winter (December to February) and 21 ~ 26°C in spring (March to May), reached the highest of about 28 °C in summer (June to August) and decreased to 23 ~ 27°C in autumn (September to November, Fig. 4, Central Weather Bureau, Taiwan). The cultured eels were fed with commercial feed twice a day and thus a higher growth rate was expected. According to the eel farm owner, the sizes of the elvers were about 50 mm and reached to marketable sizes of about 350 mm in 18 to 24 months.

2.2.3. Summary information of the eels collected

The information of the eels collected, such as sample sizes, mean (\pm SD) total lengths and weights, ages of the eels by eel origins, sexes, developmental stages, and different uses are shown in Table. 1. A total of 3,123 eels were caught from the wild, including 1996 females, 624 males and 502 sexually undifferentiated eels. They were used for evaluation of fishing gears (eel tubes vs. shrimp nets), in which the escaped cultured eels (Chu et al., 2006) were not excluded. To estimate parameters of the length-weight relationship and maturation curves, a total of 1583 females including 147 silver and 1436 yellow eels, 146 males including 51 silver and 97 yellow eels and 575 sexually undifferentiated eels during 1998 to 2007 were selected, in which the escaped cultured eels were excluded according to Chu et al. (2006). Then, 52 females including 45 silver and 7 yellow eels, 33 males including 14 silver and 19 yellow eels, and 28 undifferentiated yellow eels from the wild, as well as 3 female and 28 male cultured eels were randomly selected for validation of periodicity of otolith annuli, in which wild eels were caught during 1999 to 2003 and the cultured eels in 2007. To estimate growth parameters and select the growth models fitting the data the best, 63 wild females (55 silver and 8 yellow eels) and 57 wild males (37 silver and 20 yellow eels) were randomly selected (Table 1). The total lengths and weight of the wild eels were

log-transformed and a two-way analysis of variance (two-way ANOVA) was conducted to compare the differences between sexes, developmental stages and the sex-stage interaction. A Tukey's multiple comparison was used to find the pair-wise differences.

5 2.3. Fishing gear, fishing effort and catch per unit effort

A shrimp net was approximately 7.2m in length and composed of 25 netted cells with a mesh size of 1 cm (Fig. 5a and b). The eel tubes were made of bamboo with a mean length of 1.06 m and radius of 6.2 cm. The ends of the tube were closed by a net with a mesh size of 1.2 cm (Fig. 6a and b). A set of shrimp nets was usually consisted of 10 20 ~ 50 nets and was put along the river shore with a buoy and anchor at the first net (Fig. 7). In general, several sets were set simultaneously by different fishermen in the lower reach of the river. Eel tubes were fixed separately into the river perpendicular to the shore with a space 5 to 10 m. Both gears were set at depths less than 1 m.

Catch and fishing effort data, including number of gear units, days of operation, and 15 number and weight of eels caught, were recorded by questionnaires from August 2005 to July 2006 for shrimp nets and from August to October 2005 for eel tubes. The mean number of gears used per fisherman per day was estimated to be 50 ~ 66 for shrimp nets and 88 for eel tubes. The fishing of eels depended highly on weather, and the mean number of operation days per month varied between 12 and 31 days (Table 2). Both 20 shrimp nets and eel tubes were set in the afternoon and retrieved in the next morning, so the unit of fishing time was represented by day.

The monthly catch per unit effort (CPUE) was calculated as:

$$\text{CPUE (g} \times \text{gear number}^{-1} \times \text{fisherman}^{-1}) = \text{Total weight of eels caught a month (g)} \times (\text{number of gears})^{-1} \times (\text{number of fishermen})^{-1}$$

25 During the months when several CPUE data sets from different fishermen were available the overall monthly CPUE was estimated by averaging the CPUE from

individual fisherman.

Length compositions of the eels among years and between two gears were tested by nonparametric Kolomogrov-Smirnov test. Because the shrimp nets and eel tubes have only one mesh size, the selectivity curves of each gear were not examined. Instead, the selectivity curve in relation to eel length was represented by the empirical cumulative length distribution and the median was used an indicator of 50 % length at capture. The 2.5 ~ 97.5 percentile interval of the cumulative length distribution was used to estimate the length of eels comprising 95 % of the catch.

10

2.4. Estimation of vital parameters

2.4.1. Length-weight relationship:

The relationship between total lengths (TL) and total weights (TW) of the eels was assumed to be an allometric relationship and fitted by a multiplicative model as

$$15 \quad TW = a(TL)^b e^\varepsilon$$

where a, b are constants, and ε is the random error term which is assumed to be distributed normally with mean zero and variance σ^2 .

By taking logarithmic transformation of both sides, the length-weight relationship becomes:

$$20 \quad \log_e(TW) = \log_e(a) + b \times \log_e(TL) + \varepsilon$$

The estimates for $\log_e(a)$ and b, \hat{A} and \hat{b} , were estimated by least squares linear regression. \hat{b} could be directly used because it is an unbiased estimator for b, and a nearly unbiased estimator of a given by:

$$\hat{a} = \exp(\hat{A} + 0.5 \times \text{MSE})$$

25 where MSE is the mean sum of square errors obtained from the log-transformed linear regression between total weights and lengths (Sen & Srivastava, 1990; Hayes et al.,

1995).

2.4.2. Validation of otolith annuli and calculation of lengths-at-age

2.4.2.1 Otolith preparation

5 Each of sagittal otoliths were removed, cleaned, dried in the air, ground and polished until the primordium was exposed. The polished otolith was then etched with 5% EDTA for 2 to 3 min to enhance the visibility of the annulus. The digital picture of otolith was taken under the optic microscope with a reflected light and the age of the eel was estimated from the counts of annuli (Tzeng et al., 1994; 2002). The otolith and
10 annular radii along the longest axis from the primordium to each annulus and to the otolith edge were measured to the nearest 1 μm using the image processing software (SigmaScan Pro 5.0, SPSS Inc.).

2.4.2.2. Calculation of marginal increment ratio of the otolith of wild eels

15 The marginal increment ratio (MIR) of the otoliths of the wild eels was calculated following Lessa et al. (2006):

$$MIR = (R_C - R_L) \times (R_L - R_{L-1})^{-1}$$

where R_C , R_L and R_{L-1} are, respectively, the otolith radius from the primordium to the edge, to the last annulus and to the annulus next to the last one. The mean *MIR* in each
20 month was plotted to determine whether otolith annuli were deposited annually.

2.4.2.3. Back-calculation of lengths-at-age

The length-at-age at age i (L_{Bi}) was back-calculated using otolith radius at each age, in which two approaches, regression and proportion methods, were commonly used.
25 The regression method was not used in this study because of their low coefficient of determination ($R^2 = 0.42$ for log10-transformed data) compared to 0.98 in Jessop et al

(2004), which might be due to the variation in grinding planes among otoliths. The proportional method was suggested for incorporation of information on individual length and radii (Gutreuter, 1987). Therefore, the proportional method, Dahl-Lea method (Francis, 1990), was used to calculate the lengths-at-age as follow:

5
$$L_{Bi} = L_c \times (R_i / R_c)$$

where L_c is the length at capture, R_i is the radius from the primordium to the i^{th} annulus and R_c is the radius from the primordium to the otolith edge. Additional data compiled from Tzeng et al. (2002), in which the eels from 1998 to 2003 were added to increase the sample size.

10

2.4.3. Selection of the best growth models fitting the lengths-at-age data

2.4.3.1. Candidate growth models

Five candidate growth models were examined, namely the von Bertalanffy, generalized von Bertalanffy, Gompertz, logistic and power models. Different relationships between the instantaneous growth rate (dL/dt) and fish size are formulated in the models, with details given by Quinn & Deriso (1999).

The von Bertalanffy growth model is one of the most commonly used growth models in fisheries studies. It assumes that the growth rate linearly decreases with fish length:

20
$$\frac{dL_t}{dt} = K_1(L_\infty - L_t)$$

The solution of this differential equation is the form most used in literature as follow:

$$L_t = L_\infty [1 - e^{-K_1(t-t_0)}]$$

where L_t is the length at age t , K_1 is the von Bertalanffy growth coefficient, L_∞ is the asymptotic length, and t_0 is the theoretical age at which length is zero. L_∞ has the same biological meaning in all models described.

25

Von Bertalanffy model assumes that the instantaneous growth rate is a monotonic decreasing function with length. However, the growth of fish is sometimes sigmoidal (S-shaped). To increase model flexibility and let the shape become sigmoidal, a dimensionless factor ρ is added as the generalized von Bertalanffy growth model:

5
$$L_t = L_\infty [1 - e^{-K_1(t-t_0)}]^\rho$$

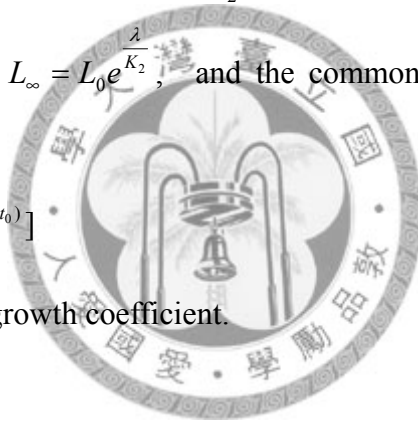
Gompertz growth model is expressed as an alternative sigmoidal one that the instantaneous growth rate is assumed to decrease exponentially with length:

$$\frac{dL_t}{dt} = \lambda e^{-K_2 L_t} \text{ with solution } L_t = L_0 \exp\left[\frac{\lambda}{K_2}(1 - e^{-K_2 t})\right].$$

10 As $t \rightarrow \infty, L_t \rightarrow L_\infty$, then $L_\infty = L_0 e^{\frac{\lambda}{K_2}}$, and the common form of Gompertz is thus derived :

$$L_t = L_\infty \exp\left[\frac{-1}{K_2} e^{-K_2(t-t_0)}\right]$$

where K_2 is the Gompertz growth coefficient.



15 The logistic growth model is another sigmoidal function and is often used in describing the population growth. The instantaneous growth rate is assumed to change according to a logistic relationship:

$$\frac{dL_t}{dt} = K_3 \times L_t \left(1 - \frac{L_t}{L_\infty}\right) \text{ with solution:}$$

$$L_t = L_\infty [1 + e^{-K_3(t-t_3)}]^{-1}$$

20 where K_3 is the logistic growth coefficient.

The growth of individual is assumed to be asymptotic, i.e. having an upper limit in length or size. However in some special cases, the growth may be non-asymptotic and thus Katsanevakis & Maravelias (2008) suggested including one non-asymptotic growth

model in the set of candidate models. Therefore, the power growth model s used in this study:

$$L_t = b_0 + b_1 t^{b_2}$$

where b_0 , b_1 and b_2 are parameters. Linear growth model is a special case of power model when b_2 equals to zero.

2.4.3.2. Estimation of growth parameters

A multiplicative error structure was assumed for the models because the residuals increased with increasing length, according to the residual plots from a preliminary examination (Quinn & Deriso, 1999). It is represented as:

$$L_t = f(t, \boldsymbol{\theta}) e^\varepsilon$$

where $f(t, \boldsymbol{\theta})$ is the growth model listed above, $\boldsymbol{\theta}$ is the parameter vector, ε is assumed to be normally distributed with mean zero and variance σ^2 . Models were fitted by nonlinear least squares using the Gauss-Newton algorithm. Fitting successfully converged in all models within a satisfactorily small number of iterations (not more than 10 iterations).

2.4.3.3. Model selection and averaging using information theory

In addition to commonly used hypothesis testing procedure for comparing different models, the model selection process based on information theory was an alternative to select the best model fitting the data from the other candidate models, in which the uncertainty in model selection was considered (Buckland *et al.*, 1997; Burnham & Anderson, 2002; Johnson & Omland, 2004). Two criteria were used: Akaike information criterion corrected for sample size (AIC_c) and Bayesian information criterion (BIC). The values of AIC_c and BIC of the model j ($AIC_{c,j}$ and BIC_j) were used,

and were calculated from the following formula:

$$AIC_{c,j} = [-2\log(L) + 2k] + \frac{2k(k+1)}{(n-k-1)}$$

$$BIC_{c,j} = -2\log(L) + k \log(n)$$

where L is the maximized likelihood value for model j , k is the number of
5 parameters, and n is the sample size.

AIC (or AIC_c) and BIC differ in concepts and believes in determining the “truth” or
the “true” model. Under AIC, the truth is believed high- dimensional that requires many
parameters to describe it. Consequent, models with more parameters tend to be selected
by AIC as sample size increases. On the other hand, under the BIC the truth is
10 considered to be dimension consistent or in low-dimensional. Therefore, the model
selected by BIC is not influenced by sample size. However, it does not imply that AIC is
inferior to BIC, but rather reflects different philosophies about the truth (Buckland *et al.*,
1997; Burnham & Anderson, 2002). Because the dimension (number of parameters) did
not differ substantially among candidate growth models, the results of model selection
15 using AIC_c or BIC were expected to be the same. Consequently, only AIC_c was used in
selecting the best growth model to describe the eel growth. On the other hand, the
dimension differed considerably among candidate models, indicating different effects of
origins and marks on the estimation of instantaneous fishing and natural mortality rates.
Therefore, the best model selected by AIC_c and BIC might be different (Burnham &
20 Anderson, 2002; Johnson & Omland, 2004). Therefore, both AIC_c and BIC were
applied in the modeling of origin and mark effects on the estimation of mortality rates.

The model with the smallest value ($AIC_{c,min}$; BIC_{min}) was selected as the best model
among the models tested with the given data. The AIC_c (or BIC) differences, $\Delta_j =$
 $AIC_{c,j} - AIC_{c,min}$ (or $BIC_j - BIC_{min}$) were computed for all candidate models. According

to Burnham & Anderson (2002), models with $\Delta_j > 10$ have essentially no support and can be omitted from further consideration, models with $\Delta_j < 2$ have substantial support, and models with $4 < \Delta_j < 7$ have considerably less support. To quantify the plausibility of each model given the data, the Akaike weight (w_j) for each model j was calculated as

$$w_j = \frac{e^{-\Delta_j/2}}{\sum_{j=1}^M e^{-\Delta_j/2}}$$

where M = number of the alternative models, w_j is interpreted as the weight of evidence in favor of model j being the actual best model among the models tested and given the observed data.

A multi-model inference approach was applied to estimate the model-averaged variance $\bar{\sigma}^2$ ($\bar{\sigma}^2$) and growth model $\bar{f}(\bar{t}, \hat{\theta})$ for the Japanese eel, which is equivalent to calculate the weighted average of the variance of the growth models and the growth model under estimated parameters $\hat{\theta}$ using w_j as weights:

$$\bar{\sigma}^2 = \sum_{j=1}^M w_j \hat{\sigma}_j^2 = \sum_{j=1}^M w_j MSE_j \quad \text{and} \quad \bar{f}(t, \hat{\theta}) = \sum_{j=1}^M w_j f(t, \hat{\theta}_j)_j$$

2.4.4. Mortality rates estimated from mark-recapture experiments

2.4.4.1. Marking, releasing, and recapturing of the eel

After anesthetized by 2-phenoxyethanol, the total length (TL) and weight (TW) of the eels were measured to the nearest 0.1 cm and 1g prior to marking. Wild and cultured eels of size larger than 30 cm were randomly selected and tagged with a microchip (MUSICC Chip™ identification system, AVID Inc., California, USA). The microchip was approximately 15 mm in length and 3 mm in radius with a unique code. The eels of sizes less than 30 cm were too small to insert the microchips. A microchip was inserted

into the dorsal musculature below the dorsal fin by the injector (Simon & Dörner, 2005). After insertion, the marked eel was checked immediately with the multimode reader (Power Track IV, AVID Inc.). If the code failed to be recognized or the code was not read correctly, the microchip was discarded and a new one was used to ensure the readability of the microchip.

The remaining wild eels were marked by pectoral fin clipping (P-FC) while the remaining cultured eels were marked by caudal fin clipping (C-FC) that the fins were clipped from the half using surgical scissors. Different types of clipping were applied to distinguish different origins and years. The left or right pectoral fins of wild eels were clipped to represent 2005 and 2006 experiment, while the apex or the lower regions of the caudal fins was clipped for the cultured eels to represent 2005 and 2006 experiment, respectively. After insertion of microchips or fin clipping, the eels recuperated in the ponds for 2 days to ensure no loss of microchip or death due to marking. Therefore, the instantaneous death rate due to marking and the instantaneous tag loss rate were negligible.

The marked eels were released approximately 1 km upstream of the fishing ground on September 28, 2005 (Fig. 3). To compare the effects of different release sites, marked eels were again released in the fishing ground on August 15, 2006 (Fig. 3). After release, eels were continuously collected from the fishing ground by 3 cooperative fishermen. All eels caught were anesthetized by ice, transferred to the Donggang laboratory, their total lengths and weights were measured and the presence of marks (microchips or clipped fins) was identified.

2.4.4.2. Analysis of the mark-recapture data

The recapture rates, defined as total number of eels recaptured divided by total eels released, were examined first between eel origins and marks applied, and then the

mortality rates estimated, as suggested by Lebreton et al. (1992). The overall recapture rate of eels released at the upstream site in 2005 (2.65 %) was much smaller than that for eels released at the fishing ground (56.78 %, test of homogeneity, $\chi^2 = 513$, $p < 0.0001$), suggesting the amount of information contained in the recapture sample from the upstream site was much less than that for the sample in the fishing ground (Burnham et al., 1995). The data from the two sites were examined separately.

2.4.4.2.1. Comparison of recapture data between origins and marks

The homogeneity in recapture rates between eels among different categories was tested by Fisher's exact test for the 2005 release (because of low recapture rate that resulted in an expected value < 5 , Zar, 1999) and by chi-square for the 2006 experiment. First, the recapture rates of the eels of different marks were tested separately in wild (P-FC vs. CHIP) and cultured eels (C-FC vs. CHIP). If the differences were not significant, the eels of different marks were pooled and the recapture rates between wild and cultured eels were then tested. Moreover, the effects of origins on the recaptures were probably confounded by the eel length at release because that of cultured eels was larger than wild eels. Hence by assuming the recapture as a binomial process, the effects of origins and length at release on the recaptures of CHIP eels (only in 2006 because of small recapture of CHIP eels in 2005) were examined by logistic regression (Dodson, 2002). Then, the maximum likelihood estimates of recapture rates were calculated using profile likelihood (Lebreton, et al., 1992; Hilborn & Mangel, 1997).

2.4.4.2.2. Estimation of mortality rates using maximum likelihood

After release, eels were continuously collected without re-release to the fishing ground and no eels released in 2005 were recaptured in 2006 (fishing for eels continued until present). Therefore, open population methods with single-release data were

applicable, in which the mortality, survival or exploitation rates are of interest (Seber, 1982). These methods are based on the idea of two competing risks, that fish were lost due either to fishing or natural causes. Let N = number of fish tagged and released at the same time, n = number of fish recaptured, t_i = known recapture time for recaptured fish i , m = combination constant = $N!/n!(N-n)!$, T = the end-point of the experiment, which is defined as the time of last recapture, F = constant fishing mortality rate, M = constant natural mortality and $Z = F + M$. Therefore, the likelihood function (L) for the experiment given the recapture data was constructed (Gulland, 1955; Paulik, 1963; Hearn et al., 1987; Farebrother, 1988; Leigh, 1988):

$$L = m \left[1 - \frac{F}{Z} (1 - e^{-ZT}) \right]^{N-n} F^n e^{-Z \sum_{i=1}^n t_i}$$

Methods with single release data were classified into two approaches: (1) Completed experiment, which indicated that marked fish not caught by fishing were all lost due to natural mortality (or implicitly due to tag-associated mortality and emigration). In other words, the study period from release to last recapture of the marked eels (T) was sufficiently large that the term e^{-ZT} can be ignored. It also implied that no live fish remained in the population at the end of the experiment, and as a result above likelihood function could be reduced. The maximum likelihood estimates of F and M were calculated by maximizing the likelihood function. (2) Uncompleted experiment, e.g. the marked fish still remained and was not all lost due to natural mortalities. It implied that the term e^{-ZT} could not be ignored. By using survival of the eel (S) = e^{-Z} and $\mu = (F/Z)(1 - e^{-ZT})$, and the likelihood function was re-parameterized as:

$$L = m(1 - \mu)^{N-n} \mu^n [-\ln(S)/(1 - S^T)]^n S^{\sum_{i=1}^n t_i}$$

The closed form maximum likelihood estimate of μ is:

$$\hat{\mu} = n / N,$$

but \hat{S} has to be estimated by solving (in R) the equation:

$$\frac{-1}{\ln(\hat{S})} - \frac{\hat{S}^T}{1 - \hat{S}^T} = \frac{(\sum_{i=1}^n t_i) / n}{T}$$

5 Once $\hat{\mu}$ and \hat{S} were calculated, estimates of F and M were obtained by

$$\hat{F} = \frac{-\hat{\mu} \ln(\hat{S})}{(1 - \hat{S}^T)} \quad \text{and} \quad \hat{M} = \ln(\hat{S}) - \hat{F}.$$

F and M values were estimated for eels of different origins and marks as well as the corresponding maximized likelihood values were calculated. Once the best model was
10 determined by the model selection process using AIC_c or BIC, the 95 % confidence intervals of F and M (completed experiment) and S and μ (uncompleted experiment) were calculated by profile likelihood.

15 **2.4.4.2.3. Comparison of mortality rates between origins and marks**

A set of candidate models about possible effects on the mortality rates were constructed. Then the model selection process was applied to find which model fitting the data the best, a process widely used for mark-recapture studies (Lebreton et al., 1992; Buckland et al., 1997; Anderson et al., 2000; Johnson & Omland, 2004). Because the
20 number of parameters in the candidate models differed substantially that the selection of best model might be influenced by model dimension, not only Akaike information criterion corrected for sample size ($AIC_{c,j}$), but also Bayesian information criterion

(BIC_j) of the model j were calculated from the likelihood values. Similarly, the model with least AIC_c or BIC was considered as the best performing model given the data. The corresponding weights based on two criterions $W_{(AIC_c/BIC),j}$ were then calculated and used to weight each model j containing different effects.

5

2.4.5. Maturation curve in relation to eel length

The eels at silver eel stage were near sexually maturing in preparation for spawning in the ocean, and thus, the maturation of the eel was referred to the silver eel stage throughout this study. Three assumptions were made before modelling the eel silvering
 10 in relation to eel length: (1) the silvering process followed a binomial process, (2) the parameters for the maturation curves were the temporally stable during the period from 1999 to 2007, (3) the parameters were not influenced by different gears, and (4) the escapement of cultured eels during 2004 did not influence the maturation curve of the wild eels. Meanwhile, the silvering of the Japanese eels was significantly different
 15 between sexes that the silver females were generally larger and older (Han et al., 2000; 2000) and thus the silvering process was fitted to females and males separately.

According to assumption (1), the silvering process of the eels was fitted by the logistic model:

$$S[L(t)] = \frac{e^{\Delta slope \times \beta_0 + \Delta slope \times \beta_1 [L(t) - \Delta L_{50}]}}{[1 + e^{\Delta slope \times \beta_0 + \Delta slope \times \beta_1 [L(t) - \Delta L_{50}]}]}$$

20 where $S[L(t)]$ is the probability of being silver eels given length L at age t , and β_0 and β_1 are parameters. ΔL_{50} and $\Delta slope$ indicated the arbitrary scalars representing the changes in the location and the slope of the maturation curve. Changes in ΔL_{50} indicated a parallel shift in the maturation curve that the length-at-50%-maturity was the only parameter changed (Fig. 8a). On the other hand, changes in $\Delta slope$

influenced the width of the range between the onset and end of the silvering process as well as the slope (or the maturation speed in relation to eel length) in this range, while the length-at-50%-maturity remained unchanged (Fig. 8b). The parameters in the maturation curves were estimated using maximum likelihood method in which ΔL_{50} at 5 0 and $\Delta slope$ was set at 1. Differences in maturation curves between sexes were evaluated by likelihood ratio test (Quinn & Deriso, 1999).

2.5. Evaluation of the eel fisheries using YPR and SPR models

2.5.1. Model describing the population dynamics of the eel

10 The population dynamics of the eels in YPR and SPR models were regulated by recruitment, growth, fishing and natural mortality, and maturation (King, 1995). The recruitment of the eel in the study area was defined as elvers recruiting to the estuaries and the growth model was selected by information theory approach from several candidate models. The maturation of the eels was described by logistic curve, and the 15 mortality rates determined the eel population size since recruit, which was described by the exponential curve:

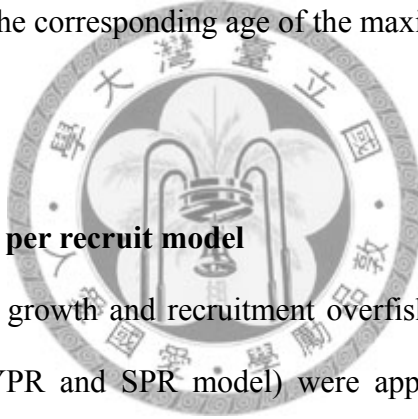
$$N(t) = \begin{cases} N_r, & t = t_r \\ N_r e^{-M(t-t_r)}, & t_r < t < t_c \\ N(t_c) e^{-M(tc-t_r)-(M+F)(t-t_c)}, & t_c \leq t \leq t_{\max} \end{cases},$$

where $N(t)$ is the population size at time t , F and M are the instantaneous fishing and natural mortality rates, respectively. Estimate of F was obtained from mark-recapture 20 experiment including two fishermen, and a totally four fishermen were operating in the study area, indicating the true fishing effort might be twice as that in the mark-recapture experiment. Therefore, by assuming constant catchability among fishermen, F_{cur} was doubled as the value estimated from mark-recapture experiment. t_r is the age at recruitment, which was set as 0.55 years, the mean age of elvers at recruitment in the

Kao-Ping River (Cheng & Tzeng., 1996). t_c was the age at capture, the corresponding age of length 200 mm (Lin & Tzeng, 2008a, a knife-edge selection for the shrimp net was assumed). When minimum legal sizes were set, t_c was replaced by t_{Lmin} , the corresponding age of the minimum legal size calculated from selected growth model (i.e. von Bertalanffy growth model). t_{max} was maximum age of capture, which was assumed as 15 years. When maximum legal sizes were set, the population size at time t becomes:

$$N(t) = \begin{cases} N_r, t = t_r \\ N_r e^{-M(t-t_r)}, t_r < t < t_c \\ N(t_c) e^{-M(tc-tr)-(M+F)(t-t_c)}, t_c \leq t \leq t_{Lmax} \\ N(t_{Lmax}) e^{-M(t-t_{Lmax})}, t_{Lmax} \leq t < t_{max} \end{cases}$$

t_{max} was replaced by t_{Lmax} , the corresponding age of the maximum legal size.



2.5.2. Yield and spawner per recruit model

To evaluate the risk of growth and recruitment overfishing, the yield and spawner per recruitment models (YPR and SPR model) were applied according to Quinn & Deriso (1999):

$$YPR = \int_{t_r}^{t_{max}} F(u)N(u)W(u)du$$

$$= e^{-M(t_c-t_r)} F \int_{t_c}^{t_{max}} e^{-zu} a \{L_{\infty} [1 - e^{-K(u-t_0)}]\}^b du \quad \text{and}$$

$$SPR = \int_{t_r}^{t_{max}} \{N(u)W(u)S[L(u)]\}du$$

$$= \int_{t_r}^{t_{max}} e^{-M(u-t_r)} a \{L_{\infty} [1 - e^{-K(u-t_0)}]\} \frac{1}{(1 + e^{\beta_0 + \beta_1 L(u)})} du$$

$$+ e^{-M(t_c-t_r)} \int_{t_c}^{t_{max}} e^{-Z(u-t_c)} a \{L_{\infty} [1 - e^{-K(u-t_0)}]\} \frac{1}{(1 + e^{\beta_0 + \beta_1 L(u)})} du$$

$$+ e^{-M(t_c-t_r)} e^{-Z(t_{Lmax}-t_r)} \int_{t_{Lmax}}^{t_{max}} e^{-M(u-t_{Lmax})} a \{L_{\infty} [1 - e^{-K(u-t_0)}]\} \frac{1}{(1 + e^{\beta_0 + \beta_1 L(u)})} du$$

where t_{Lmax} is the corresponding age of the maximum legal size.

YPR and SPR values were calculated numerically using *integrate* procedure incorporated in R (version 2.8.1, Owen, 2006). F_{max} and $F_{0.1}$ were derived from YPR model, which represented the F value at which the YPR was maximal (at YPR_{max}) and the F value at which the slope of YPR curve was one-tenth of that when F equals to zero. The two biological reference points (BRPs) were calculated from solving the two formulae numerically by built-in function in R:

$$\left. \frac{\partial YPR}{\partial F} \right|_{F=F_{max}} = 0$$

$$\left. \frac{\partial YPR}{\partial F} \right|_{F=F_{0.1}} = 0.1 \left. \frac{\partial YPR}{\partial F} \right|_{F=0}$$

SPR under current fishing mortality (F_{cur}) and without fishing mortality was denoted by $SPR_{F_{cur}}$ and SPR_0 and their values were calculated from SPR model. The relative SPR ($\%SPR$) is defined as the SPR value under divided by the SPR value without exploitation ($F = 0$). It was calculated from:

$$\%SPR = 100 \times \frac{SPR|_{F_{cur}}}{SPR|_{F=0}}$$

Two biological reference points, i.e. $F_{40\%}$ and $F_{50\%}$ were derived from SPR model, which correspond the F values resulting in $\%SPR$ equals 40 and 50, respectively. Threshold level of $\%SPR$ was set at 50 % of the unfished level for *A. japonica* due to its catadromous life history (Hoyle & Jellyman, 2002), and the commonly used level of 40 % (Clark, 2002) was set as the limiting level. Consequently, F_{max} and $F_{40\%}$ were used as the limit reference point, while $F_{0.1}$ and $F_{50\%}$ were as the threshold reference points indicating growth and recruitment overfishing, respectively (Gabriel & Mace, 1999; King, 2007).

To evaluate the effects of different minimum and maximum legal sizes on YPR and SPR, the minimum and maximum legal lengths (L_{min} and L_{max}), which were not

enforced for the eel fishery examined, were incorporated in YPR and SPR analyses. L_{min} increased from current unregulated level of 200 mm to 700 mm for both sexes, in which 200 mm corresponded to the current minimum catching length of the eels by the shrimp nets (Lin & Tzeng, 2008). L_{max} decreased from 800 to 400 mm in females and 700 to 300 mm in males, respectively. Values of BRPs, i.e. F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$ and key YPR and SPR values, i.e. YPR_{max} , $SPR_{F_{cur}}$, SPR_0 and $\%SPR$ were calculated under three minimum legal sizes (L_{min}), 200, 300, and 400 mm and under the maximum legal sizes were set at 800, 700 and 600 mm for females and 700, 600 and 500 mm for the males, respectively.

10

2.5.3. Incorporation of uncertainties into the YPR and SPR models

The uncertainty in parameter estimation was incorporated into the YPR and SPR models using Monte Carlo simulation following Chen & Wilson (2002) and Grabowski & Chen (2004), in which 10,000 simulations were conducted. Two kinds of random errors, additive (δ) and multiplicative errors (ε), were generated from assumed probability functions. The additive errors were directly added to the models, while the multiplicative errors were exponential transformed and multiplied to the models.

15

The multiplicative error (ε_{LW}) entered into the length-weight relationship as:

$$W^s(t) = aL^s(t)^b e^{\varepsilon_{LW}}$$

20

where $W^s(t)$ and $L^s(t)$ are simulated total weight and length at age t , a and, b are parameters, ε_{LW} is the multiplicative error term assumed to follow a normal distribution, i.e. $\varepsilon_{LW} \sim N(0, \sigma_{LW}^2)$.

The error in growth model was also assumed to be multiplicative:

25

$$L^s(t) = L_{\infty} [1 - e^{-K(t-t_0)}] e^{\varepsilon_{GR}}$$

where ε_{GR} is the multiplicative error in growth model.

The errors in instantaneous natural mortality rates (M) and maturation parameters (β_0 and β_1) were assumed to be additive:

$$M^s = M + \delta_M,$$

5
$$\beta_0 = \beta_0 + \delta_{\beta_0}, \text{ and } \beta_1 = \beta_1 + \delta_{\beta_1}$$

where M^s is the simulated value of M . δ_M , δ_{β_0} and δ_{β_1} are the additive errors in natural mortality, and maturation parameters, β_0 and β_1 , respectively.

To cope with the correlation between natural mortality and growth (Pauly, 1980) and between maturation parameters β_0 and β_1 , a multivariate normal distribution was used to

10 simulate the random errors for these correlated processes:

$$\begin{bmatrix} \varepsilon_{GR} \\ \delta_M \end{bmatrix} \sim \mathbf{N}_2(\mathbf{0}, \Sigma_{GR,M}), \text{ where } \Sigma_{GR,M} = \begin{bmatrix} \sigma_{GR}^2 & \rho_{GR,M} \sigma_{GR} \sigma_M \\ \rho_{GR,M} \sigma_{GR} \sigma_M & \sigma_M^2 \end{bmatrix} \text{ and}$$

$$\begin{bmatrix} \delta_{\beta_0} \\ \delta_{\beta_1} \end{bmatrix} \sim \mathbf{N}_2(\mathbf{0}, \Sigma_{\beta_0,\beta_1}), \text{ where } \Sigma_{\beta_0,\beta_1} = \begin{bmatrix} \sigma_{\beta_0}^2 & \rho_{\beta_0,\beta_1} \sigma_{\beta_0} \sigma_{\beta_1} \\ \rho_{\beta_0,\beta_1} \sigma_{\beta_0} \sigma_{\beta_1} & \sigma_{\beta_1}^2 \end{bmatrix}$$

where $\rho_{GR,M}$ was the correlation between growth and natural mortality, which is assumed to be 0.8 according to Pauly (1980). ρ_{β_0,β_1} is the correlation between β_0 and β_1 , which is

15 calculated directly from the asymptotic covariance matrix in estimation of maturation curve.

For better plasticity and prevention of unrealistic (negative) values, the distribution of F was assumed to be gamma distribution:

$$F^s \sim \Gamma(s_1, s_2)$$

20 where $s_1 = \hat{F}^2 / \sigma_F^2$ and $s_2 = \sigma_F^2 / \hat{F}$ are parameters of the gamma distribution. To consider the information about the variability in F due to changes in fishing effort, constant catchability of shrimp nets and independence between estimation of fishing

mortality and the use of fishing gear were first assumed. Then the uncertainty in estimation of fishing mortality as well as the variation in the number of shrimp nets used per fishermen (Lin & Tzeng, 2008a) was also incorporated into the model by: $\sigma_F^2 = (CV_{Est}^2 + CV_{Gear}^2)\hat{F}^2$

5 where CV_{Est}^2 is the coefficient of variation from estimation of F from mark-recapture data, and CV_{Gear}^2 is the coefficient of variation from number of fishing gears used during study period. Estimated values and corresponding variations in the estimated parameters are listed in Table 3, in which the only mortality rate for wild eels was used.

10 **2.5.4. Risk of growth and recruitment overfishing**

F_{max} , at which the yield per recruit is at maximal, was regarded as the limit reference point and $F_{0.1}$, at which the rate of increase in yield per recruit is 10 % of that when $F = 0$, was used as the threshold reference point for growth overfishing. Thus the growth overfishing is defined as the situation when current fishing mortality (F_{cur}) is larger than
15 F_{max} . $F_{0.1}$ is considered as a more conservative measure and a threshold of growth overfishing that if F_{cur} lies between $F_{0.1}$ and F_{max} , the growth overfishing is likely or near to occur.

Threshold level of spawner-biomass per recruit was set at 50 % of the unfished level for *A. japonica* due to its catadromous life history (Hoyle & Jellyman, 2002), and a
20 reduction in SRP of 50 % is found resulting in higher mean recruitment than threshold in examined populations (Mace, 1994). The commonly used level of 40 % (Clark, 2002) was set as the limiting level. Thus, $F_{40\%}$ and $F_{50\%}$ was the limit and threshold reference point for recruitment overfishing (Gabriel & Mace, 1999; King, 2007) Then the risks of growth and recruitment overfishing were estimated by calculating the one-tailed
25 probability of the distribution of F_{cur} in relation to the distribution of the limit or

threshold biological reference points (Fig. 9, Chen & Wilson, 2002).

2.5.5. Sensitivity analysis

Because a certain degree of uncertainty might still exist, e.g. natural variability, a sensitivity analysis was conducted to evaluate the effects of misspecification or the stochastic variation of some key parameters, such as growth coefficient, fishing and natural rates, ΔL_{50} and $\Delta slope$ on the estimate and standard deviation of F_{max} , F_{cur} , % SPR , risks of growth and recruitment overfishing, respectively. Nineteen scenarios were designed in which either the mean or the variance of a parameter was changed in a scenario. Each scenario was simulated for 2,000 times (Table 4) and the mean and standard deviation of the biological reference points were calculated. The percentage change of one specific biological reference point in scenario j (PC_{BR}^j) is defined followed King (1995) as : $PC_{BR}^j = \frac{BR^j - BR^{ref}}{BR^{ref}} \times 100$ where BR^j indicates the statistic (mean or standard deviation) of a biological reference point (e.g. F_{max}) in scenario j , and BR^{ref} indicated the statistic for this biological reference point in the reference case. Meanwhile, we were especially uncertain in determining F_{cur} , which apparently influenced the risk of growth and recruitment overfishing and the sustainable use of the eel resources. Consequently, a special scenario called “varying F” was conducted that values of F_{cur} increased from 0.5 to 4 times to the current value and corresponding risks of growth and recruitment overfishing were calculated accordingly. All statistical tests, computation and simulation were conducted in SAS ® (Version 8.01, Stokes et al., 1996) and R (version 2.7.2, Owen, 2006; Seefeld & Linder, 2007). Significance level (α) was set at 0.05 throughout.

3. Results

3.1. Eel catch profiles from 1999 to 2007

3.1.1. Numbers by sex

During 1999 to 2003, the catch of the eels was low, comprising about 100 females, 20 males and 30 sexually undifferentiated eels annually. In 2004, the catch of females and males increased dramatically, reaching a peak of 502 females and 686 males, while the sexually undifferentiated eels only marginally increased to 84 eels. After 2004, the catch of the females remained considerably high, ranging from 401 to 684 eels annually. On the other hand, the catch of males also decreased drastically that was 209 individuals in 2005 and only 9 males were caught in 2007. The catch of sexually undifferentiated eels also increased gradually after 2004, being 199, 148 and 272 eels in 2005, 2006 and 2007, respectively (Fig. 10a).

3.1.2. Annual variation in mean lengths and weights by sex

The mean total length of females caught ranged from 300 to 500 mm with standard deviation from 72 to 107 mm, and decreased significantly with time during the period from 1999 to 2007 (slope = -14.47, $t = -2.85$, $p = 0.0247$). The mean lengths of males ranged from 400 to 550 mm, and those of sexually undifferentiated eels were between 300 to 400 mm (Fig. 10b). The mean lengths of neither males nor the undifferentiated eels showed significant relationship with time during 1999 to 2007 ($t = -0.88$ and -0.81 , $p = 0.4082$ and 0.4464 , respectively).

The total weight of the eel caught varied much than the total weight (Fig. 10c). The mean total weights of the females and males ranged from 62 to 300 g, while those of sexually undifferentiated eels were between 20 to 150 g. The temporal trends in mean total weights were not significant for females, males and sexually undifferentiated ($t = -2.07$, -1.27 and -0.72 , $p = 0.0767$, 0.2446 and 0.4968 , respectively).

3.1.3. Comparison of the lengths of the wild eels by sex and stag

The mean total lengths and weights were significantly different between sexes (female, male and sexually undifferentiated eels), stages (yellow and silver stage) and the sex-stage interaction (log-transformed two-way ANOVA, both $p < 0.0001$, Table 1).

5 The females had the largest lengths and heaviest weights, followed by the males, and the sexually-undifferentiated eels had the smallest length and weight. Within sex, the lengths and weights of the silver eels were significantly larger than those of the yellow eels (Tukey's multiple comparison), consistent with the previous studies (Tzeng et al., 2000; 2003; Kotake et al., 2005; Okamura et al., 2008).

10

3.2. Changes in length composition and CPUE of the eel fishery

3.2.1. Annual length composition from 1999 to 2007

Most of the eels caught in 1999 to 2007 were between 200 mm and 800 mm (Fig. 11a to i). The length compositions among 1999 to 2007 were significantly different
15 among years (Kolomogrov-Smirnov test, $p < 0.0001$). From 1999 to 2003, the females were dominated ($> 70\%$) and most were larger than 400 mm ($> 88\%$). The male eels of sizes about 400 mm increased greatly in 2004 (41 %, Fig. 11f) and substantially decreased in 2005 (18.9 %, Fig. 11g) and 2006 (6 %, Fig. 11h), and in 2007 the catch of males was very few (9 eels, Fig. 11i). The changes in eel size composition in the catch
20 are apparent. Eels larger than 400 mm contributed 88 % of the catch from 1999 to 2003 and 86 % in 2004, but eels less than 400 mm comprised nearly half of the catch in 2005 (49.5 %, Fig. 11g), 2006 (51 %, Fig. 11i) and increased substantially in 2007 (81 %, Fig. 11i).

25 3.2.2. Length composition by fishing gears

The cumulative length distribution of eels caught differed significantly between

gears (Fig. 12, Kolmogorov-Smirnov test, $p < 0.0001$). Eels caught by shrimp nets were significantly smaller (median length 410 mm) than those by eel tubes (median length 512 mm) (Mann-Whitney test, $p < 0.001$). The 2.5th and 97.5th percentiles were also larger for the shrimp nets (266, 657 mm) than for the eel tubes (330, 605 mm),
5 indicating that the length range vulnerable to fishing is larger for the shrimp net than for the eel tubes.

3.2.3. Monthly length composition

Due to low eel catches from 1999 to 2003 for plotting changes in monthly length
10 composition, and to exclude the effect of escaped cultured eels in the fall of 2004, and eel tube information that was available only for three months in 2005, the monthly eel length compositions were represented by data only from the shrimp nets. The monthly length compositions were similar from October to December 2005 (Kolmogorov-Smirnov test, all $p > 0.05$), but eels less than 400mm became dominant
15 ($p < 0.0001$) in January and February 2006. However, larger eels were also found in May and June 2006 but the small eels were dominated again in July 2006 (Fig. 13).

3.2.4. Monthly CPUE of the shrimp net

The mean catch weight per unit effort (CPUE) of the eel tubes and shrimp nets
20 fluctuated with months. The CPUE ($\text{g} \times \text{gear number}^{-1} \times \text{fisherman}^{-1}$) for shrimp nets was high in September, and then decreased substantially from 40 to around 8 ~ 14 in autumns (October to December) before reaching a minimum of about 2 in January to April of the next year. Mean monthly CPUE peaked again in May and June, and then decreased in July, indicating a summer high and winter low in mean CPUE for the
25 shrimp net fishery. CPUE data for eel tubes was available only during August to October 2005. It decreased from 35 in August to 8 in October 2005 (Fig. 14).

3.3. Length-weight relationships

The relationships between the lengths and weights by sexes were summarized in Fig. 15 and the estimates of parameters in Table 5. The estimated value of a (g mm^{-1}) was the largest in the male eels (3.54×10^{-7}), followed by sexually undifferentiated eels (6.85×10^{-8}) and the smallest in the female eels (1.33×10^{-8}). On the contrary, the exponent b (no unit) was the largest in females (3.74), then in the sexually undifferentiated eels (3.46), and the smallest in males (3.22). The length-weight relationship in general fitted the observed values well that the R-square was not less than 0.9 (Table 5). According to the estimated relationship, females attained higher weights than the males and sexually undifferentiated eels as the length increased. This implied the growth rate in weight of females was higher, while the gains in weight of for the males and sexually undifferentiated eels were probably similar each other.

3.4. Validation of otolith annuli

3.4.1. By known-age cultured eels

The presumed annuli in otoliths in sagittal plane of cultured eels of known ages were compared with those of wild eels with unknown ages under the optic microscope with reflected light (Fig. 16a and b). The primordium (P), the metamorphosis check (MC) and elver check (EC) corresponded to the initial growth point of the otolith, the metamorphosis from the leptocephalus to the glass eel stage and the elver stage at estuarine arrival. The region from primordium to EC appeared dark and grey after being etched by EDTA. Beyond EC, the otolith growth rate varied among different growth axes. It was the fastest in the post-rostrum axis, followed by the rostrum, and the slowest in ventral and dorsal axis in both wild and cultured eels. The annuli were discriminated by the clearest and the most distinct increments, but some thinner and less clear composite bands with lighter color were also found between the two successive

rings in both wild and cultured eels. This indicated the eels did not stop growth at annulus formation. Two discernible annuli after the elver check were found in 26 individuals (83.9 %) out of the 31 cultured eels (Fig. 16a) and the remaining 5 individuals (16.1 %) were aged either 1 or 3. The mean (\pm SD) age of the cultured eels was 1.97 ± 0.4 years, which matched the rearing period of two years. Accordingly, the annulus in otolith of the eel is validated. The annulus pattern in otoliths of wild eels was also similar to that of cultured ones, which suggested that the otolith annulus was also deposited annually in the wild eels.

3.4.2. Monthly marginal increment ratios in otoliths of wild eels

Monthly changes in marginal increment ratio (MIR, mean \pm SD) of otoliths in wild eels caught from Kao-Ping River are shown in Fig. 17. The water temperature in the study area fluctuated from around 23°C in winter (December to February) and rose to ~25-26°C in spring (March to May), reached the highest (~ 28°C) in summer (June to August), and decreased to 25 ~ 26°C in late summer and autumn (September to November) and in winter (Fig. 17). Although the sample size varied from 0 eels in April, 3 in March and 28 in August, a seasonal pattern of MIR was recognizable. MIR was low (about 0.5) in winter and early spring (January to March), increased in March (or April) and reached a peak of around 1.0 in May and June. It then decreased from 0.6 in July to 0.7 in October, and then decreased to 0.5 again in November and December. The single mode in the monthly changes of mean MIR over a year period implied that the presumed otolith annulus was deposited once a year. Moreover, the patterns in mean MIR corresponded to the seasonal changes in mean water temperature of Kao-Ping River, implying the annulus might be deposited during the period of low temperature in winter.

3.5. Selection of the best growth models

3.5.1. Best model for the females and males

The model selection process for the five candidate growth models was conducted by sexes to examine whether the best model chosen differed between the sexes. The von Bertalanffy growth model was the best model fitting the data for both females and males (w = 0.468 and 0.410, Table 6), but other models were also substantially supported by the data. For females, the power, generalized von Bertalanffy, and Gompertz growth models were supported because of relatively high Akaike weights ($\Delta = 1.749, 2.013$ and 2.184 , respectively). For males, the Gompertz, power, and generalized von Bertalanffy models were the second, third and fourth best selections ($\Delta = 1.272, 1.698$ and 2.019 , respectively). The logistic model could probably be excluded for females ($\Delta = 8.147$ and $w = 0.008$), but had considerable support for males ($\Delta = 5.433$ and $w = 0.028$) and probably should be incorporated when model averaging.

3.5.2. Model-averaged growth model by sexes

The model-averaged growth models for females and males were computed from the suggested growth models based on their Akaike weights (Fig. 18). Different growth models for both females and males were essentially indistinguishable from ages 1 to 4, but diverged considerably after ages 6 ~ 7. The averaged growth model nearly overlapped the von Bertalanffy growth model for females and was only slightly different for males. The generalized von Bertalanffy growth models were generally close to the averaged models for both sexes, but its lengths at older ages were slightly smaller than those of averaged and von Bertalanffy growth models. At older ages, the lengths from the power model were the highest, while those of the Gompertz (Fig. 18a) and logistic models (Fig. 18b) were the smallest.

3.5.3. Model with sex-specific parameters

Since the best model selected was the von Bertalanffy growth model for both females and males, ten models were constructed including the five candidate growth models in which the parameters were assumed to be either the same or different
5 between sexes. The von Bertalanffy growth model with sex-specific parameters was the best model fitting the data ($w = 0.671$, Table 7). The sex-specific power, Gompertz, and generalized von Bertalanffy growth models also had substantial support ($\Delta = 3.448$, 3.457 and 4.024, $w = 0.120$, 0.119 and 0.090, respectively), but the fit for the sex-specific logistic model was very poor ($\Delta > 13$, $w < 0.001$). The Akaike differences
10 for the five sex-pooled growth models were quite large (all Δ 's > 20), suggesting that the growth of the eels should be modelled separately for each sex.

3.5.4. MSE from averaged model and sexual differences

The parameter estimates, their asymptotic standard errors and the model-averaged
15 mean sum of errors (MSE) are shown in Table 8. The averaged MSE was 3.100×10^{-2} , which was about 1.6 % higher than that of the suggested von Bertalanffy growth model with sex-specific parameters (3.095×10^{-2}). Sex dimorphism in parameters was found in the asymptotic models (von Bertalanffy, Gompertz and generalized von Bertalanffy), such that the females had larger asymptotic length and smaller growth coefficients (K ,
20 K_2 and K_4) than the males. The averaged growth model also differed between sexes (Fig. 19). The predicted length of females was always higher than that of males and the differences became larger at older ages. The males also had a smaller asymptotic length and reached their asymptotic length earlier than did females.

3.6. Estimation of mortality rates by mark-recapture experiments

3.6.1. Number of eels recaptured

Marked eels started to be recaptured one day after release (September 28 for 2005 experiment and August 15 for 2006). The fishing and collecting for eels continued at least until December, 2008, but none of marked eels were recaptured. The overall recaptures of the eels in the experiment in 2005 was low, with only 19 marked eels recaptured until the last recapture (146 days after releasing) from the 717 marked eels released, including 3 cultured eels with CHIP, 5 cultured eels with C-FC, 5 wild eels with CHIP and 6 wild eels with P-FC. More eels (444 marked individuals) were recaptured during the 2006 experiment, including 72 cultured eels with CHIP, 310 cultured eels with C-FC, 23 wild eels with CHIP and 39 wild eels with P-FC from the 782 eels released. Generally, the cultured eels were larger (46.0 ~ 92.5 cm and 127 ~ 1326 g) than the wild eels (21.1 ~ 86.5 cm and 5 ~ 917 g, Table 9).

3.6.2. Comparison of the recapture rates by origins and marks

When the eels were released in the upstream site in 2005, the first recapture was 15 days after release and the last recapture was after 146 days. Most of the marked eels (89 % of 19) were recaptured in the fishing ground within 60 days after the release. The recaptures did not decrease with time and not depended on their origins and marks (Fig. 20a). For the 2006 experiment when the marked eels were released directly in the fishing ground, the first recapture was made on the next day and the recapture rate decreased substantially with time (Fig. 20b). Most eels (more than 90 %) were recaptured during the first 8 days, and occasionally to 60 days after release. A substantial number of the CHIP wild eels were recaptured about 30 ~ 62 days after release (Fig. 20b). However, few eels were recaptured after two months, except for 4 P-FC cultured eels recaptured between 132 and 220 days after release (Fig. 20b).

For the data from the 2005 experiment, differences in the recapture rates were not significant between wild eels marked by CHIP and P-FC (Fisher's exact test, $p = 0.10$) and between cultured eels marked by CHIP and C-FC ($p = 0.12$). When the eels of different marks were pooled, the recapture rate of cultured eels (1.5 %, 8 out of 519) was significantly smaller than that of the wild eels (5.6 %, 11 out of 198, $p = 0.0067$). For the experiment in 2006, the recapture rates did not differ between wild eels marked by CHIP and P-FC ($\chi^2 = 0.32, p = 0.57$) and between cultured eels marked by CHIP and C-FC ($\chi^2 = 2.82, p = 0.09$). In contrast to the 2005 experiment, the recapture rate of cultured eels (71.3 %, 382 out of 536) was significantly higher than that of the wild eels (25.2 %, 62 out of 246, $\chi^2 = 63.0, p < 0.0001$). Therefore, the recapture rates of eels differed between cultured and wild eels but not between the eels marked by different tags in both 2005 and 2006. Also, the differences in recapture rates for the CHIP eels were significantly influenced by their origins (logistic regression, $p < 0.001$), but not by their length at release for the 2006 experiment ($p = 0.38$). The recapture rate (95 % CIs) was 1.54 % (0.71 ~ 2.85 %) for the cultured eels and 5.56 % (2.92 ~ 9.33 %) for the wild eels in 2005, and 71.27 % (67.34 ~ 74.99 %) and 25.20 (20.05 ~ 30.87 %), respectively, in 2006 (Table 10).

3.6.3. Differences in mortality and survival rates between origins and marks

For the 2005 experiment with the complete method, the best model suggested by AIC_c ($W_{AIC_c} = 0.334$, Table 11) was the cultured + mark model; the estimates of mortality rates differed among cultured eels marked by CHIP, C-FC and the wild eels in which the marks were pooled. The optimal model was followed by the full model ($W_{AIC_c} = 0.246$) and the origin model ($W_{AIC_c} = 0.208$). On the other hand, the simplest null model was suggested by BIC ($W_{BIC} = 0.975$) and the weights of other models were much smaller. When the uncompleted method was used to estimate the survival rates (S),

meaningful estimates ($1 \geq S \geq 0$) were produced only in the null and mark models, so that the model selection was not conducted (Table 12). A few eel recaptures in the 2005 experiment did not justify the construction of complex models and parameter estimation was only conducted in the null model; the estimates (95 % CIs) of F , M , S and μ were
5 1.45×10^{-3} ($8.86 \sim 22.14 \times 10^{-3}$), 0.053 (0.039 ~ 0.073), 0.959 (0.924 ~ 0.984) year⁻¹ and 0.026 (0.016 ~ 0.040), respectively (Table 13). Moreover, the estimates of F and M using the uncompleted methods were smaller (1.20×10^{-3} and 0.0441 year⁻¹, Table 13).

For the 2006 experiment, the best model was the wild + mark model according to both AIC_c and BIC after fitting the data by the completed method ($W = 0.765$ and 0.997,
10 Table 11). The uncompleted method obtained nearly identical data weights (Table 12). The full model was the second best model, but its weights were much smaller ($W = 0.235$ and 0.003) than those of the best model, indicating that the estimates of F , M , S and μ were influenced by both eel origins and the marks. The mark (CHIP vs. P-FC) effects were significant in wild eels and appeared insignificant in the culture eels (CHIP
15 vs. C-FC). The estimates and 95 % CIs of F , M , S and μ under the selected model were also listed in Table 13.

3.7. Maturation parameters

The maturation curves among females, males and the sex-pooled were shown in
20 Fig. 21, and the estimated values of parameters with corresponding standard errors were in Table 14. The maturation curves were significantly different between females and males (Likelihood ratio test, $p < 0.0001$). The models predicted that 95 % of females became silver eels at the sizes ranged from 474 to 751 mm, while those of males were from 350 to 709 mm. The males became silver eels with a wider size range than females
25 (Fig. 14). The sex-pooled model was fairly similar to the curve of the females, probably due to that the sample size of females (1,583 eels) was larger than the males (148 eels).

3.8. Evaluation of the exploitation status

3.8.1. YPR and SPR without uncertainty in parameter estimation

YPR and SPR in relation to fishing mortality rates by sexes were demonstrated in Fig.2. YPR of females were higher than those of males (Fig.22). Calculated F_{max} was 0.156 and 0.186 and $F_{0.1}$ was 0.111 and 0.128 year⁻¹ for females and males, respectively. Maximal YPR of females (62.22 g ind⁻¹) was higher than that of males (42.48 g ind⁻¹)(Table 15). Current fishing mortality rate ($F_{cur} = 0.120$) exceeded the $F_{0.1}$ value of females and was closed to $F_{0.1}$ value of males, indicating that the growth overfishing has likely occurred on the females, and was close to growth overfishing for the males.

Without exploitation, i.e. $F = 0$, the females had higher SPR ($SPR_0 = 957.46$ g ind⁻¹) than that of males (591.34), but SPR of females decreased slightly lower than that of males when fishing mortality increased (Fig.2). Under F_{cur} , SPR was reduced to 32.66 and 37.23 % of SPR_0 for females and males, respectively. Therefore, it was reasonable that F_{cur} exceeded $F_{50\%}$ (0.073 for female and 0.082 year⁻¹ for males), as well as $F_{40\%}$ (0.097 year⁻¹ for females and 0.110 for males, Table 15), indicating the recruitment overfishing might have occurred.

When minimum legal sizes (L_{min}) were enforced, YPR values increased with increasing F and L_{min} in both sexes (Fig. 23). At F_{cur} , YPR of females was highest (around 75 g ind⁻¹) at L_{min} of around 500 mm (Fig. 23a), and YPR of males was highest (around 45), at L_{min} of around 420 mm (Fig. 23b). Given F was between 0 and 1 year⁻¹, YPR of females exceeded 120 when L_{min} was larger than 680 mm and F was higher than 0.7. YPR of males exceeded 70 when L_{min} was between 500 to 620 mm and F was larger than 0.55.

Relative SPR also increased with increasing L_{min} for both sexes (Fig. 24). At F_{cur} , the L_{min} that produced highest YPR (500 and 420 mm for females and males) resulted in a relative SPR of slightly higher than 50 % for both sexes. However, at L_{min} of larger

than 680 mm and F higher than 0.7 with highest YPR of females, the relative SPR seemed less optimistic, ranging from approximately 20 to 40 % (Fig. 24a). At L_{min} values between 500 to 620 mm that produced highest YPR of males, relative SPR varied between 20 to 50 % (Fig. 24b).

5 Compared to the L_{min} , the enforcement of maximum legal lengths (L_{max} , mm) resulted in a decreased YPR for both sexes (Fig. 25). When L_{max} decreased from unregulated (above 800 mm) to 400 mm and from above 700 to 300 mm, the YPR value substantially decreased to from approximately 60 and 40 to 5 and lower than 5 for the females and males, respectively. Moreover, the YPR increased more slowly with
10 increasing F at smaller L_{max} . On the other hand, relative SPR drastically increased with decreasing L_{max} (Fig. 26). At F_{cur} , the relative SPR increased greatly from approximately 33 % without regulation of L_{max} to more than 70 % when L_{max} was larger than 800 and 650 mm for females and males, respectively. The increase in relative SPR slowed down when L_{max} further decreased. When L_{max} was smaller than 600 for females and 500 mm
15 for males, the relative SPR nearly appeared not affected by L_{max} and only decreased with F (Fig. 26).

3.8.2. YPR and SPR with uncertainty in parameter estimation

When the uncertainty in parameter estimation were incorporated, the means of F_{max} ,
20 $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$ were nearly the same with the case without this uncertainty. However, the YPR and SPR values (YPR_{max} , $SPR_{F_{cur}}$ and SPR_0) were substantially higher and %SPR was slightly higher (Table 15 and 16).

F_{max} and $F_{0.1}$ were found to had smaller coefficient of variation (CV, 0.8 ~ 1.1 %) and their distributions were symmetric and analogue to normal distribution. On the
25 other hand, $F_{40\%}$ and $F_{50\%}$ had relatively higher CV (7.4 ~ 8.8 %). Their distributions were likely symmetric or slightly skewed, and were flatter (platykurtic) than F_{max} and

$F_{0.1}$ (Fig. 27).

Estimated YPR and SPR values (YPR_{max} , $SPR_{F_{cur}}$ and SPR_0) fluctuated more greatly than the BRPs, that the CV were between more than 50 % to more than 100 %, indicating these values were highly affected by the uncertainty in parameters.

5 Moreover, the distribution of YPR_{max} , $SPR_{F_{cur}}$ and SPR_0 were highly skewed with a long tail extending to the right, analogues to exponential or Poisson distributions that extremes of high YPR and SPR value occurred at a low probability. %SPR varied moderately with CV of 24.7 to 28.9, and its distribution became symmetric around the mean (Fig. 28). These indicated that extremes of SPR occurred simultaneously in each
10 simulation, and thus canceled each other. Distributions of possibilities that hat F_{cur} was larger than F_{max} and $F_{0.1}$ were nearly symmetric, while those of possibilities that hat F_{cur} was larger than $F_{40\%}$ and $F_{50\%}$ were left-skewed (Fig.29).

Probabilities that F_{cur} was larger than F_{max} were small, 1.7 to 4.7 % for the females and 1.0 to 2.0 % for the males as the confidence level change from confidence level of
15 larger than 99.95 % to less than 0.05 % (Fig. 30). The probability that F_{cur} was larger than $F_{0.1}$ was substantial, 30.6 to 39.7 % for the females and 31.0 to 37.0 % for the males. It was considerable for $F_{40\%}$, 23.9 to 84.8 % for the females and 28.5 to 79.5 % for the males and much high for $F_{50\%}$, 67.0 % to 97.6 % for the females and 70.0 to 95.5 % for the males. This suggested that the risk of growth overfishing was small to
20 substantial, and the risk of recruitment overfishing was considerable to high for the eel fishery.

3.8.4. Effects of L_{min} and L_{max}

Means and corresponding coefficient of variations of BPRs (F_{max} , $F_{0.1}$, $F_{40\%}$ and
25 $F_{50\%}$) and %SPR with increasing L_{min} were illustrated in Fig. 31 and 32, and those with decreasing L_{max} were in Fig. 33 and 34, respectively. The four BPR associated with

fishing mortality rate, i.e. F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$, increased with stricter limitation in fisheries, namely increase L_{min} and decrease in L_{max} . The degree of increase from L_{min} of 200 to 600 mm was more apparent in F_{max} (440 % in females and 1200 % in males) than $F_{0.1}$ (260 % in females and 270 % in males). The degree of increase in $F_{40\%}$ and $F_{50\%}$ was less apparent that $F_{40\%}$ increased 290 % and 460 % and $F_{50\%}$ increased 270 % and 380 % in females and males, respectively. Moreover, the increase in four BPRs accelerated with increasing L_{min} (Fig. 31), indicating a stricter L_{min} appeared more efficient to against growth and recruitment overfishing. %SPR also substantially increased from 33 to 63 % for females and 39 to 72 % for males with decreasing with increasing L_{min} (Fig. 32).

F_{max} and $F_{0.1}$ increased 550 and 540 % when L_{max} changed from 800 to 400 mm in females, and 980 and 890 % when L_{max} changed from 650 to 300 mm in males. $F_{40\%}$ and $F_{50\%}$ increased 940 and 950 % for females, and 140 and 160 % for males, respectively (Fig. 33). %SPR also increased with decreasing L_{max} , from 76 to 89 % for females and 78 to 89 % for males, respectively (Fig. 34). Similar to the case of L_{min} , F_{max} and $F_{0.1}$ also accelerated with stricter L_{max} , but $F_{40\%}$, $F_{50\%}$ and %SPR seemed demonstrating the phenomenon of “saturation” or “plateau”. Although L_{max} can effectively protect the spawning biomass, its marginal effects decreased with stricter L_{max} . In other words, it was not practical and inefficient to set L_{max} below a certain level, especially setting set L_{max} would result in decreased YPR (Fig. 25).

In addition, the variation of BRPs and %SPR also changed with stricter L_{min} and L_{max} . CV of BRPs increased with increasing L_{min} , while decreased with decreasing L_{max} (Fig. 31 and 33), but CV of %SPR decreased with stricter L_{min} and L_{max} (Fig. 32 and 34). It indicated that the uncertainty of estimating BRPs increased with stricter L_{min} , but decreased with stricter L_{max} , and uncertainty of %SPR decreased with stricter L_{min} and L_{max} .

3.8.5. Sensitivity analysis: consequences of misspecification of parameters

Percentage changes of the means and standard deviations of four BRPs (F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$), key YPR and SPR values (YPR_{max} , $SPR_{F_{cur}}$ and SPR_0) and %SPR in 19 scenarios were listed from Table 17 to 20 for females and males. Mean and standard deviations of the probability that F_{cur} was larger than F_{max} (P_{Grow}), $F_{0.1}$ ($P_{Grow0.1}$), $F_{40\%}$ ($P_{Recruit40}$) and $F_{50\%}$ ($P_{Recruit50}$) in 19 scenarios were listed in Table 21 and 22 for females and males, respectively. It was showed that M and K were important vital parameters to which all BRPs, key YPR and SPR values were highly sensitive. Besides, $SPR_{F_{cur}}$ and %SPR were also sensitive to mean and variance of F_{cur} , and affected by changes in lengths at 50 % maturity and steepness of maturation curve in a smaller degree (Table 19 and 20). P_{Grow} and $P_{Grow0.1}$ were closely related to mean and variance of F_{cur} , and mean of K , while $P_{Recruit40}$ and $P_{Recruit50}$ were considerably affected by mean and variance of F , mean and variance of M , mean of K , and by length at 50 % maturity, and steepness of maturation curve in a lesser degree (Table 21 and 22).

Because F_{cur} and M were highly uncertain, a risk analysis of misspecification in F_{cur} and M was conducted and shown in Fig. 35 and 36, respectively. As expected, P_{Grow} , $P_{Grow0.1}$, $P_{Recruit40}$ and $P_{Recruit50}$ of both sexes increased with increasing F_{cur} (Fig. 35), and decreased with increasing M (Fig. 36), in which the probabilities of both growth overfishing (P_{Grow} and $P_{Grow0.1}$) and recruitment overfishing ($P_{Recruit40}$ and $P_{Recruit50}$) of females were all larger than that of males. If F_{cur} was in fact 1.5 to 2 times higher to the estimated value, it was quite certain (nearly 100 %) that the growth overfishing would occur for both sexes (Fig. 35a and b). On the other hand, the recruitment overfishing was more easily to happen. If F_{cur} was underestimated that the real value was 125 to 150 %, then the risk of recruitment overfishing reached near 100 % for sexes (Fig. 35c and d). Meanwhile, if M was underestimated, then the probabilities of overfishing decreased, and vice versa (Fig. 36). However, the risks of growth overfishing decreased greatly

with increasing M that P_{Grow} and $P_{Grow0.1}$ reached nearly zero for both sexes (Fig. 36a and b). But the risks of recruitment overfishing was still considerable ($P_{Recruit40}$ and $P_{Recruit50}$ of females were 41 and 75 % for females, and those of males were 14 and 47 %, respectively) even the M was three times higher than the value used (Fig. 36a and b)

- 5 These implied that (1) *A. japonica* in study area was more vulnerable to recruitment overfishing than growth overfishing, (2) females were more vulnerable to the fishery exploitation than the males, and (3) misspecification of F_{cur} was probably more serious to result in overfishing than use of an unrepresentative M .



4. Discussion

4.1. General view of Japanese eel catches in the Kao-Ping River

4.1.1. Effects of fishing gears and escaped cultured eels on the length composition

The changes in the sex ratio from female dominance in 1999 to 2003 to the male
5 dominance in 2004 were probably due to the escape of large (about 500 mm) cultured
eels in the lower reach of the Kao-Ping River caused by Typhoon Mindulle (Chu et al.,
2006). The larger lengths of the males than the females, which contradicted to that
females are generally larger than males for both yellow and silver Japanese eels in the
wild (Han et al., 2000; Tzeng et al., 2002; 2003; Kotake et al., 2005; Han & Tzeng
10 2006), further indicated the effect of escaped cultured eels. The escaped cultured eels
estimated as 30,000 eels drastically changed the sex ratio and length composition in the
wild, implying the smallness and fragility of the wild eel population. However, the
impact of cultured eels on the wild eel population did not last longer than 2 years. After
escaping from the ponds, the cultured eels might either die because of failure to find
15 food and escape possible predators, or they could become silver eels and migrating to
sea for spawning, as indicated by younger ages and male-dominance sex ratios of the
silver eels after 2004 (Lin et al., unpublished data). However, these hypotheses required
further examination.

20 4.1.3. Impacts of shrimp nets on the eel population

The length compositions of the eel catches differed between fishing gears, with
smaller eels and a wider length range by the shrimp nets than that by the eel tubes.
Moreover, the length compositions in 2005 and 2006 were composed markedly by eels
less than 400 mm, probably due to the wide use of shrimp nets. Thus, more eels with
25 smaller length might be vulnerable to fishing by the newly introduced shrimp nets than

by the traditional eel tubes. The more small eels in the catch, occurs more likely the growth overfishing in the future (King, 1995; Haddon, 2001).

Meanwhile, how many eels might be caught by the newly introduced shrimp nets in a year? A simple and rough estimation was: (mean CPUE) × (mean gear used per day) ×
5 (mean operation days in one month) × 12 × (approximate number of fishermen) × (median weight)⁻¹ = 11.3 × 61 × 24 × 12 × 4 × 110⁻¹ = 7,219 eels. This is a quite disturbing estimate because the local population size in the lower reach of Kao-Ping River was estimated as 5,000 to 20,000 eels (Han & Tzeng, 2006). Although this estimate was likely unrealistic, it gave a simple illustration of the large potential
10 influence of the shrimp nets on the local eel population. According to the local fishermen, at least four more fishermen were willing to use shrimp nets, while virtually no fishermen were willing to use eel tubes in 2008. Thus, the high potential in harvesting the eels and the greater vulnerability of small eels might further indicate that the increasing and unregulated use of shrimp nets might reduce the eel population
15 further in the lower reach of Kao-Ping River.

4.2. Validation of otolith annuli

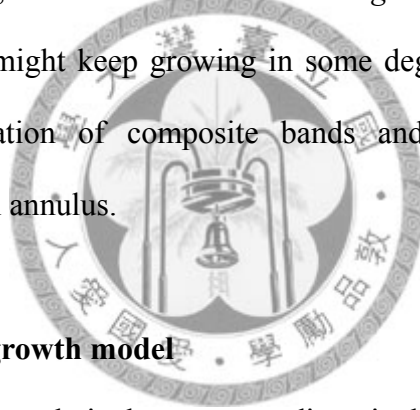
Annual periodicity of otolith annuli was validated using fish in rearing condition with known ages of European eel *Anguilla anguilla* (Deelder, 1981), and bluegills
20 *Lepomis macrochirus* in controlled laboratory conditions (Schramm, 1989). When cultured fish are applied to validate ages estimated from hard structures, the environment should be kept as similar as where the wild fish were in (Campana, 2001). In this study, the cultured eels were reared in the outdoor ponds, so that the experiences of temperature and photo period of the cultured eels were subjected similarly to those of
25 wild eels. However, the seasonal changes in the otolith deposition rate resulted from seasonal changes in somatic growth due to environmental fluctuation were suggested to

be a reason for annuli deposition (Campana, 2001). However, the growth of cultured eels was generally fast without growth disruption due to virtually unlimited food resources all the year around (Deelder, 1981; Chu et al., 2006). The otolith annuli were found to be deposited in annual schedule as least for the two-year old cultured Japanese eels in this study, further implying that the food intake and the changes in somatic growth rate were probably not the only factors for the annuli deposition of the otoliths in the eels in tropical southern Taiwan as previous suggested (Campana, 2001).

On the other hand, the annual periodicity of otolith annuli was also validated by the monthly variation in MIR of the wild eels. Longhurst & Pauly (1987) noted that a temperature difference of 4 to 5 °C was necessary for formation of the otolith annuli. Interpretable increments or rings were found in the pomacentrid fish in the western tropical Atlantic where temperature fluctuated only within 3°C (Caldow & Wellington, 2003). The difference in annual water temperature in the study area was around 7°C (approx. 20°C to 28°C, Fig. 4), which might be enough for annuli formation for the Japanese eels. However, the eels in the study area were less-active and the catch was lowest in winter (Lin & Tzeng, 2008a). The metabolic rate of the eels might be decreased at low temperature and subsequently lead to reduced somatic and otolith growth rates. Guan et al. (1994) speculated that the otolith annulus in Japanese eels might be formed during January to March in the subtropics (25°30'N). Accordingly, the otolith annulus of the Japanese eel was likely to be formed once per year, as temperate anguillids as mentioned above and other tropical fishes (Morales-Nin, 1989; Caldow & Wellington, 2003; Morales-Nin & Panfilli, 2005).

Although the difficulty of resolving the margins of otolith increments for MIR analysis may influence its validity (Campana, 2001), it has been useful for validating the annual periodicity of the annulus in numerous fish species (e.g., Dwyer et al., 2003; Brouwer & Griffiths, 2004; Williams et al., 2005). Three possible sources of bias may

confound the MIR analysis, i.e. insufficient sample size, excessively extended sample periods and lack of a defined reproductive period (Lessa et al., 2006). In this study, the wild eels in the Kao-Ping River were recruited by elvers arriving to the estuary regularly during winter (November to February), so the effect of undetermined reproductive period was negligible. The large SD in mean MIR in each month indicated a high variability in MIR among individuals. This might result from small sample size in some months, multiple age classes, variability in resolving increments, and differences in the timing of the increment formation. Although the growth rate and activity might reduce, the wild eels probably did not completely stop feeding under a water temperature of around 20°C during winter, similar to Indian eel *A. bengalensis* in the tropics (Pantulu, 1956), so that the otolith might keep growing in some degree during the winter. This may result in the formation of composite bands and introduced variability in determination of the otolith annulus.



4.3. Selection of the best growth model

Information theory is a relatively new paradigm in biological sciences, such as estimation of wild life abundance, population biology, ecology, and mark-recapture experiments (Buckland et al., 1997; Anderson et al., 2000; Burnham & Anderson, 2002; Johnson & Omland, 2004). It has recently been used to select the best model describing the absolute or relative growth of invertebrates (Rabaoui et al., 2007), chondrichthyan fishes (Coelho & Erzini, 2007), and bony fishes (Katsanevakis, 2006; Katsanevakis & Maravelias, 2008).

Results from an information theory approach depend on the data used and the set of candidate growth models. To keep the number of growth models in the set appropriate, models irrelevant to the biological questions being asked should be omitted (Chatfield, 1995). A balance should be recognized between keeping the set small enough to focus

only on plausible models and making the set sufficiently large to ensure that a good model was included (Burnham & Anderson, 2002). The widely used von Bertalanffy growth model becomes the generalized von Bertalanffy sigmoid and more flexible by adding a scale parameter ρ (Quinn & Deriso, 1999). The Gompertz and linear growth model, which is a special case of the power model when the exponent of age b_2 equals one, have also been applied to model the eel growth (Graynoth & Taylor, 2004; Jessop et al., 2004; Walsh et al. 2006). The logistic model has been used in other growth studies (Katsanevakis, 2006; Coelho & Erzini, 2007; Katsanevakis & Maravelias, 2008; Rabaoui et al., 2008). A more general and flexible growth model, i.e. the Schnute and Richards growth model (Schnute & Richards, 1990), was fitted in the preliminary study but failed to converge. Therefore, the five models considered were probably sufficiently plausible for modelling the eel growth (Katsanevakis & Maravelias 2008).

4.3.1. Candidate models for the eel growth

Von Bertalanffy growth model has been used in most studies of anguillids (e.g. Guan et al., 1994; Poole & Reynolds, 1996; Tzeng et al., 2000; Lin et al., 2007; Simon, 2007; Okamura et al., 2008). It was also the model best fitting the data in this study. Small differences in mean sum of square errors and nearly overlapped growth trajectories between the von Bertalanffy and averaged models (Fig. 18a and b), indicated that the von Bertalanffy growth model probably fit the data nearly as well as the averaged growth model.

However, von Bertalanffy growth model did not always fit the eel growth well (Sparre, 1979). Alternative models, such as the Gompertz (Jessop et al., 2004) and linear model with various effects (Walsh et al., 2006) were also applied to model the eel growth. Because different mechanisms were presumed in different models, their growth trajectories differed substantially even when the same data was used (e.g. Fig. 18a and

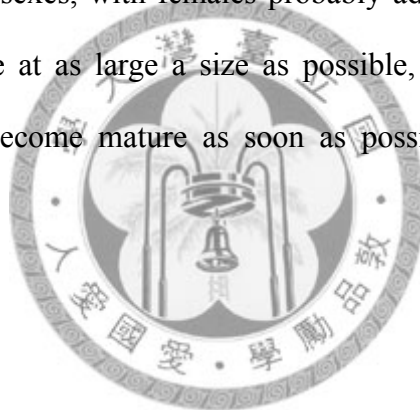
b), and thus, the extrapolation of the lengths at older ages was of high uncertainty. Moreover, the asymptotic lengths from logistic and Gompertz models were generally smaller than those of von Bertalanffy and generalized von Bertalanffy models (Table 12; Katsanevakis & Maravelias 2008), indicating the effects of the selection of different growth models that further strengthened the importance of the model selection.

4.3.2. Comparison of growth models among subgroups

Differences in growth among subgroups (e.g. sexes or geographical populations) may be represented by two conditions: different forms of the growth models (Coelho & Erzini, 2007) and different parameters within the same growth model (Rabaoui et al., 2008). A sequential examination of the former was tested first, followed by a test of the latter in this study. The simultaneous comparison of models among the subgroups greatly increased the difficulty of model selection because the number of possible scenarios increased dramatically. For example, if the growth models differed between the sexes, then there are $5 \times (5 - 1) = 20$ possible scenarios. If the growth model for each sex was the same and the parameters were either the same or different, then $5 \times (2^1) = 10$ possible scenarios were produced. Since either condition was equally likely, there were simultaneously $20 + 10 = 30$ possible scenarios in the set of candidate models, rather than the 10 considered by Rabaoui et al. (2008). Moreover, the number of scenarios became even larger when one wished to know which parameter(s) differed among subgroups. Consequently, the parameter estimation and calculation for these possible scenarios needed huge computation labor and time. A properly designed sequential examination could greatly reduce computation requirements and is recommended for comparison among subgroups. Computation requirements are further reduced by not including models with little relevance to the question of interest.

4.3.3. Implication of sexual dimorphism

Although the best model fitting the data was the same for each sex, the fitting of other growth models differed slightly between the sexes. For females, the power model was better than the Gompertz growth model and vice versa for the males. The logistic growth model was poorly fit for females but fitted better for males (Table 10). The higher support given to the Gompertz and logistic growth models at smaller asymptotic lengths (Fig. 18a and b) resulted in divergent model-averaged growth curves, because females attained higher lengths-at-age than did males (Fig. 19). The observed sexual dimorphism in growth for Japanese eels which might be due to differences in life history strategies between sexes, with females probably adopting a “size maximizing” strategy to become mature at as large a size as possible, while males apply a “time minimizing” strategy to become mature as soon as possible (Helfman et al., 1987; Oliveira, 1999).



4.4. Estimation of mortality rates by mark-recapture experiments

4.4.1. Validity of assumptions in mark-recapture experiments

Assumptions in mark-recapture experiments, such as negligible immigration and emigration, constant F , M , S and μ , no tag loss (short-term instantaneous tag loss or long-term tag shedding), no tag-associated mortality and all tags were found and reported are very important. A high degree of the violation or deviation from these assumptions may consequently influence the estimation or conclusion of the mark-recapture experiments (Seber, 1982; Schwarz & Seber, 1999).

4.4.1.1. Assumptions of constant F and M , all marks reported and no mark-associated mortality

Constant F and M among eels of the same origin and mark throughout the study period from release to the last recapture were probably not violated in some degree. The fishing efforts remained stable (66 ± 13.6 units fisherman⁻¹ day⁻¹) (Lin and Tzeng, 2008a), and thus, the assumption of constant F seemed reasonable during study period. The duration of the mark-recapture study was relatively short (146 and 220 days), of which constant M could be reasonably assumed (Paulik, 1963). All eels caught by the cooperative fishermen were all examined for marks and tags at the Fisheries Research Institute of Taiwan in Donggang. Therefore, it was sure that all recaptures were reported and recapture dates were recorded correctly.

All eels marked with CHIP, C-FC or P-FC survived during the 2-day recovery period and instantaneous tag-associated mortality was zero in both 2005 and 2006 experiments. The long-term mortality due to marking has been found to be small for other anguillids. The mortality rate due to coded wire tag was 0 % for farmed European eel *A. anguilla* during 1, 3 or 4 weeks (Thomassen et al., 2000; Simon & Dörner, 2005). Zero mortality was also found in *A. rostrata* marked by hot branding after 50 days of rearing (Caron et al., 2003). Therefore, long-term mortality due to insertion of microchip was probably small as found in *A. anguilla* and *A. rostrata*. However, the long-term mortality due to fin-clipping was unclear, which might consequently influence the estimation of mortality rates.

4.4.1.2. Assumptions of no tag/mark loss

The instantaneous loss rate of microchips was also zero for both 2005 and 2006 experiments, because the loss was checked by immediately after insertion and during the 2-day recovery period, but the long-term tag shedding rate was still unclear.

According to Thomassen et al.(2000) and Simon & Dörner (2005), the loss rate of coded wire tag after 1 week for small- sized European eels (mean TW of 3.8 g) was (2.6 %) higher than 0.4 % of large-sized eels (mean TW of 10.2g). Microchips were inserted in the dorsal musculature according to Simon & Dörner (2005), and the eels were even larger in this study (larger than 50g), so the long-term tag shedding rate for the microchip was probably small. On the other hand, the long-term shedding of fin clipping resulted from the fully regeneration of the clipped fin and disappearance of the identifiable scars. For the common carp in the tropical Bangalore, the identification rates of clipped pectoral and caudal fins after 6 months ranged from 96.7 to 100 %. In addition, pink and identifiable kinks were found in the clipped caudal fins (Basavaraju et al., 1998). Most of the eels were recaptured within 2 months after release, which might be relatively short for the clipped fins to regenerate without identifiable scars. The recapture of C-FC culture eels after 220 days in 2006 also implied the fins did not fully regenerate. Therefore, the influences of tag loss (microchip or fin clipping) on the estimate of mortality rate, either due to short-term instantaneous tag loss or long-term tag shedding, were assumed to be negligible.

4.4.1.3. Assumptions of no emigration and immigration

The assumption of no emigration and immigration are also important because the two kinds of movement may confound the estimates of F and M and are hard to discriminate them without proper experiment designs (Seber, 1982). The marked or tagged anguillids are sedentary and show considerable fidelity to the homing area, and are usually recaptured near their release site (Oliveira, 1997; Baras et al., 1998; Lamonte et al., 2000; Aoyama et al., 2002, Jellyman & Sykes, 2003; Laffaille et al., 2005). Moriarty (1986) concludes that the recapture rates of 5.5 ~ 18.5 % can be expected if the eel population is non-migratory. For the 2006 experiment, observed

recapture rates (71.3 and 25.2 % for culture and wild eels) indicated that the marked eel population exhibited restricted movement range that most of the marked eels were believed to remain in the fishing ground during the study period of 2006.

Small eels (TL of around 200 mm) recruited in the study area and became
5 vulnerable to the shrimp net fishery mainly in January and February (Lin & Tzeng, 2008a), while the large silver eels in the catch are found almost only in the period from November to January (Han et al., 2000). Most eels were recaptured within two months after release, before October 14, 2006, for 2006 experiment, indicating that the
10 examined population was less influenced by the immigration of new recruits or downstream migration of the silver eels. Therefore, the immigration and emigration of the eels might play a minor role for the 2006 experiment.

Small recapture rate for the 2005 experiment (1.5 ~ 5.6 %) also suggested a limited
downstream movement of the eels released from the upstream release site to the fishing
ground in the lower reach. Only marked eels that moved to the fishing ground were
15 vulnerable to the fishery and were thus recaptured and therefore, the assumption of negligible emigration was probably not valid for the 2005 experiment. Moreover, the low number of recaptures (19 eels) appeared too small to provide reasonable estimation of mortality rates and thus only the estimates of F and M from the 2006 experiment were used in the following assessment.

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4.4.2. Different recapture rates between origins and marks

Recapture rates differed significantly between the eel origins but not between the
marks (CHIP vs. C-FC in cultured eels and CHIP vs. P-FC in wild eels) for both 2005
and 2006 experiment. The recapture of CHIP eels was not influenced by the length at
25 release for the 2006 experiment. All wild eels released were previously caught by the shrimp nets and the net avoidance of the marked eels was found not significant (Dekker,

1989). Therefore, it was hypothesized that the behavioral differences between wild and culture eels were the possible reasons resulting in the differences in recapture rates between culture and wild eels, while the length related selection by the shrimp nets as well as the size-related differences in activities (Glova & Jellyman, 2000) were less influential.

Wild eels were possibly better accustomed to find natural shelters, such as crevices under rocks or to bury themselves into the bottom sand or mud (Dou & Tsukamoto, 2003; Aoyama et al., 2005). The inexperienced cultured eels, which spent most of their life in the culture ponds, might choose all possible shelters, including the shrimp nets.

As a result, they were more vulnerable to the fishing gear, leading to the higher recapture rate, especially in the first two days after release in the 2006 experiment (Fig. 20b). The lower recapture rate of cultured eels in the 2005 experiment probably also indicated a different movement pattern for the cultured eels that the cultured eels were less willing to move downstream or suffered a higher mortality at the release site.

However, the number of recaptures was insufficient to make a further hypothesis.

4.4.3. Different mortality rates between origins and marks

Estimates of mortality rate seemed to be affected by both origins and marks, and their relationships were probably highly complicated. The fishing mortality rate (F) of the cultured eels was about 10 times higher and the survival rate was about 77 % lower than those of wild eels marked by CHIP. The lower survival rate of culture eels was consistent with that for reared salmon in a wild environment (Saloniemi et al., 2004; Jonsson & Jonsson, 2006). The high F value of cultured eels resulted from the high number of recaptures and early recapture dates, which were probably related to the activity of seeking suitable shelter. Compared to F , the M value of cultured eels was 24 % higher than that of CHIP wild eels, implying that the adaptability and survival of

cultured eels in the wild environment were only marginally poorer than for wild eels. This was supported by the fact that the cultured eels were still caught after two months (Fig. 20*b*). The escaped cultured eels in July 2004 due to Typhoon Mindulle could be found in the eel catches in following 2005 and 2006 (Chu et al., 2006; Lin & Tzeng, 5 2008*a*), which further supported the ability of cultured eels to survive in the study area.

Higher F and M values for wild eels marked by P-FC were unexpected because the recapture rates of the wild eels marked by CHIP and P-FC did not differ significantly. More than 97 % of the wild eels marked by P-FC were recaptured in the first two days after release and none were recaptured after two weeks (Fig. 20*b*), which consequently 10 resulted in the high values of F and M . Pectoral fin regeneration (Croombs et al., 1990; Rogers et al., 2005) seemed unlikely because the recapture period from release to last recapture was extremely short (14 days after release). Emigration of marked eels overestimated the fishing mortality and underestimated the natural mortality (Seber, 1982), which appeared insufficient to explain observed higher values in both F and M . 15 Possible explanations were (1) size dependent mortality and (2) behavioral change from fin clipping. The body size of wild eels marked by P-FC was smaller than those by CHIP and these small-sized wild eels probably experienced a higher mortality than larger eels, and the pectoral fin is important for the movement and locomotion and the clipping might reduce its mobility. Wild eels with a clipped pectoral fin might be less 20 able to escape the shrimp nets and resulted in higher fishing mortality. The remainders escaping the nets finding shelters might be more sedentary, less active during recovery from the clipping, or have a smaller home range than the wild eels marked by CHIP and hence were not available to the following sampling. However, evidences in this study were not enough and future studies are needed.

4.5. Sex-specific maturation curves

The significant differences in the maturation (silvering) curves between sexes of the Japanese eel that the females attained a larger size than the males implied a sexual dimorphism of the eels, which was also common in *A. anguilla*, *A. rostrata*, *A. australis* and *A. dieffenbachia* (Poole & Reynold, 1996; Oliveira, 1999; Jellyman, 2001; Tzeng et al., 2003). This might relate to sex-dependent life history strategies. The females probably adapted a “bigger is better” strategy that they tended to have a longer growing period (yellow eel stage) to reach a larger size. Bigger the size of silver eels, higher the fecundity and better egg quality might be. Compared to females, the males seemingly adapted a contrary strategy called “faster is better” that they tended to become silver eels as sooner as they can to avoid the loss of reproduction potential due to mortality in the older ages (Helfman et al., 1987; Oliveira, 1999; Jellyman, 2001). However, this hypothesis neither indicated that the size was not important in the silvering of the males, nor indicated that they could become silver eels with an extremely small size. The size of the eels were important for silvering of both female and male eels because the eels have to store enough energy required for long-distance spawning migration (van Grinneken & van den Thillart, 2000, van Grinneken & Maes, 2005), which was highly related to the length, weight, fat content or condition factor (Larsson et al., 1990; Han et al., 2000). This implied the existence of a “critical” or “minimum” length required for the silvering the eels to reach the spawning ground, which also indicated that the silvering of the eels modeled by lengths was more reasonable than by age.

Moreover, other than the logistic model, the generalized logistic model including an asymptotic maturation rate was proposed to describe the silvering process because not all eels in the longer length classes became silver eels in some cases (De Leo & Gatto, 1995; Bevacqua et al., 2006). However, in the preliminary examination, the estimates of asymptotic maturation rate in both females and males reached one, indicating that the

common logistic curve was necessary to describe the maturation process of the eel in the study area.

4.6. The exploitation status of the eel fishery

5 4.6.1. Criterion level of spawner per recruit for self-sustainable

It has been suggested that at 30 % of unfished SPR, 80 % of the European and American fish stock studied were able to produce sufficient offspring to replace themselves (Mace & Sissenwine, 1993). A %SPR of 35 to 40 % was also proposed for better protection of spawner biomass under random or serially correlated recruitment
10 (Clark, 1993; 2002). However, the fishery exploitation might reduce the spawner biomass of anguillid more due to its catadromous life history, longer life span and slower growth rate and hence a more conservative level of 50 % of unfished spawner per recruit was suggested (Hoyle & Jellyman, 2002). Under current exploitation level, %SPR was about 32 to 37% of the unfished level, and therefore, the recruitment
15 overfishing probably has occurred in the study area. Although the catch of glass eel in Taiwan seemed not showing signs of decreasing (Tzeng, 1997; 1998; 2006), the time lag of 7 to 14 years for *A. anguilla* between recruitment decline and adult stock decrease (Feunteun, 2002; McCarthy et al., 2008) might mask the declining trend in population size. This further stressed the importance of precaution approach (Russell & Potter,
20 2003), as to maintain sufficient level of spawner biomass before the beginning of the reduction in catch of glass eels.

4.6.2. Risks of overfishing

F_{cur} was substantially possible to be larger than $F_{0.1}$ (30 to 40 %) and less likely to
25 be larger than F_{max} (1 to 5 %), thus the eel fishery in the study area was probably fully-exploited stage in the view of YPR. On the other hand, the recruitment overfishing

might have been occurred, as indicated by the high risks of F_{cur} being larger than $F_{40\%}$ and $F_{50\%}$ (23 ~ 98 %). The risk of recruitment overfishing was higher for females than for males, and higher than that of growth overfishing. Moreover, under current F_{cur} , mean %SPR has decreased to be lower than the critical level, implying that the Japanese eels were more easily to suffer a deficiency in spawners, similar to other anguillids (Hoyle & Jellyman, 2002). The eels were mainly harvested as glass eels and thus, it was more reasonable to retain the spawning population, rather than harvesting the eels in yellow eel stage under “optimum level” from YPR model. Because the recruitment overfishing has likely occurred with high probabilities, the eel fisheries in the study area that the eel resources seemed in the “red line”, in which the recruitment overfishing occurred. As the results, the management of the eel fishery and control of eel escapement are urgently needed.

4.6.3. Sensitivity analysis of the parameters

F_{max} and $F_{0.1}$ depended mainly on two processes: natural mortality and growth and $F_{0.1}$ seemed more robust to variation in M and K and was independent to F_{cur} , which was in consistent with King (1995). The variance of F_{max} and $F_{0.1}$ fluctuated more than the mean, indicating that the uncertainty in the parameter estimation influenced variation of F_{max} and $F_{0.1}$ more than the means. On the other hand, $F_{40\%}$ and $F_{50\%}$ was mainly affected by M , K and F_{cur} , indicating its major impacts on spawner biomass. The sensitivity of risks of growth and recruitment overfishing, i.e. P_{Grow} , $P_{Grow0.1}$, $P_{Recruit40}$, and $P_{Recruit50}$ was much complicated than the mean and variance of the biological reference points. P_{Grow} and $P_{Grow0.1}$ were influenced by the means and variances of F_{cur} and M , while K played a smaller role, in contrast to the case of F_{max} and $F_{0.1}$. $P_{Recruit40}$ and $P_{Recruit50}$ depended on more factors, such as mean and variance of F and M , mean of K , changes in length-at-50% maturity, and steepness of maturation curve in a small

degree (Table 21 and 22). Different sensitivities between biological reference points and risks of overfishing might be due to that both mean and variance of the distributions of biological reference points were influenced by uncertainty in parameter estimation.

In traditional approach of using YPR and SPR models, only the location of the limiting biological reference point (ex. F_{max}) was calculated from available estimates of parameters and the inferences were made by comparing whether current state (F_{cur}) was larger than limiting biological reference point. In this approach, the uncertainties in parameter that influenced both mean and variance was neglected, and thus the determination of overfishing might be thus biased and the corresponding decision might be away from reality (Chen & Willson, 2002). This highlighted the importance of incorporation of uncertainty from more aspects to provide an estimate of risk with more reality.

Besides, we were highly uncertain that whether the estimated F and M were near to real values or not because of the lack of comparing studies. Especially for F because the fishing effort, namely number of shrimp nets used, seemed at a high level that might result in high exploitation pressure (Lin & Tzeng, 2008a). Therefore, it was necessary to consider the worse situation when the current fishing mortality rate was higher than our estimates. An fishing mortality rate of $0.15 \sim 0.20 \text{ year}^{-1}$ with corresponding exploitation rate of $40 \sim 57 \%$ led to recruitment and growth overfishing with nearly 100 % confidences for both sexes, which appeared not unrealistic for the eel population. Moreover, the spawning biomass of the eels was much reduced even under mild exploitation rate that %SPR was below 50 % under the exploitation rate of 10 % for *A. australis* (Hoyle & Jellyman, 2002). Therefore, the exploitation of eel resources in the study area seemed not sustainable and it was again recommended that the eel fishery needed to be managed and controlled.

4.6.4. Different vulnerabilities to overfishing between sexes

It seemed worse that females were found to be more vulnerable to both growth and recruitment overfishing, as indicated by the departure of risks of both growth and recruitment overfishing between the females and males (Fig. 30). Different vulnerabilities between sexes were probably due to the slower growth rate (smaller K) and larger size at maturity for the females. Moreover, because (1) the females were dominant in the study area (Han & Tzeng, 2006), (2) the silver eels were contributed more by females residing in the brackish study area (Han & Tzeng, 2007) and (3) the biomass of females might be more related to recruitment of elvers than the males, management of the eels based on the females appeared more practical in increasing the spawning biomass.

4.7. Possible sources of uncertainties

For selection of best growth models, the errors in lengths-at-ages were assumed to be independent but in fact were not because the back-calculated lengths-at-ages were retrospective. However, the effects of the retrospective lengths-at-ages data on the shape of the growth model and on parameter estimation was probably small (Jones, 2000) and less influential. The otolith age estimates for the *A. japonica* studied were validated in Lin & Tzeng (2008b), but the random effects on the estimation of growth due to variation in ageing among readers were not evaluated (Cope & Punt, 2007). Also, the two-stage von Bertalanffy growth model proposed by Melià et al. (2006) or more generally, any two-stage growth model for sexually undifferentiated and differentiated eels was not considered in the set of candidate growth models because one crucial parameter, the length at sex differentiation was unknown for *A. japonica*. Such kind of uncertainty requires further study.

In the estimation of mortality rates using mark-recapture data, it was more unclear

that why the wild eels marked with pectoral fin clipping had higher fishing and natural mortality rates. If this was due to size-related mortality and mark-associated mortalities, additional uncertainties might be introduced to the YPR and SPR models. Also, the wild eels were unfed during the acclimation period, because they did not eat the commercial feed at all (the culture eel did). The wild eels marked with pectoral fin clipping were smaller in length than wild eels marked by microchips. Therefore, the pressures resulting from the starvation period in the accommodation period might be more serious for the smaller eels, which might partly account for their higher mortality rates. According to the growth parameters, the natural mortality of the eels in the study area was 0.292 year⁻¹ by Pauly's empirical formula (Pauly, 1980), similar to 0.177 year⁻¹ from mark-recapture. However, other source the level of fishing mortality rate was limited and thus we were more uncertain about the current level of fishing mortality rate. Although sensitivity analysis provided some insight on the consequence of misspecification of current fishing mortality rate, we should be more conservative in determining the current state of the eel population.

The uncertainties in estimation of length-weight relationship, growth parameters, fishing and natural mortality rates, and maturation parameters with the fluctuation in number of shrimp nets used were incorporated into YPR and SPR models using Monte Carlo simulation, but it did not indicate that all kinds of uncertainties were included in our simulation model. The uncertainties in model selection for growth model was probably small, but our model still suffered uncertainties in model selection due to the uses of allometric growth for length-weight relationship, exponential curve for mortality and logistic curve for maturation *a priori* without considering alternatives (Rabaoui et al., 2007). Although the effects of variation in parameters of length-weight relationship on the YPR models were small (Chang et al., 2008), how this kind of the uncertainty affected the assessment models (e.g. YPR or SPR models) was still not fully examined.

The YPR and SPR models in this study were basically deterministic because the parameters were implicitly assumed to be constant among different cohorts and the natural variation in parameters was not considered. Introduction of natural variations in the parameters into the YPR and SPR models was more or less analogue to increase the variations of parameters in our sensitivity analysis, resulting in enhanced variation of related biological reference points (Table 19 and 20) and in changed risks of growth and recruitment overfishing (Table 21 and 22). A lack of knowledge about the natural variation in the parameters made this assessment difficult. The steady state of the population structure was assumed in per-recruit models, which was hard to be verified that the exploitation itself might make the population not steady (King, 1995). Although the recruitment of the eels were relatively regular that occurred in winter, it was highly variable in annual catch numbers in Taiwan (Fig. 2.). A more conservative limit SPR level was suggested to cope with varying recruitment (Clark, 1993), but our YPR and SPR models were still subject to varying recruitment of the eels, which was necessary to be evaluated in the future studies.

4.8. Recommendations for management and conservation of the eels

The sizes and CPUEs of eels caught varied seasonally, which can provide useful information on the fishery management. According to the dominance of small eels in the shrimp nets, most of the eels recruited to the fishing ground and became vulnerable to the shrimp nets in winter (January and February), one or two months after the elver recruitment (Tzeng, 1984; Tzeng 1997; Tzeng, 1998; Tzeng, 2006). The temporal changes in the CPUE and length composition were similar, that reached to the largest in summer, decreased in fall and winter, and increased again the next spring. The winter may be least favorable season for using shrimp nets because the catch might largely consist of small eels less than 400 mm. If the shrimp nets were reduced or ceased in

winter, it might reduce the pressure of growth overfishing due to smaller exploitation pressure, especially on the small eels.

The control of fishing mortality rate and exploitation rates, as well as the regulation of minimum and maximum legal sizes has been proposed as the candidate management acts for the eel fishery in study area. Current fishing mortality rate seemed critical in possibilities of both growth (P_{Grow} , $P_{Grow0.1}$) and recruitment overfishing ($P_{recruit40}$, $P_{recruit50}$). Control of fishing mortality rate or exploitation rate was effective in control of overfishing, and a 40 to 50 % reduction in F_{cur} can make the F_{cur} below $F_{50\%}$ with a possibility more than 70 %. The restriction in minimum legal size was effective in reducing P_{Grow} and $P_{Grow0.1}$ but it was relatively less efficient in reducing $P_{recruit}$. On the other hand, the restrictions in maximum legal sizes can better maintain the spawning biomass than minimum legal size, but subsequent YPR also decreased accordingly. Since the risk of recruitment overfishing was more urgent for the eel fishery and maintaining sufficient spawning biomass was of more interest (McCarthy et al., 2008), the control of fishing mortality rate with the restriction in the minimum and maximum legal size was preferred. Therefore, a 40 % reduction in current fishing mortality and enforcement of minimum legal length of not less than 500 mm, along with a maximum legal length of not larger than 850 were suggested to maintain sufficient amount of spawning biomass and make the exploitation on the elvers sustainable for this eel fishery in the lower reach of Kao-Ping River.

5. Conclusion

Japanese eels *Anguilla japonica* in the lower reach of Kao-Ping River have been harvested from elver, yellow and silver eels. Its population structure, such as sex ratio and length compositions in the study area, were found to be significantly influenced by both escapement of cultured eels and use of shrimp nets. The effect of escaped cultured eels on local population structure lasted less than 2 years. The continuous and increasing use of shrimp nets might influence the eel population more than the traditional fishing gear, eel tube, because small eels were more vulnerable to the shrimp nets.

To understand the eel population dynamics, the growth was estimated by otolith annulus readings, mortality rates by mark-recapture data and maturation curves by logistic curves. The otolith annulus of the eels was reliable in age estimation, as validated by known-age cultured eels and marginal increment ratios of the wild eels. Among the five candidate models, information theory indicated that von Bertalanffy growth model with sex-specific parameters fitted the lengths-at-age data and provided nearly the same fit to the averaged model. It was considered as the best one to describe the eel growth. The estimates of fishing and natural mortality rates by mark-recapture experiment were affected by both eel origins (wild and cultured) and marks (microchips and fin clipping). The parameters in maturation curves described by logistic curves were different between sexes, reflecting sex-dependent life history strategies of the eels.

The increasing use of shrimp nets might increase the fishing mortality rate and subsequently increase the risks of both growth and recruitment overfishing. The risk of growth overfishing was considerable as indicated by the yield per recruit model, and the risk of recruitment overfishing was higher and probably has occurred. The eel population in the study area was fully-exploited in the sense of YPR and overfished in the sense of maintaining sufficient spawning biomass. According to sensitivity analysis, the uncertainties in fishing and natural mortality rates, growth parameters and maturity

curves might influence the risks of overfishing.

According to our analysis, control of fishing mortality rate (or exploitation rate) and the restriction of the minimum and maximum legal size were the preferred management tactics against both growth and recruitment overfishing. A 40 % reduction in current
5 fishing mortality and enforcement of minimum legal length of not less than 500 mm, along with a maximum legal length of not larger than 850 were suggested to maintain sufficient amount of spawning biomass and make the exploitation on the elvers sustainable for this eel fishery. These can be implemented by regulating the total number of fishermen, the number of gears, eels harvested per fisherman, fishing
10 limitation in certain seasons, and restriction of the maximum legal size. Other possible management acts, such as setting the protection area and release of elvers, yellow or silver eels, still need to be evaluated in the future.



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5



Figures

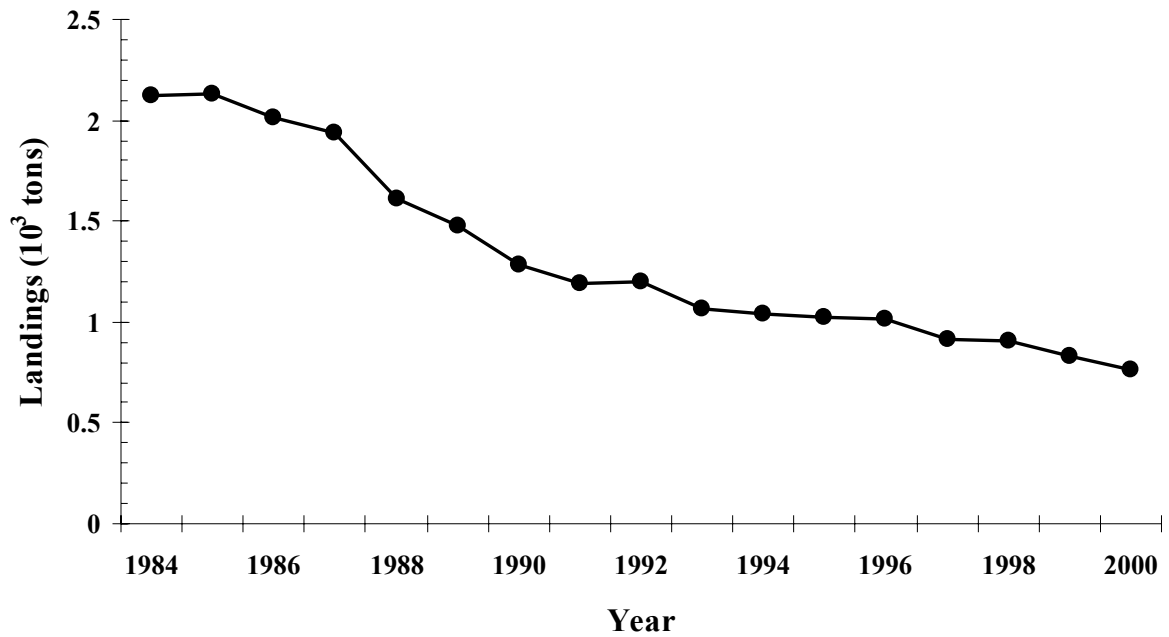


Fig. 1. Annual landings of the adult Japanese eels from 1984 to 2000 in mainland China, Korea and Japan (from FAO statistic).

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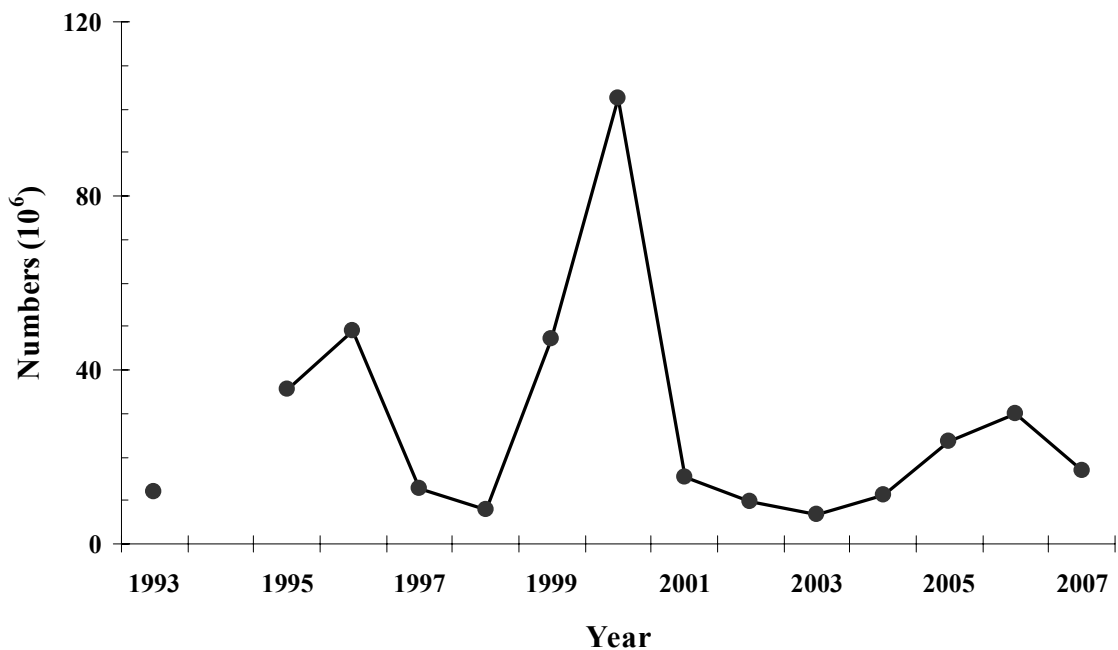


Fig. 2. Annual catches of glass eels in Taiwan during the period from 1993 to 2007 (compiled from the Taiwan Fisheries Yearbooks, Fisheries Agency, Council of Agriculture).

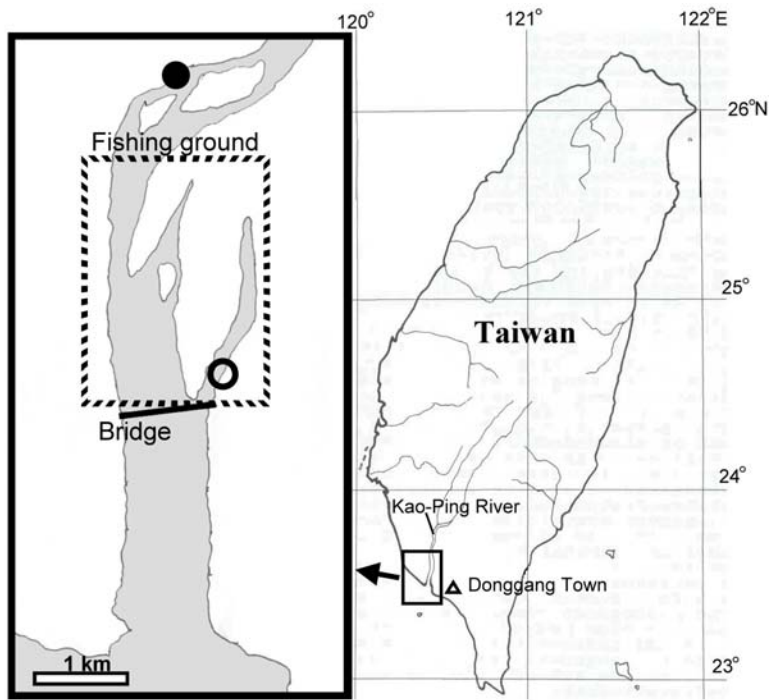


Fig. 3. The study area (Open solid line in the square area represented the lower reach of Kao-Ping River in southern Taiwan; and open triangle was the Donggang-Town where cultured eels were collected; broken line indicated the fishing ground of the Japanese eel (*Anguilla japonica*) in the lower reach of the Kao-Ping River. Solid circle, the release site in 2005; open circle, the release site in 2006.

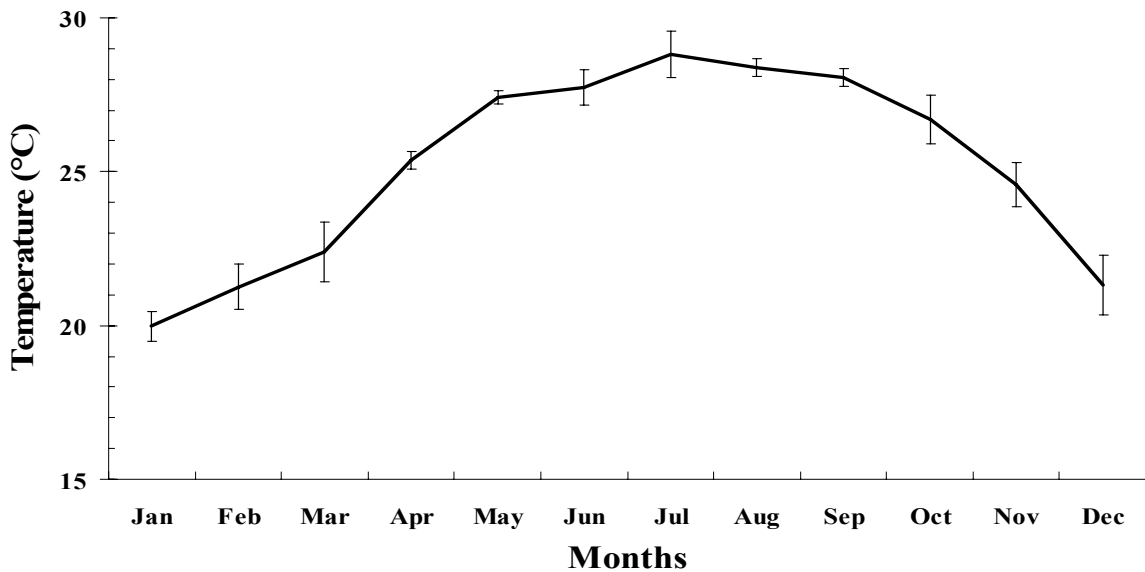


Fig. 4. Monthly bottom temperature (mean \pm SD) at the mouth of Kao-Ping River from 2001 to 2006 (Redraw from Chen et al. 2005, 2007).

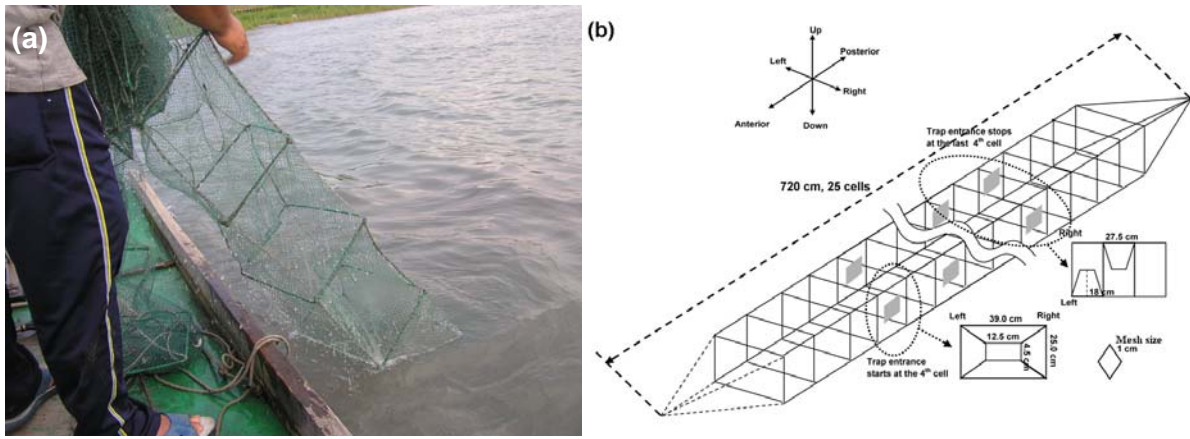


Fig. 5 (a) Retrieving shrimp nets on a small boat. (b) The structure and mesh sizes of a shrimp net unit.

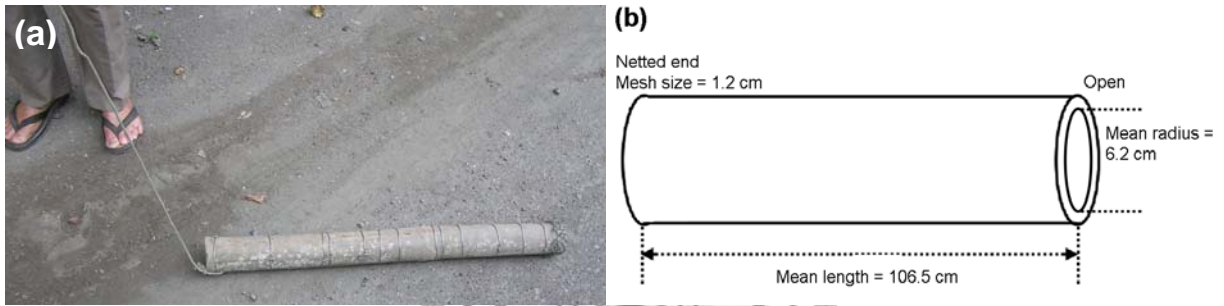


Fig. 6 A diagrams of (a) the bamboo eel tube and (b) the eel tube.

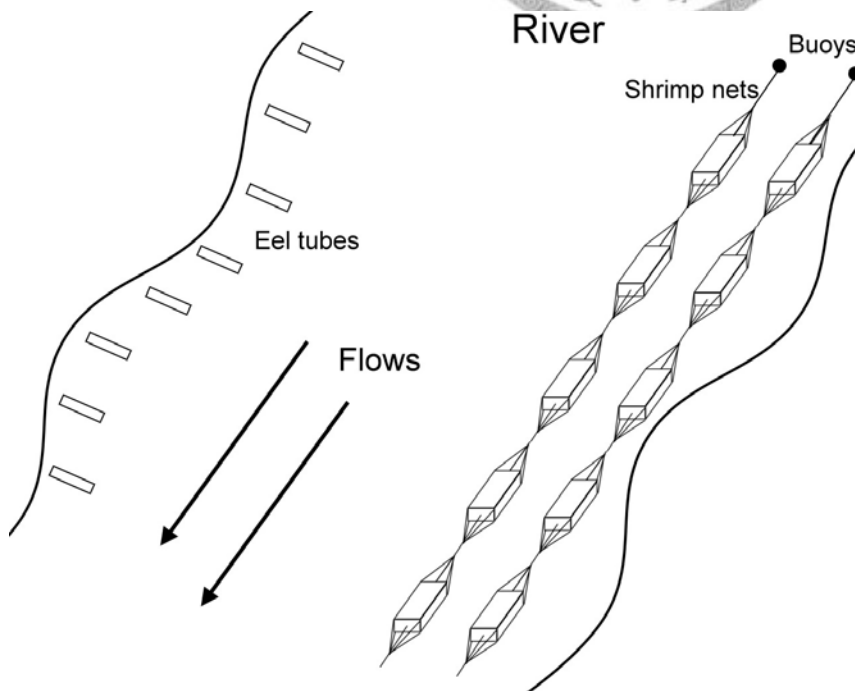


Fig. 7. The way how the two gears were set along the river bank by the fishermen.

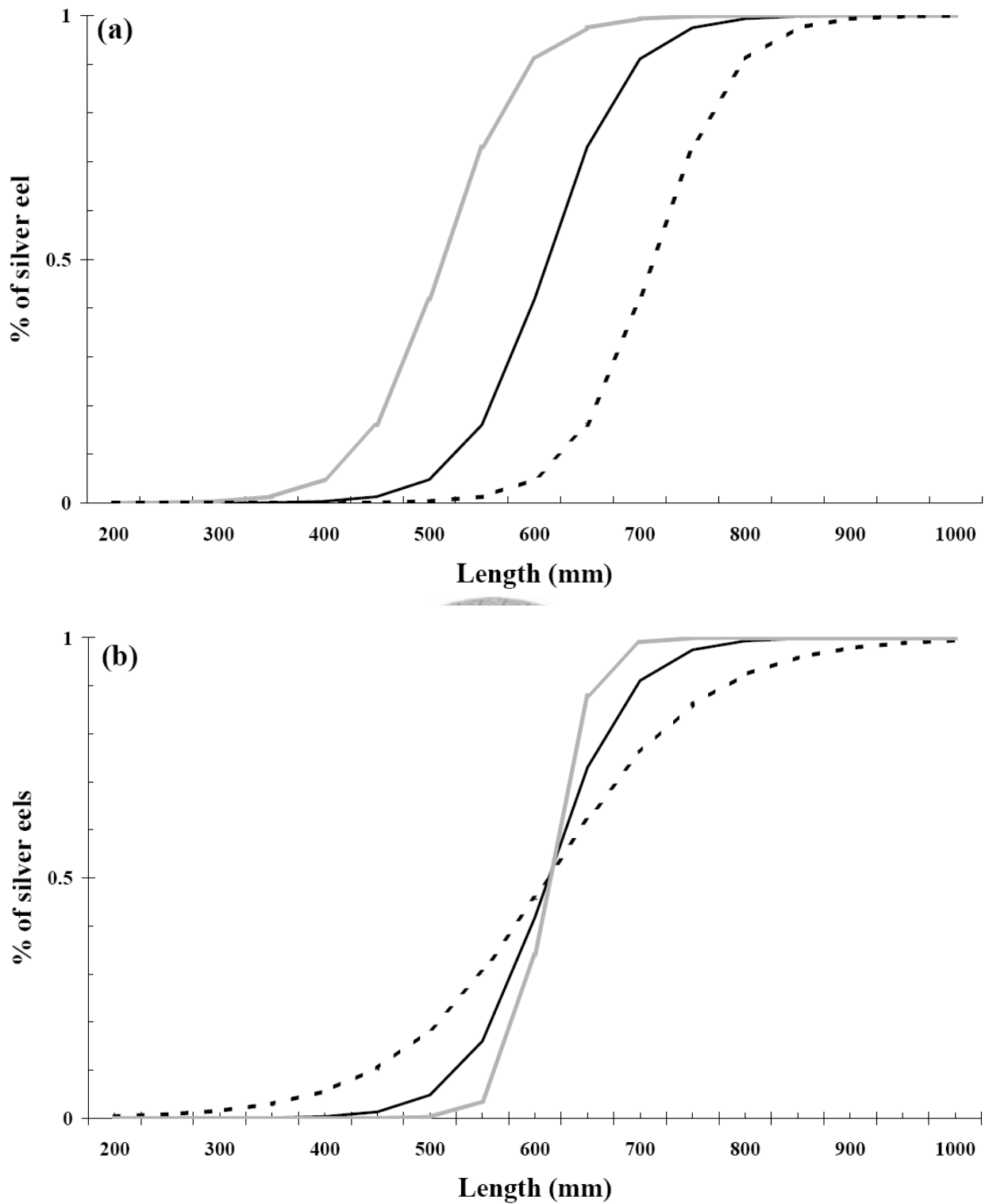


Fig. 8. Logistic maturation curves of the female Japanese eel with (a) $\Delta L_{50} = 0$ (black solid line), 100 (black broken line) and -100 (grey solid line) and (b) $\Delta slope = 1$ (black solid line), 0.5 (black broken line) and 2 (grey solid line), respectively.

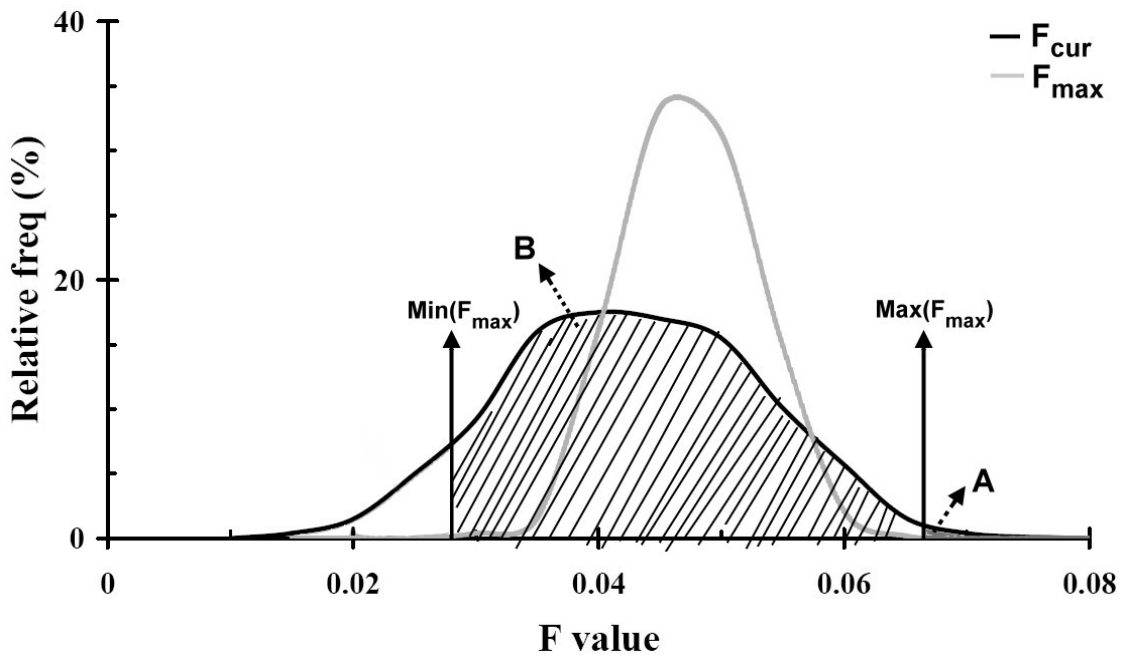
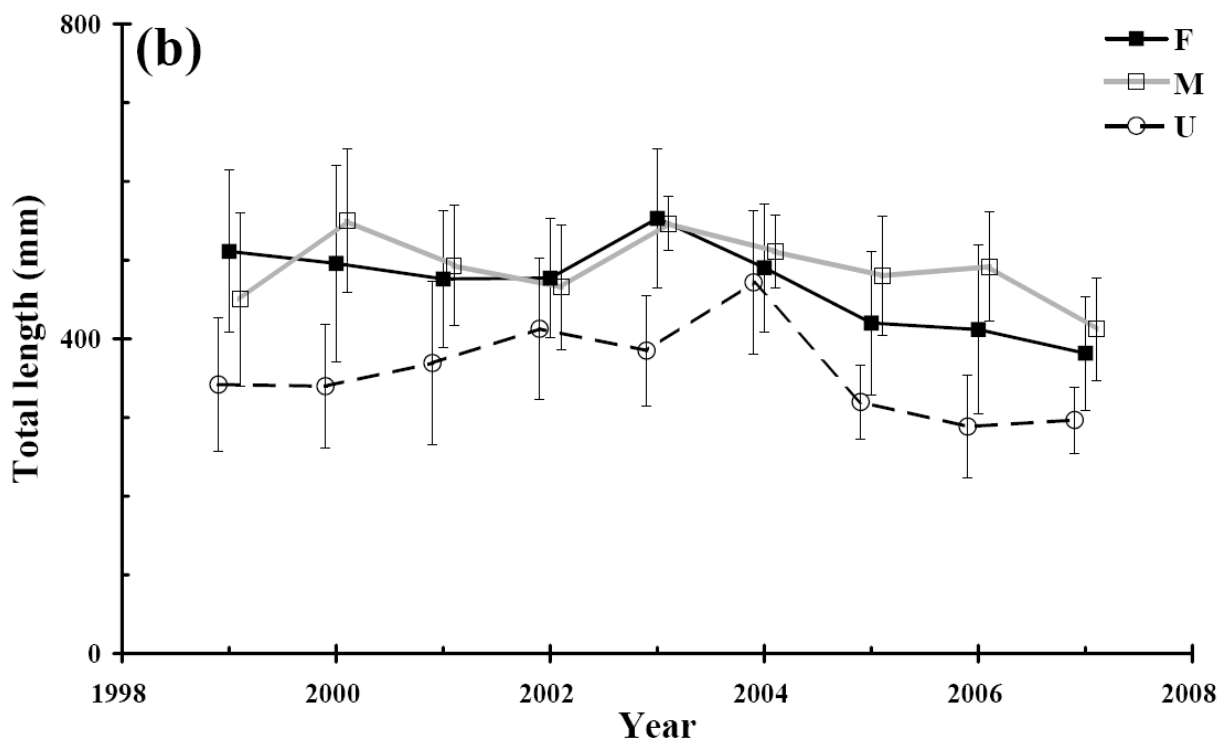
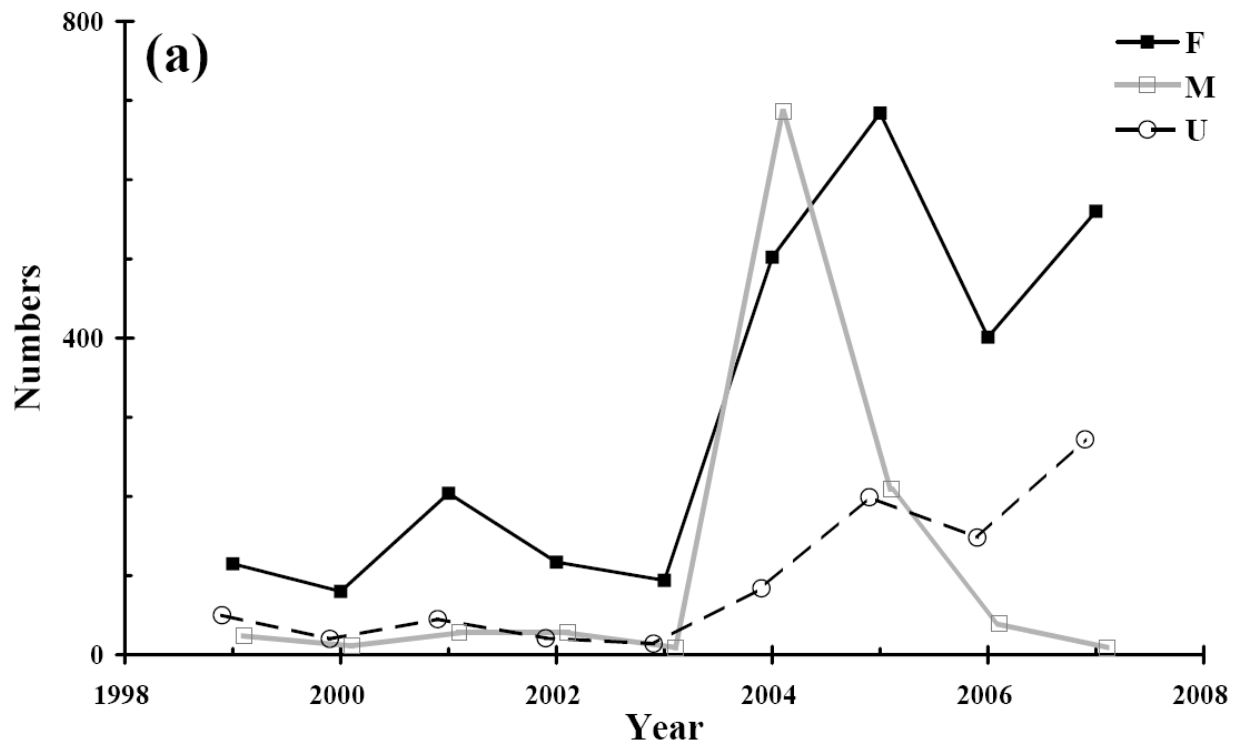


Fig. 9. Diagram showing calculation of the probabilities that current fishing mortality rate (F_{cur}) was larger than a specific BRP, in which F_{ma} was used as an example. Distribution of F_{cur} , (black line) overlapped with that of F_{max} (grey line). The probability that F_{cur} was larger than F_{max} was the cumulative probability of F_{max} corresponded to different confidence level of F_{cur} . The minimal value corresponded to the tailed area from the maximal value of F_{max} (Max(F_{max}), grey area A), indicating we had nearly 100 % that F_{cur} was below this value. The maximal value corresponded to the minimal value of F_{max} (Min(F_{max}), shaded area B), indicating F_{cur} was hardly lower than this value.



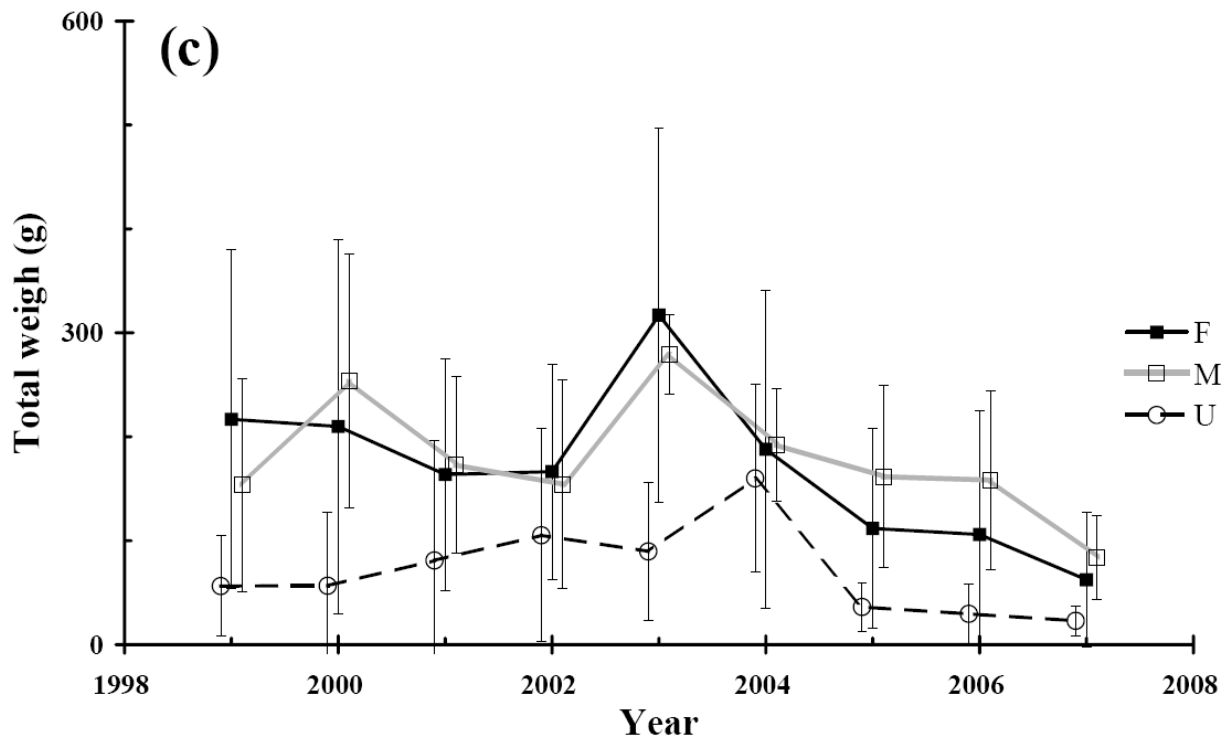
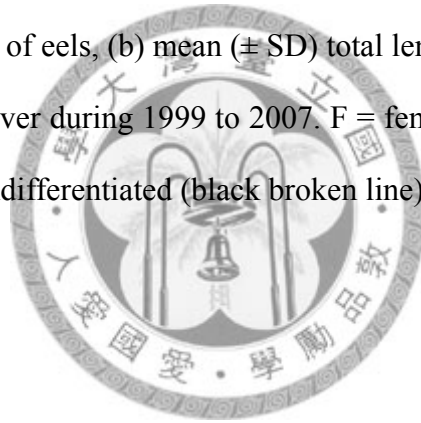
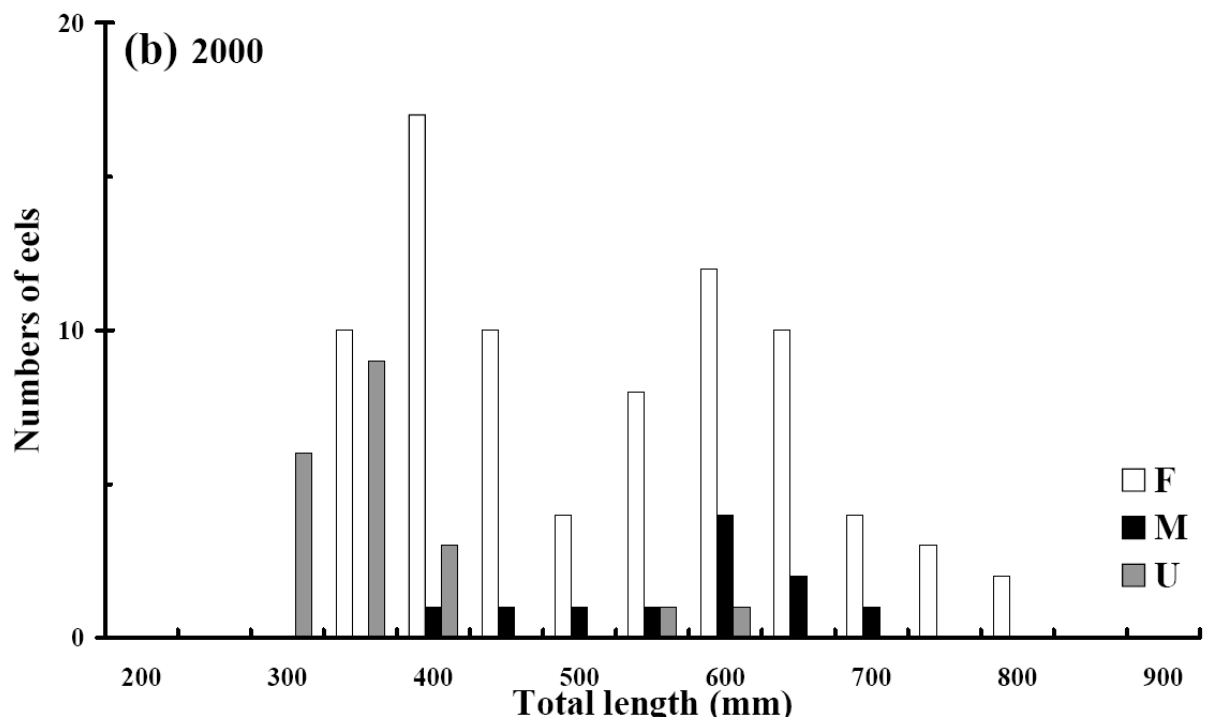
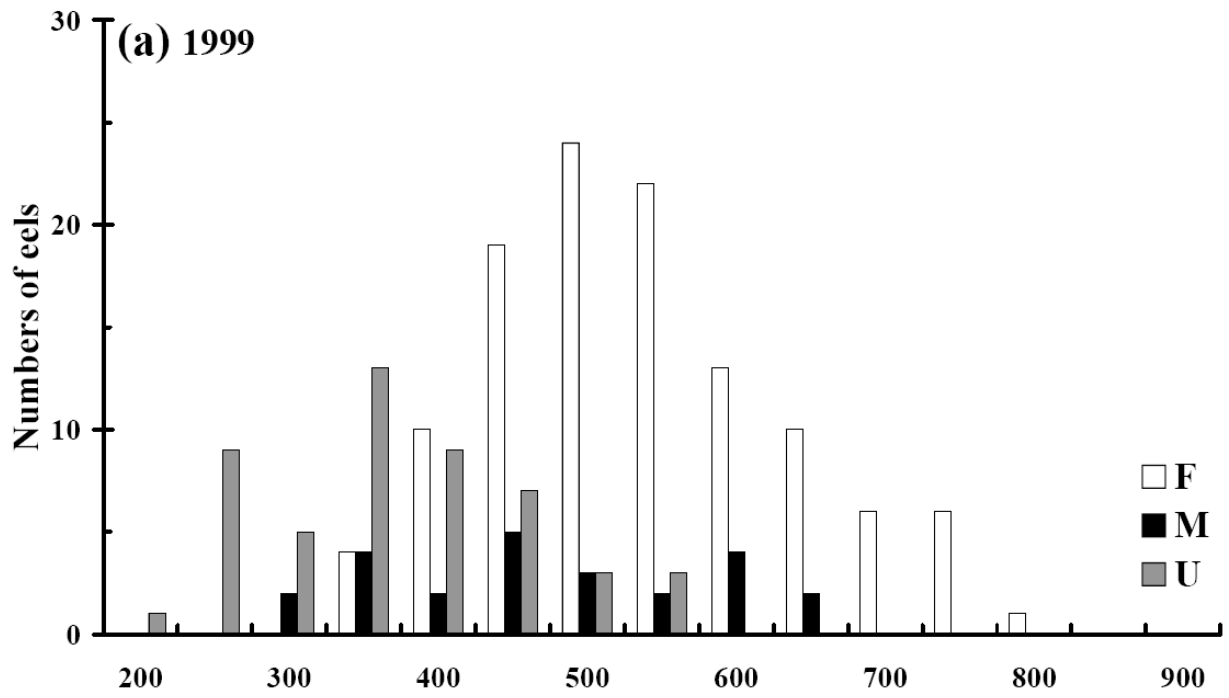
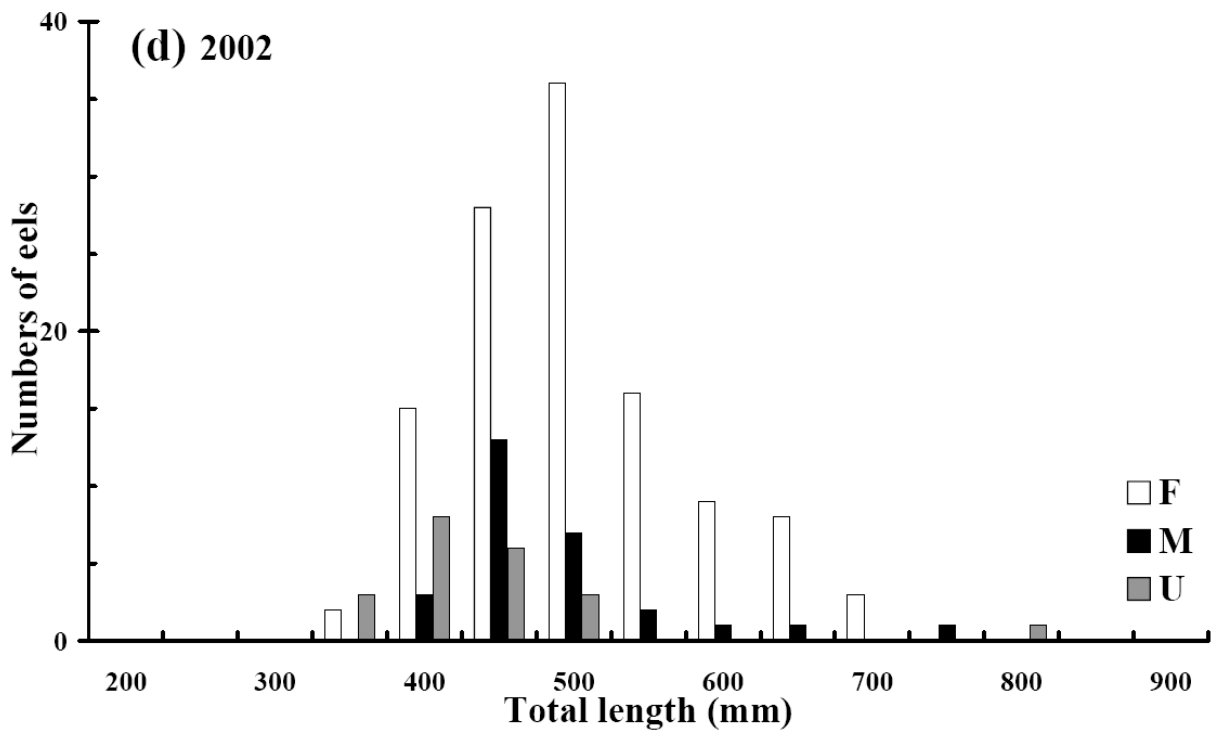
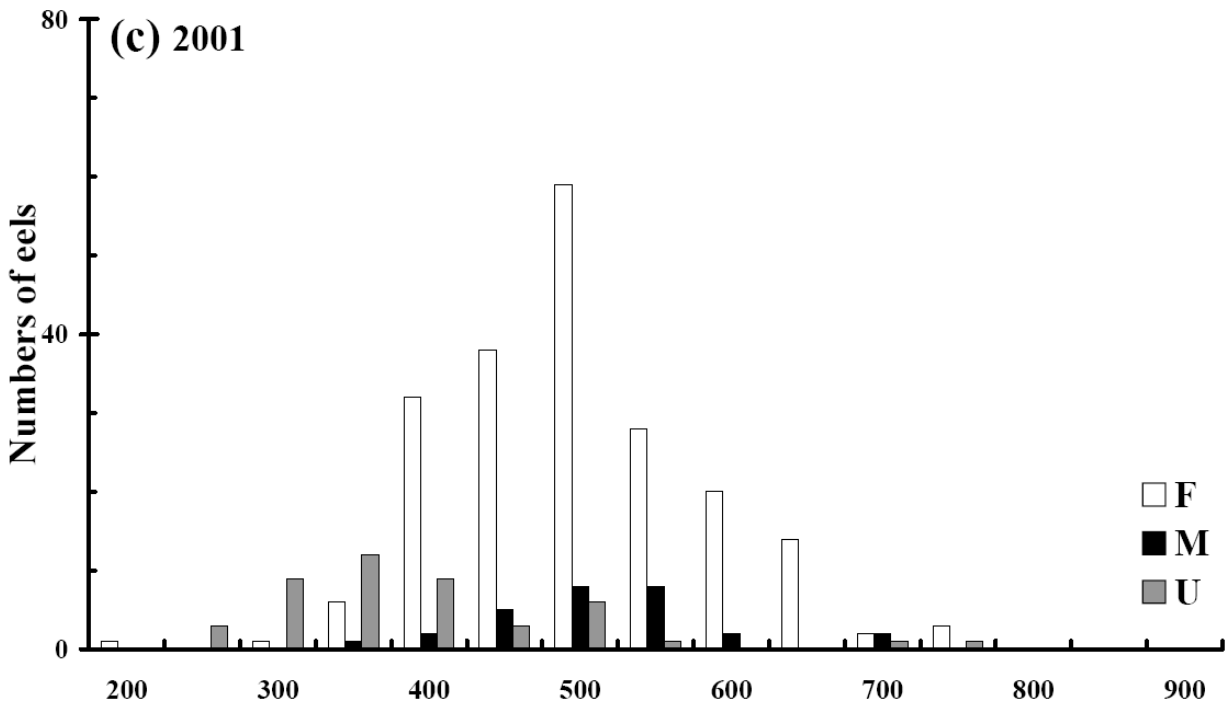
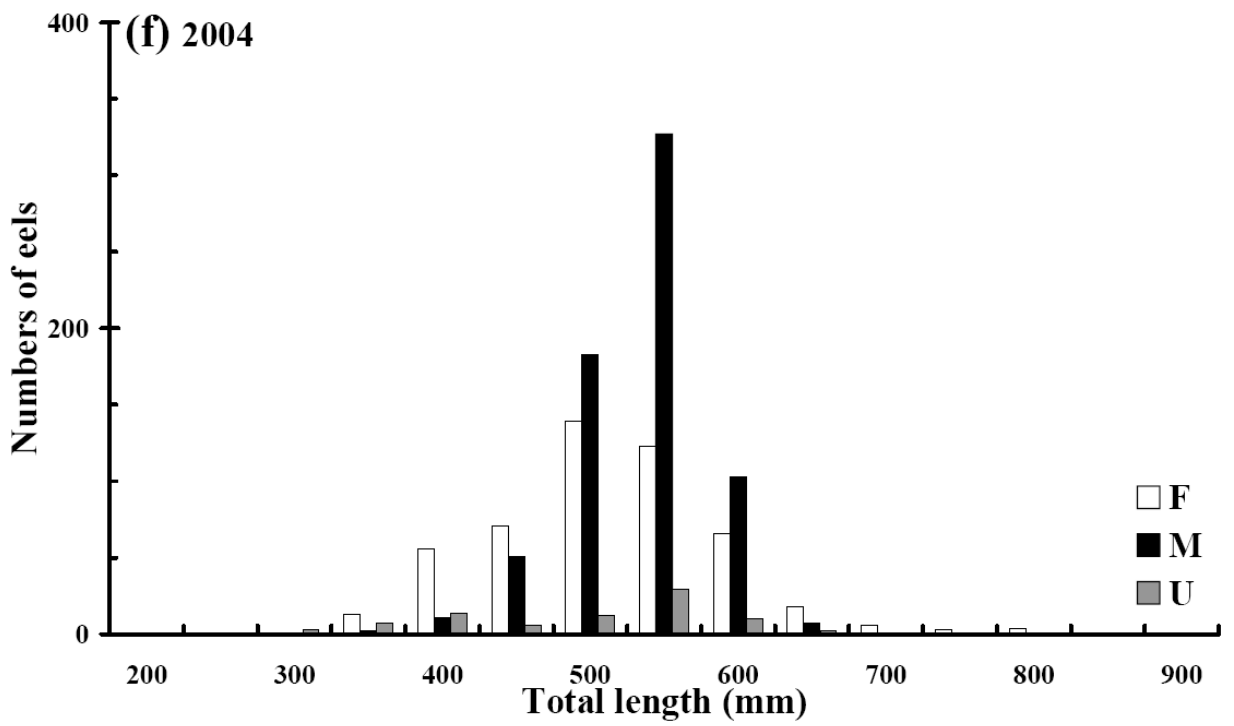
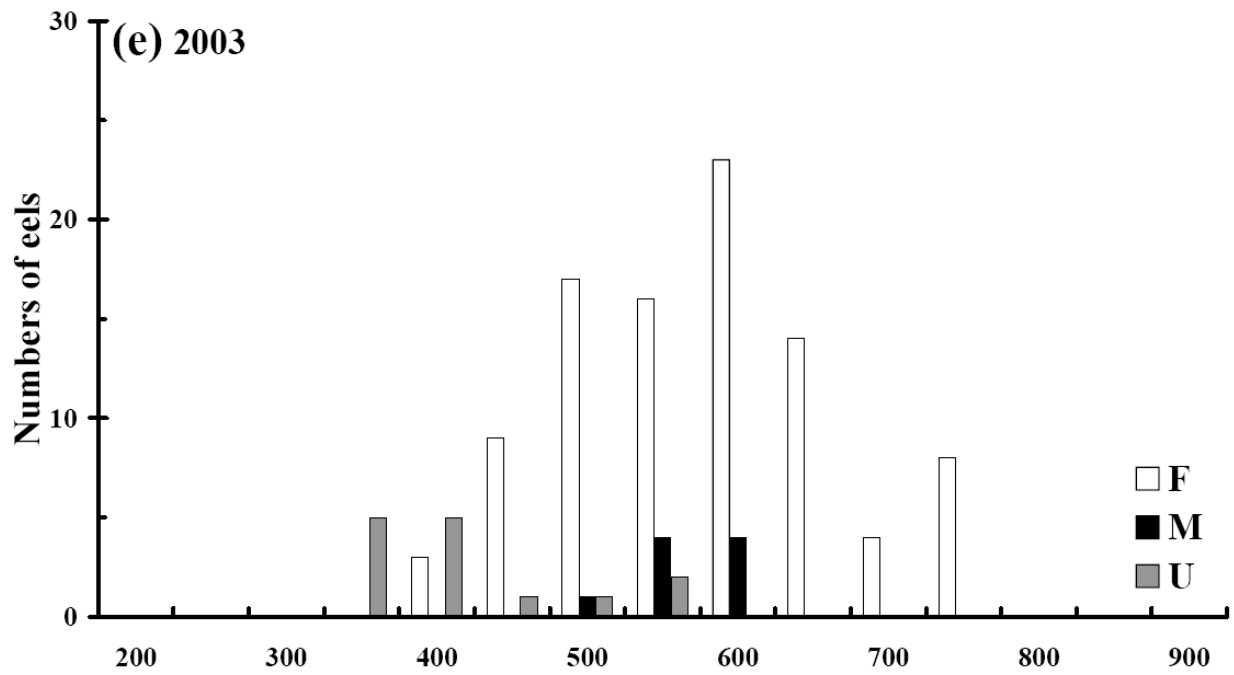


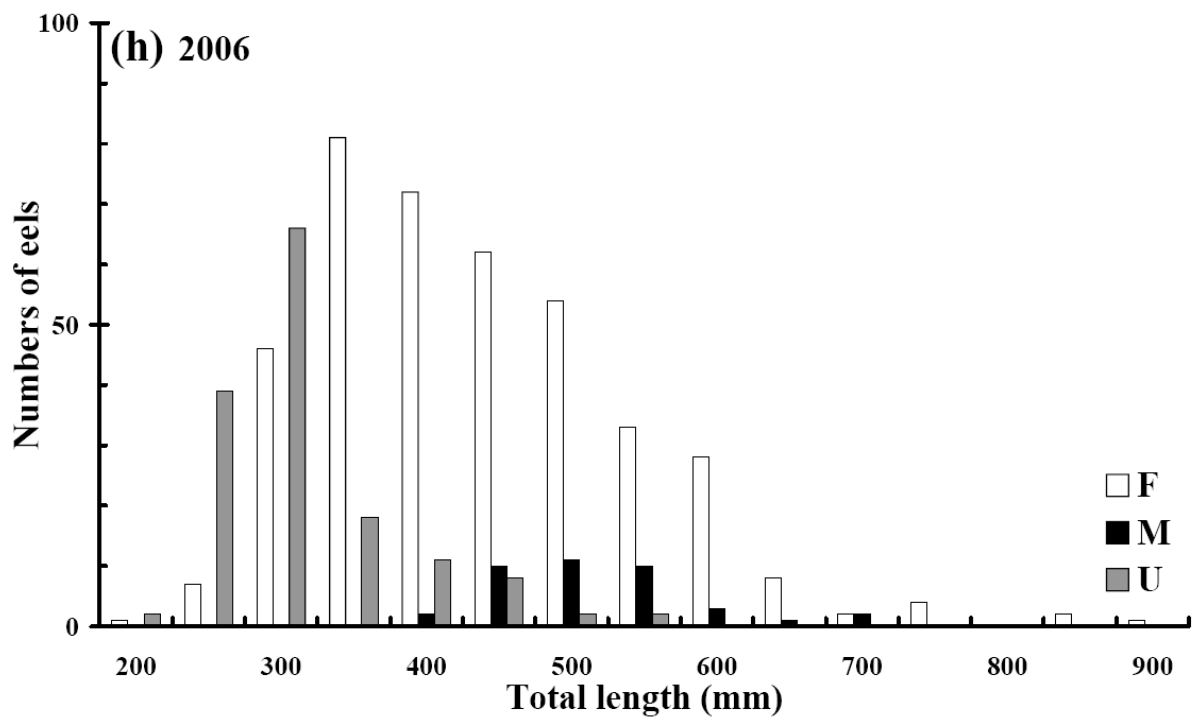
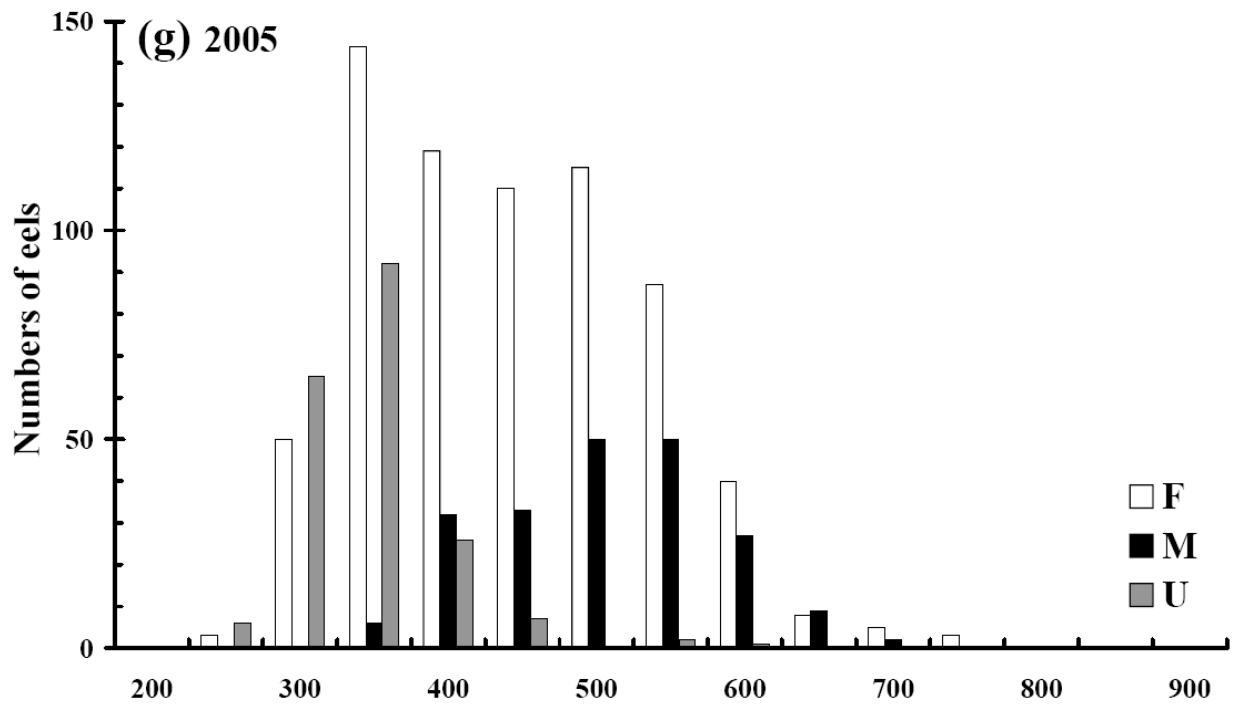
Fig. 10. (a) Catches in numbers of eels, (b) mean (\pm SD) total length (b, mm) and weight (c, g) in the lower reach of Kao-Ping River during 1999 to 2007. F = female (black solid line), M = male (grey solid line) and U = sex undifferentiated (black broken line).











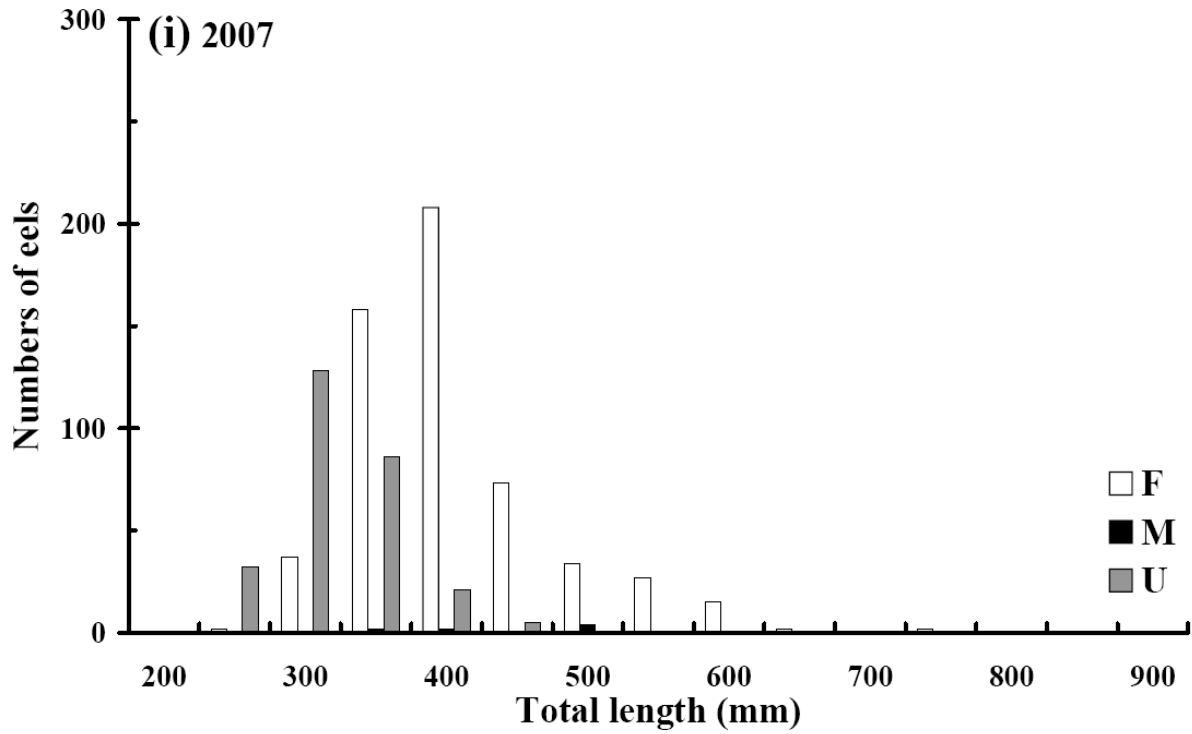
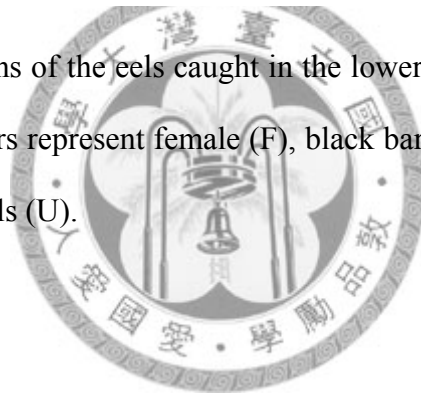


Fig. 11. The length compositions of the eels caught in the lower reach of Kao-Ping River during 1999 to 2007 (a to i). White bars represent female (F), black bars for male (M) and grey bars for the sexually undifferentiated eels (U).



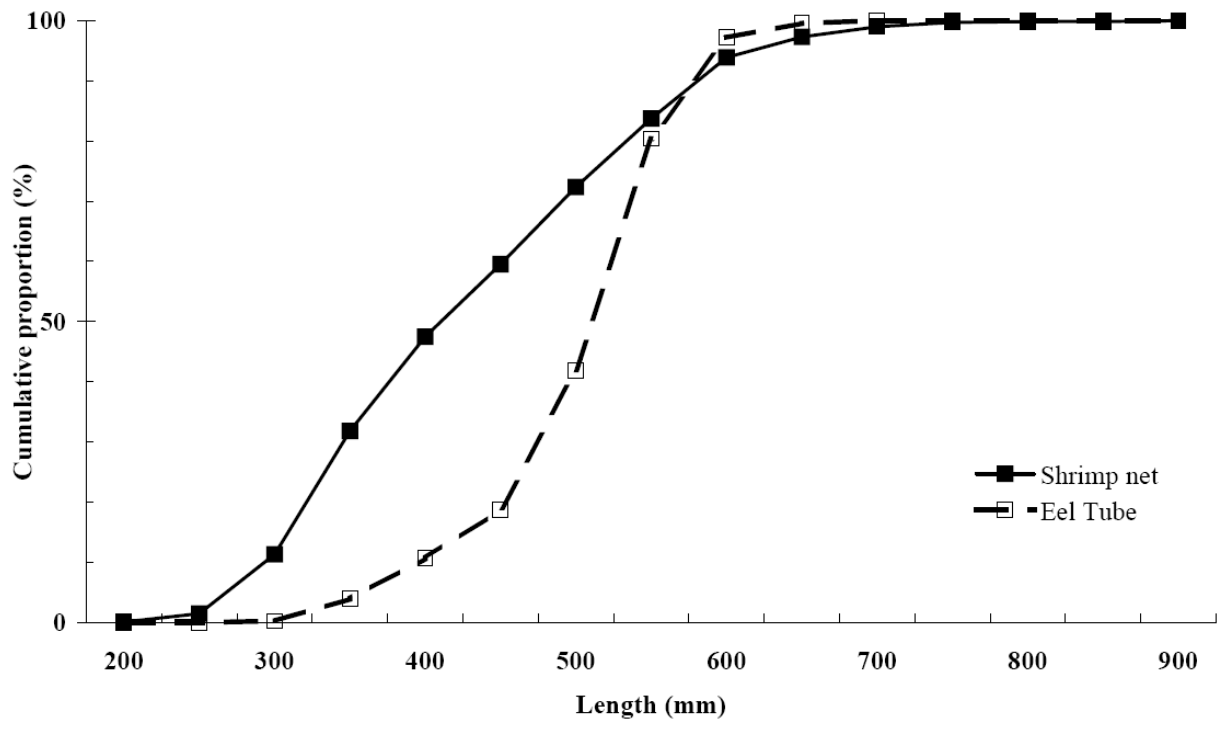


Fig. 12. Cumulative proportion of eels caught by different gears. Solid line = shrimp nets and broken line = eel tube.



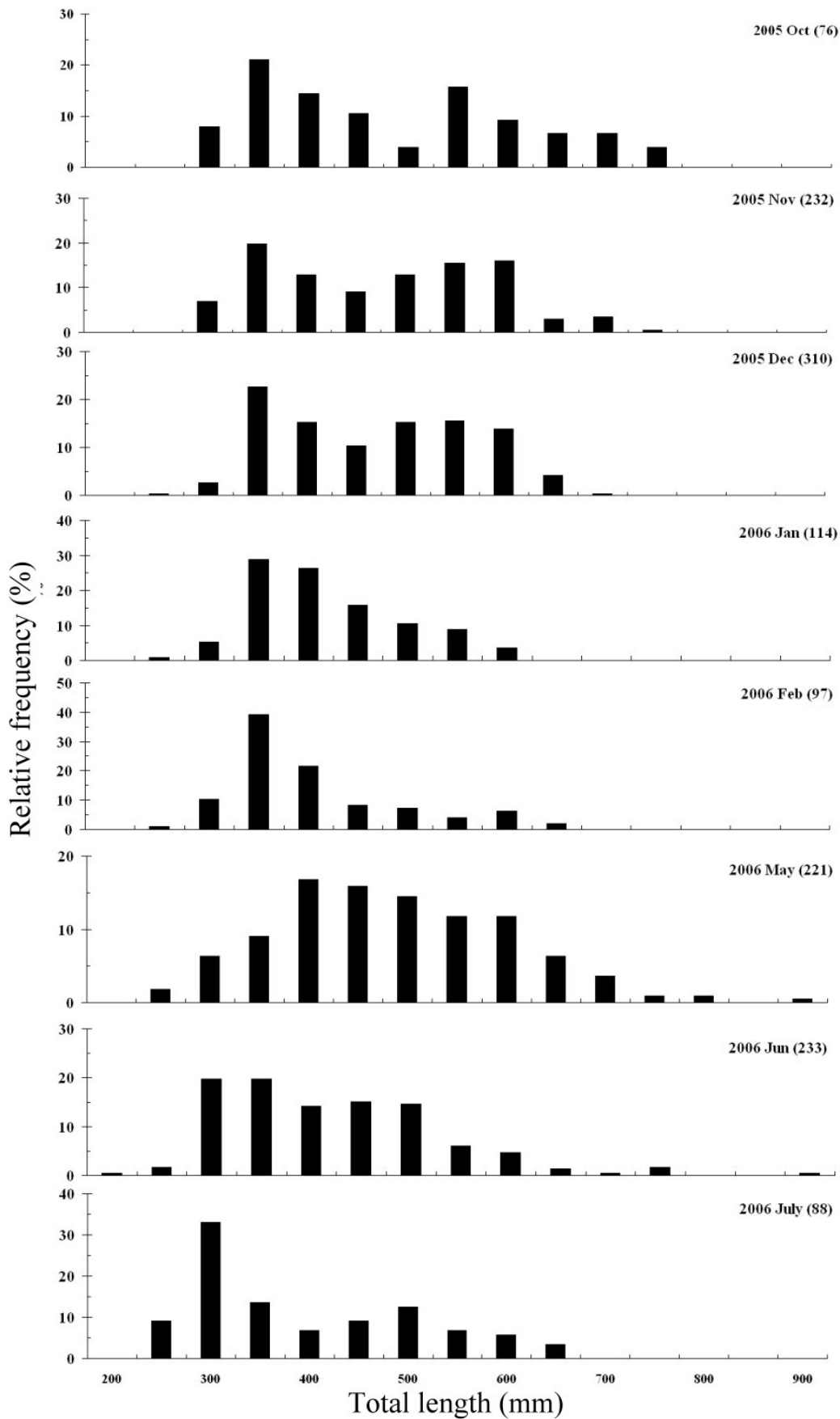


Fig. 13. Monthly changes in length compositions of the eels caught by the shrimp nets during the period from September 2005 to July 2006. Numbers in the brackets are the sample size.

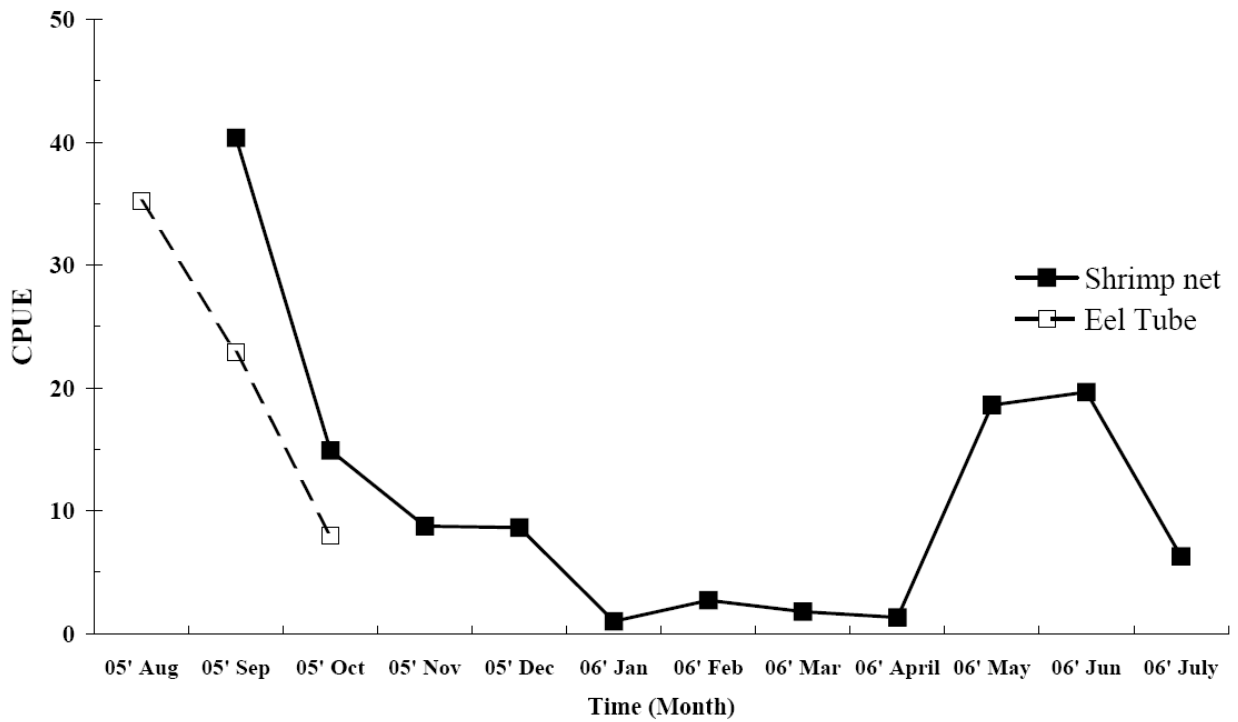
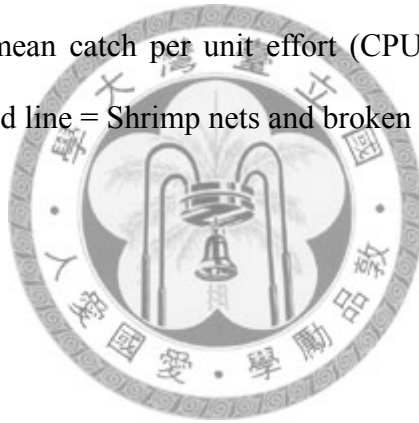


Fig. 14. Monthly changes in mean catch per unit effort (CPUE, $\text{g} \times \text{gear unit}^{-1} \times \text{fisherman}^{-1}$) from Sep 2005 to Jul 2006. Solid line = Shrimp nets and broken line = eel tubes.



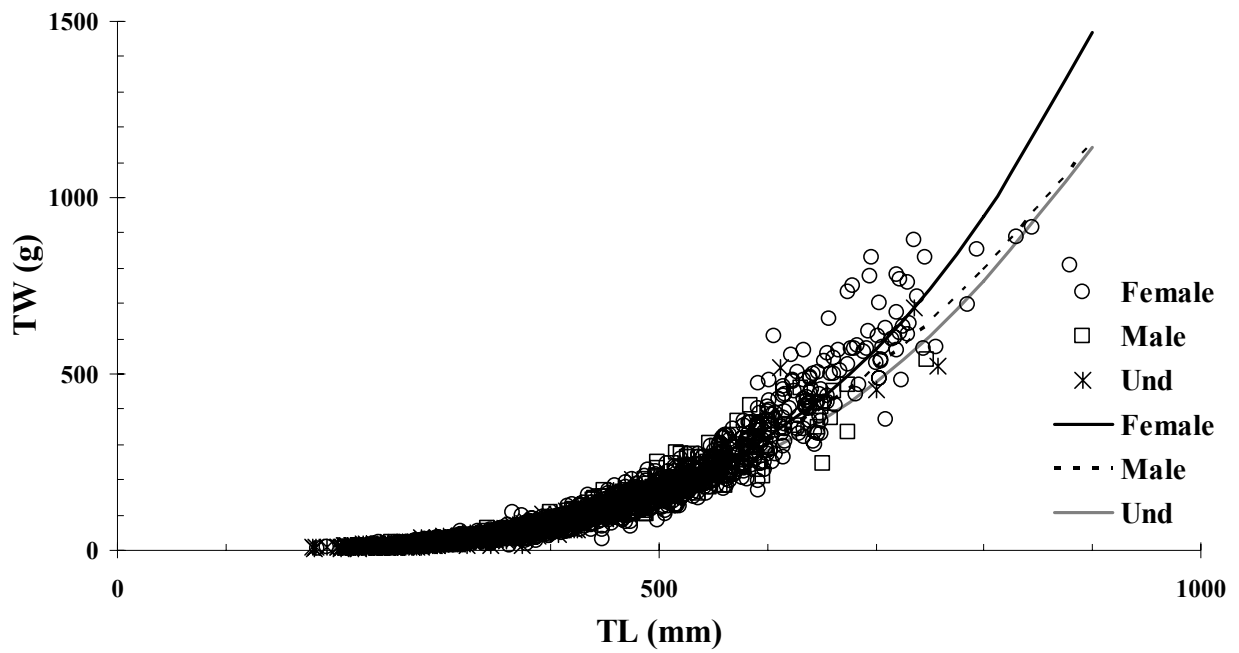


Fig. 15. Relationship between the length and weights of the female (open circles), male (open squares) and sex-undifferentiated (Und, asterisks) Japanese eel in the studied region. Black solid line, black broken line and grey solid lines were the estimated length-weight line of the females, males and sex-undifferentiated eels, respectively.

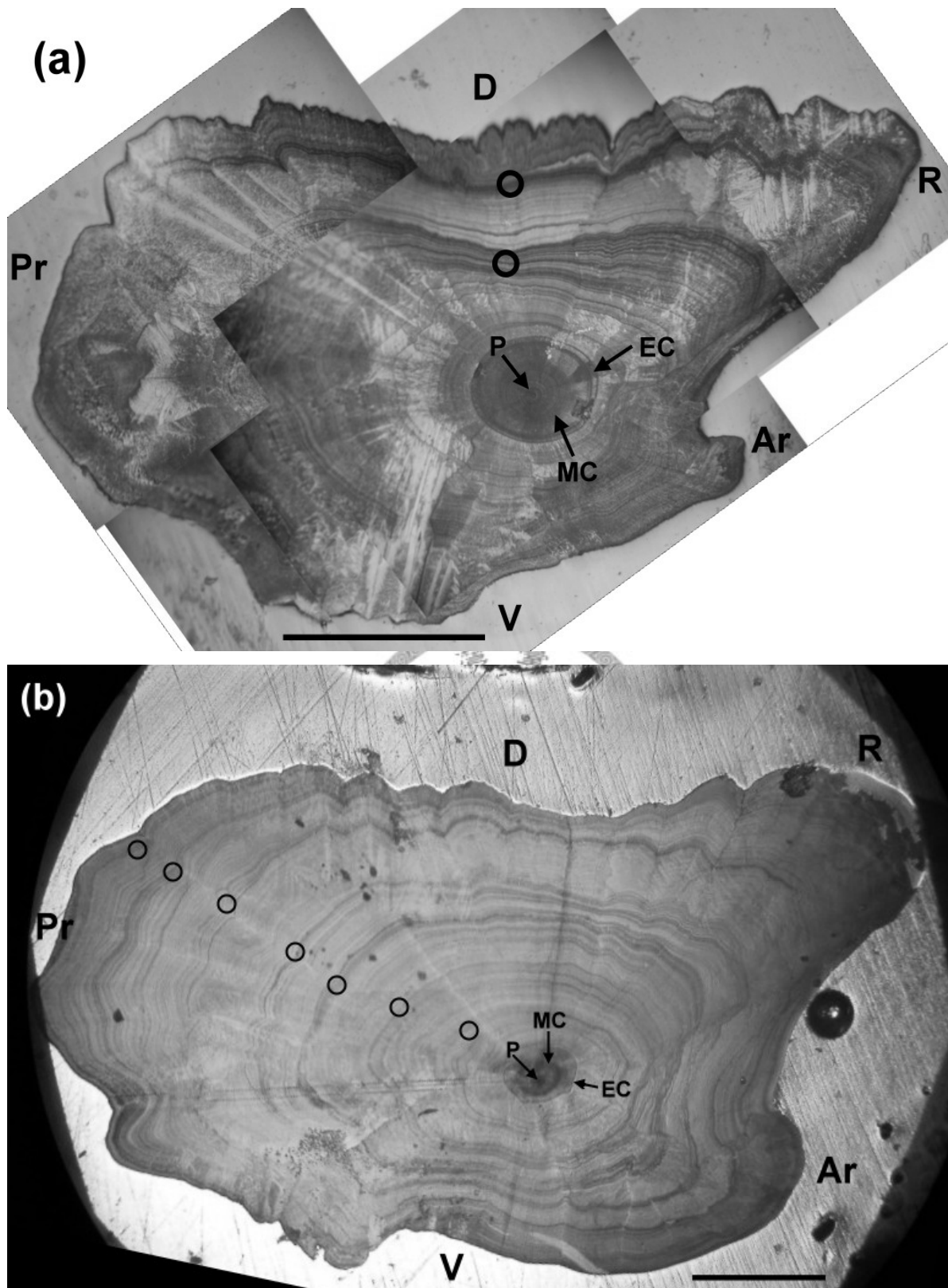


Fig. 16. Annuli (open circles) in the otolith of (a) 2-years-old cultured eels from Donggang Town, and (b) a 7-years-old wild eel from the lower reach of Kao-Ping River. P = primordium, MC = metamorphosis check and EC = elver check. R = rostrum, Ar = Anti-rostrum, Pr = post-rostrum, D = dorsal and V = ventral axis. Scale bar = 500 μm.

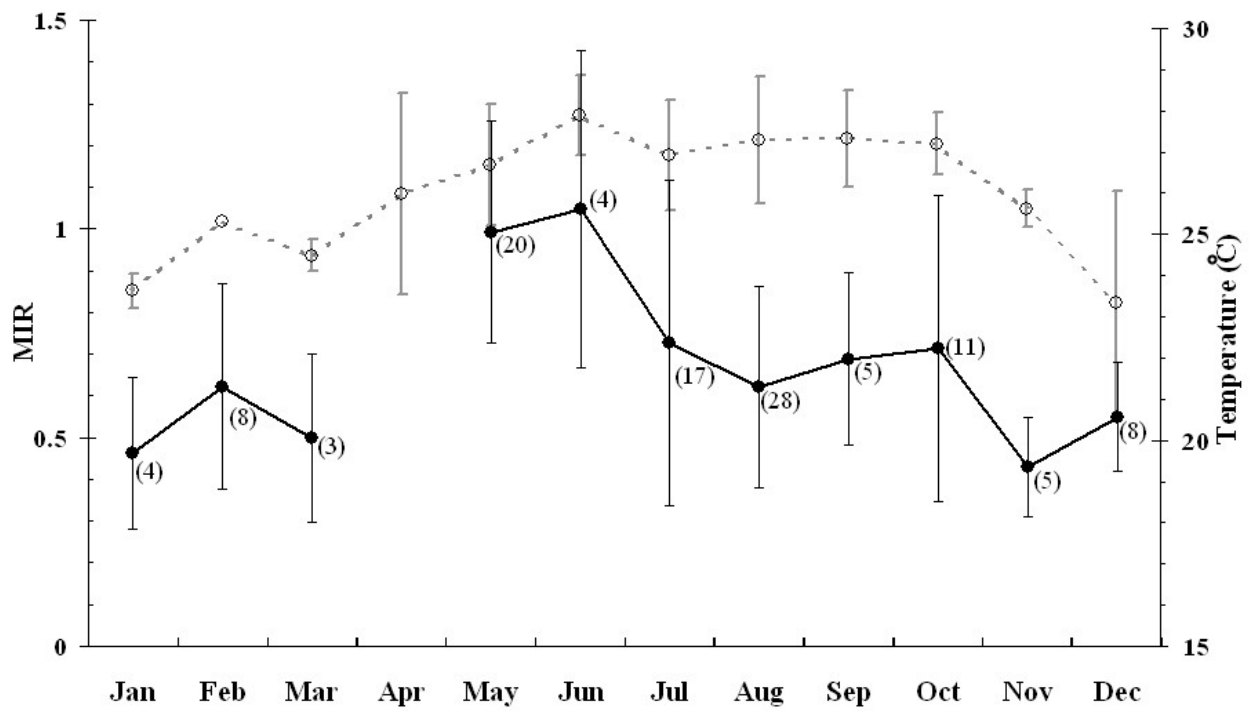
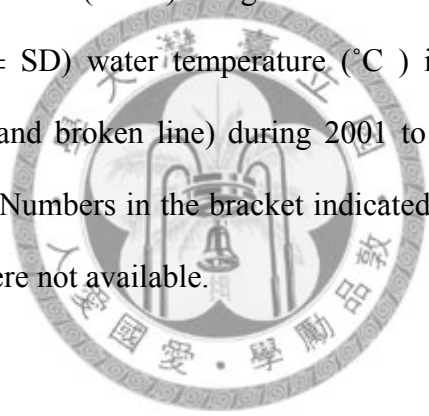


Fig. 17. Monthly changes in mean (\pm SD) marginal increment ratio (MIR, solid circles) of otoliths in wild eels. Mean (\pm SD) water temperature ($^{\circ}$ C) in the bottom of the mouth of Kao-Ping River (open circles and broken line) during 2001 to 2006 were derived from Chen (2005) and Chen et al. (2007). Numbers in the bracket indicated number of the eels collected in that month, and eels in April were not available.



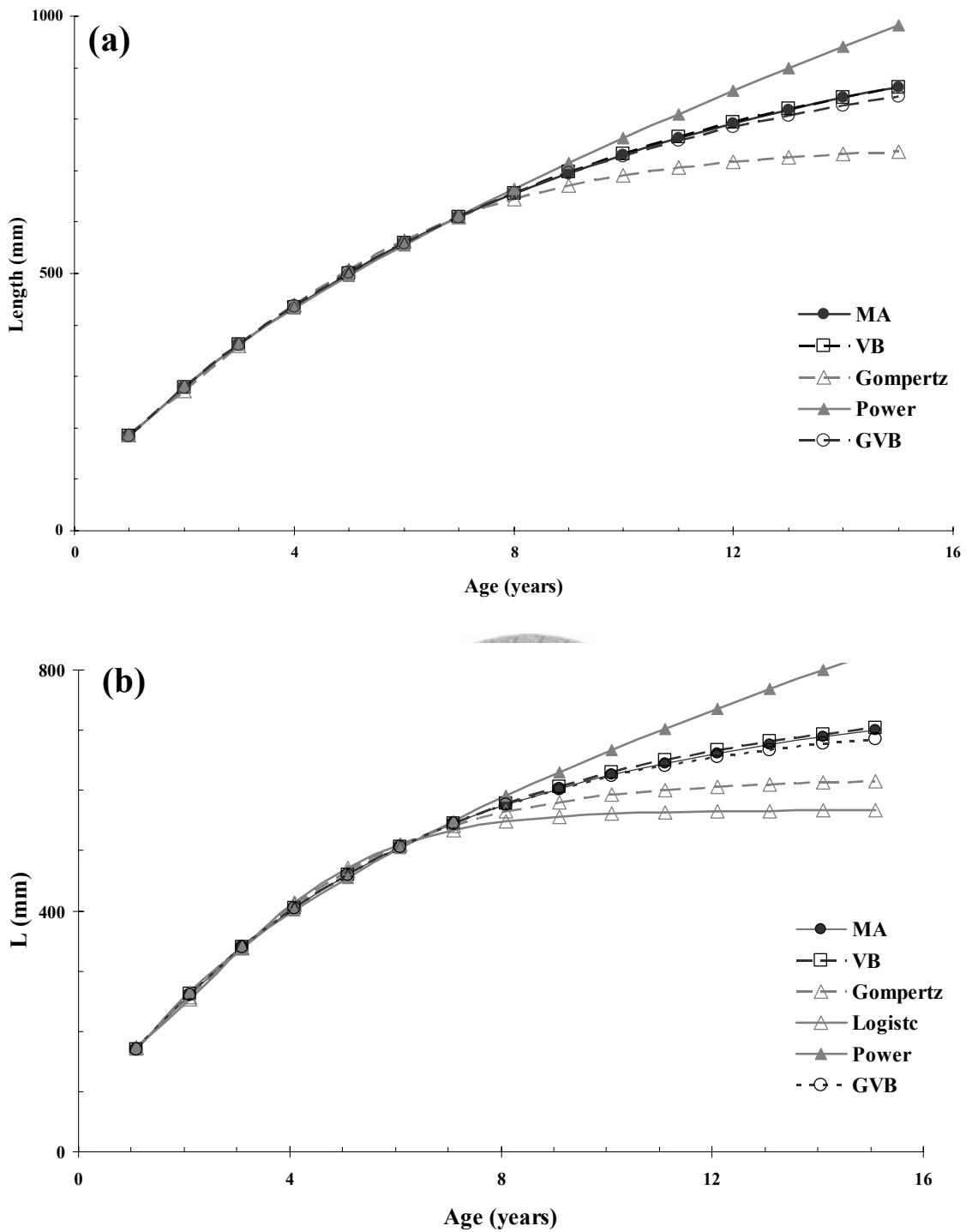


Fig. 18. Model-averaged growth model (MA, black solid line with solid circles), von Bertalanffy (VB, black broken line with open squares), Gompertz (grey broken line with open triangles), logistic (grey solid line with open triangles), power (grey solid line with solid triangles) and generalized von Bertalanffy growth model (GVB, black broken line with open circles) for (a) female and (b) male *Anguilla japonica*. The logistic growth model of females was not shown because of its small Akaike weight (0.008).

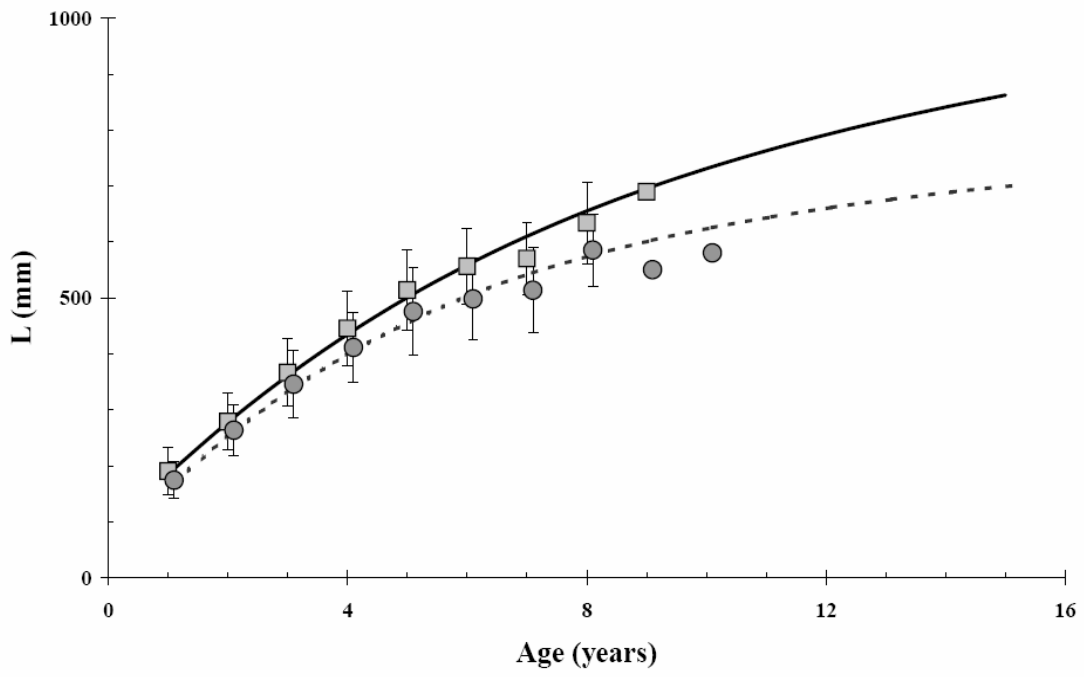


Fig. 19. Model-averaged model and observed mean lengths-at-age (\pm SD) between females (solid line and solid squares) and males (broken line and solid circles).



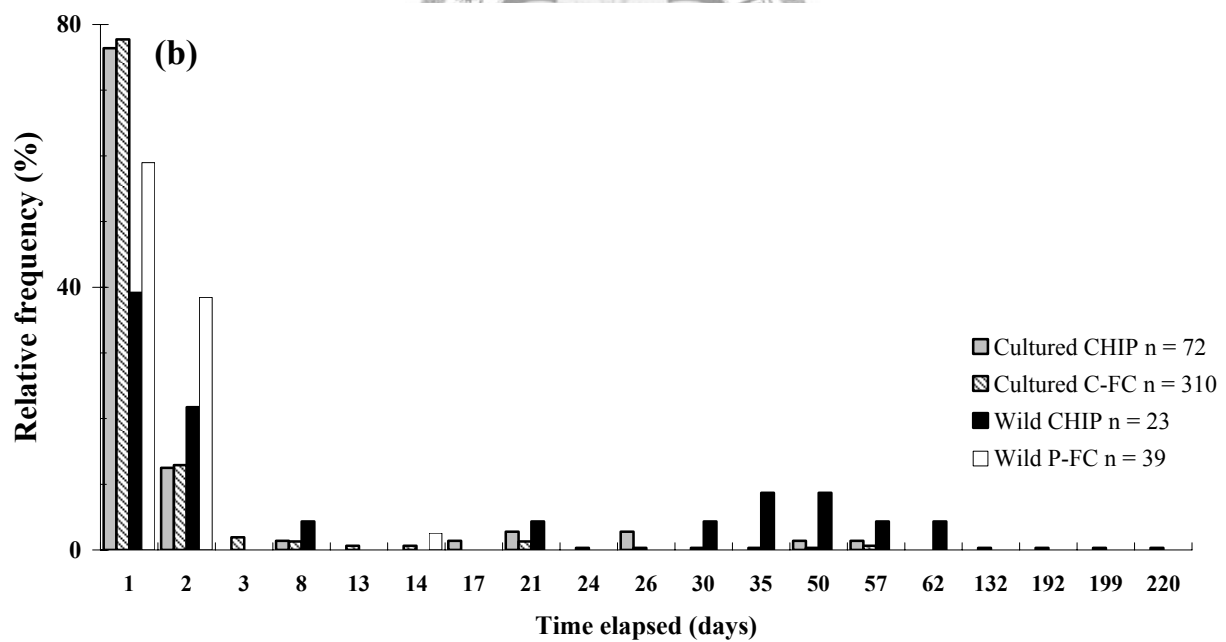
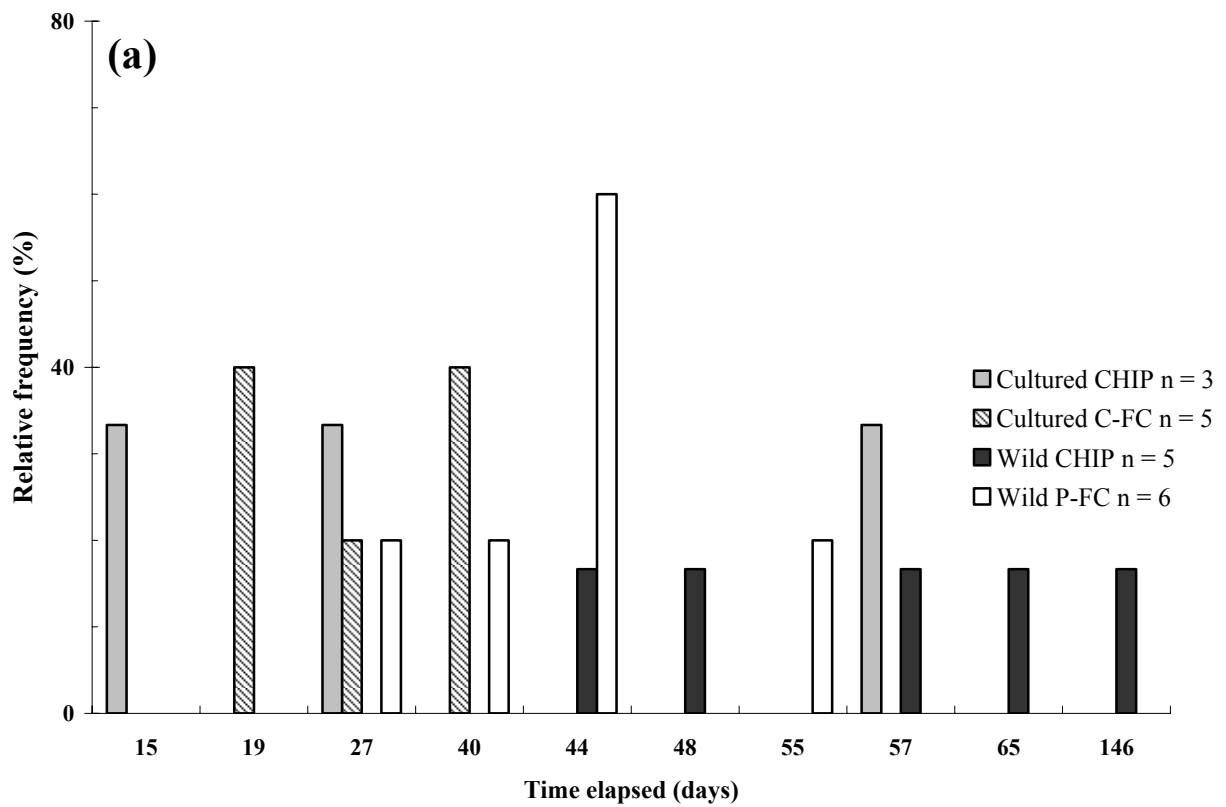


Fig. 20. The relative frequency distribution of the recapture times from release to recapture for the marked eels released (a) 1 km upstream of the fishing ground in 2005 and (b) at the fishing ground in 2006 by eel origin and mark (CHIP = microchip, C-FC = caudal fin clip and P-FC = pectoral fin clip).

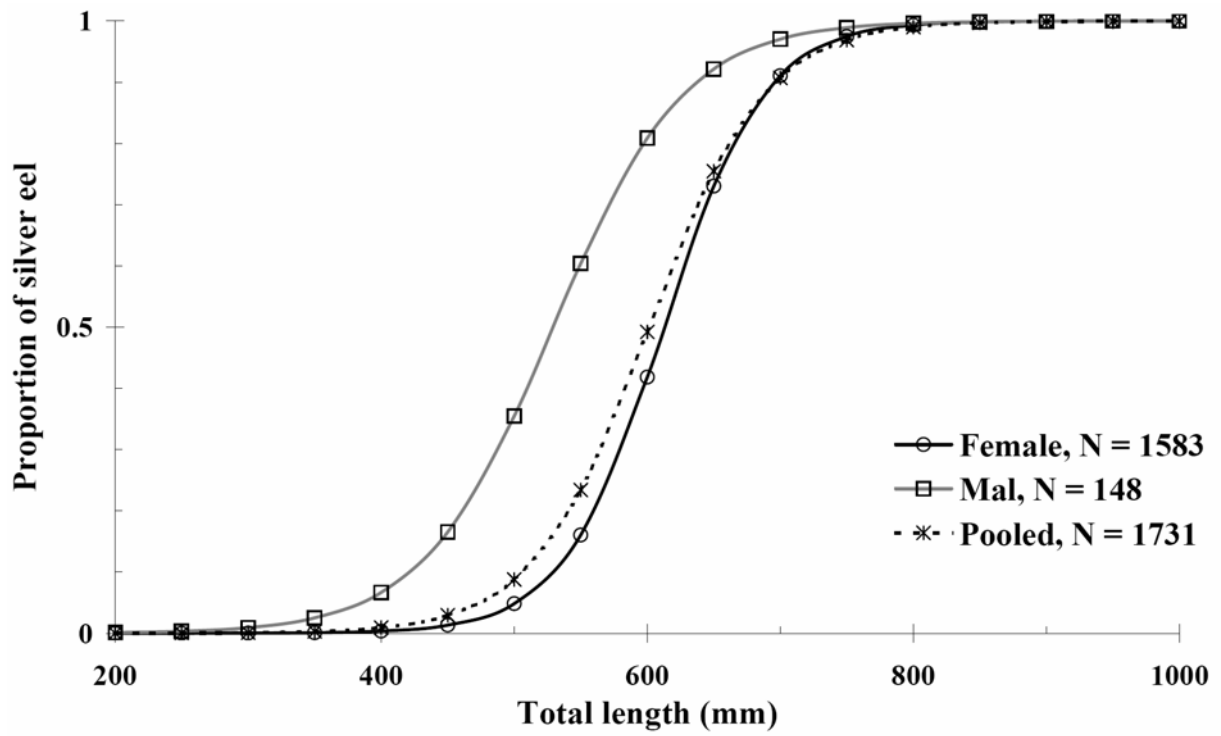
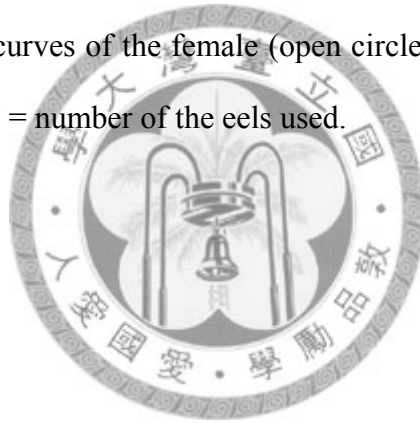


Fig. 21. Estimated maturation curves of the female (open circles), male (open squares) eels and sex-pooled model (asterisks). N = number of the eels used.



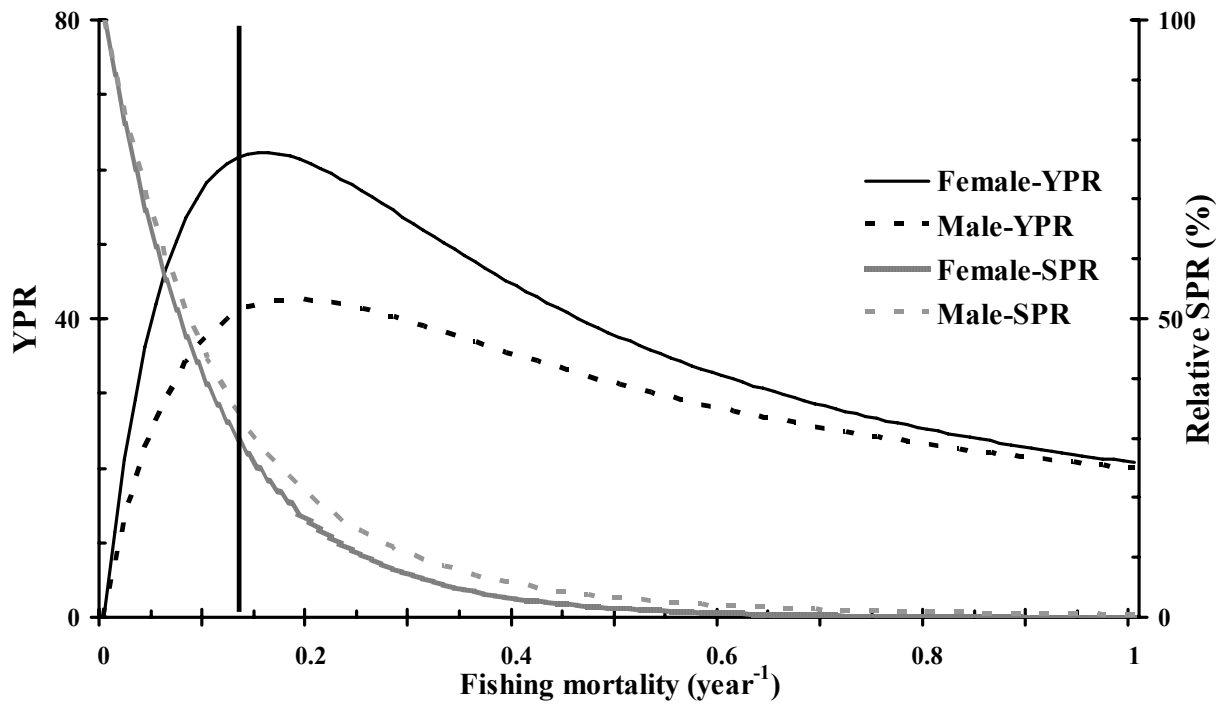
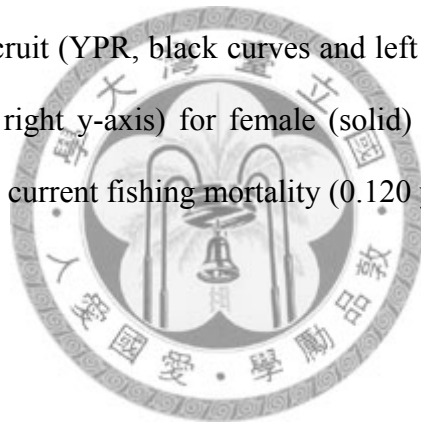


Fig.22. Calculated yield per recruit (YPR, black curves and left y-axis) and relative spawner per recruit (SPR, grey curves and right y-axis) for female (solid) and male (broken) *A. japonica*. Vertical black line indicated the current fishing mortality (0.120 year⁻¹).

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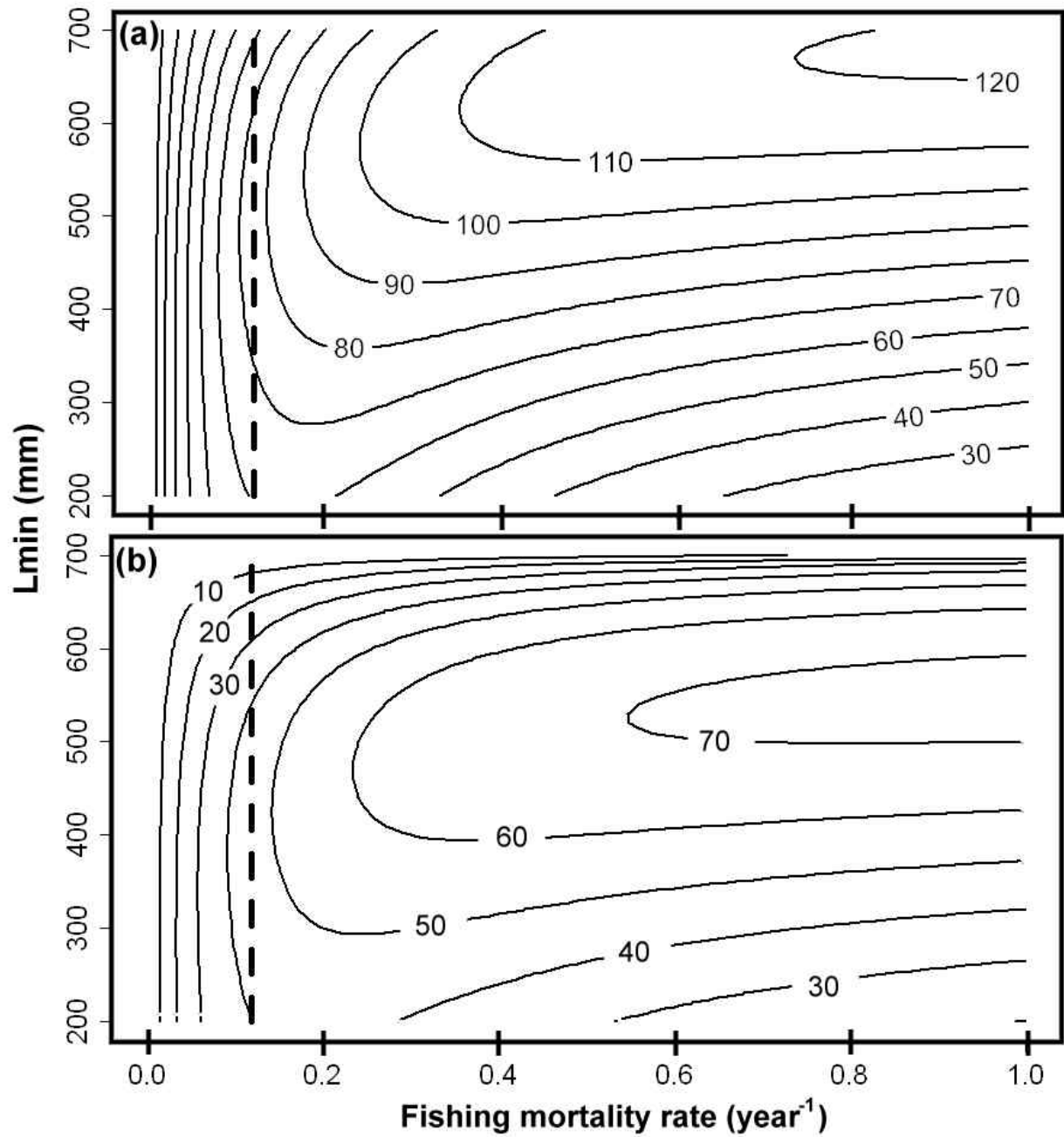


Fig. 23. Isopleths of YPR under different combinations of fishing mortality rates and minimum legal lengths (L_{min}) for (a) females and (b) males.

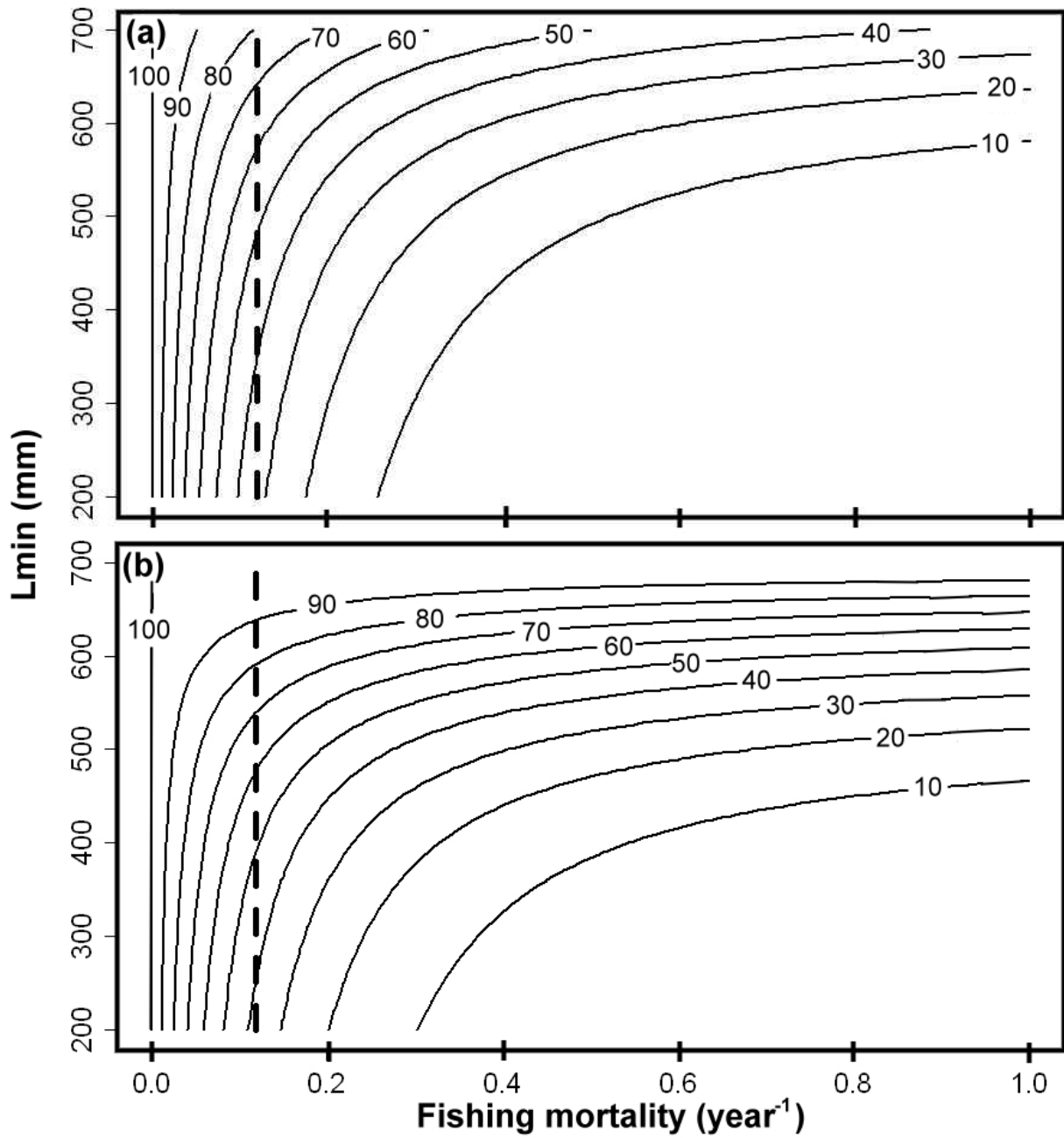


Fig. 24. Isopleths of relative SPR under different combinations of fishing mortality rates and minimum legal lengths (L_{min}) for (a) females and (b) males.

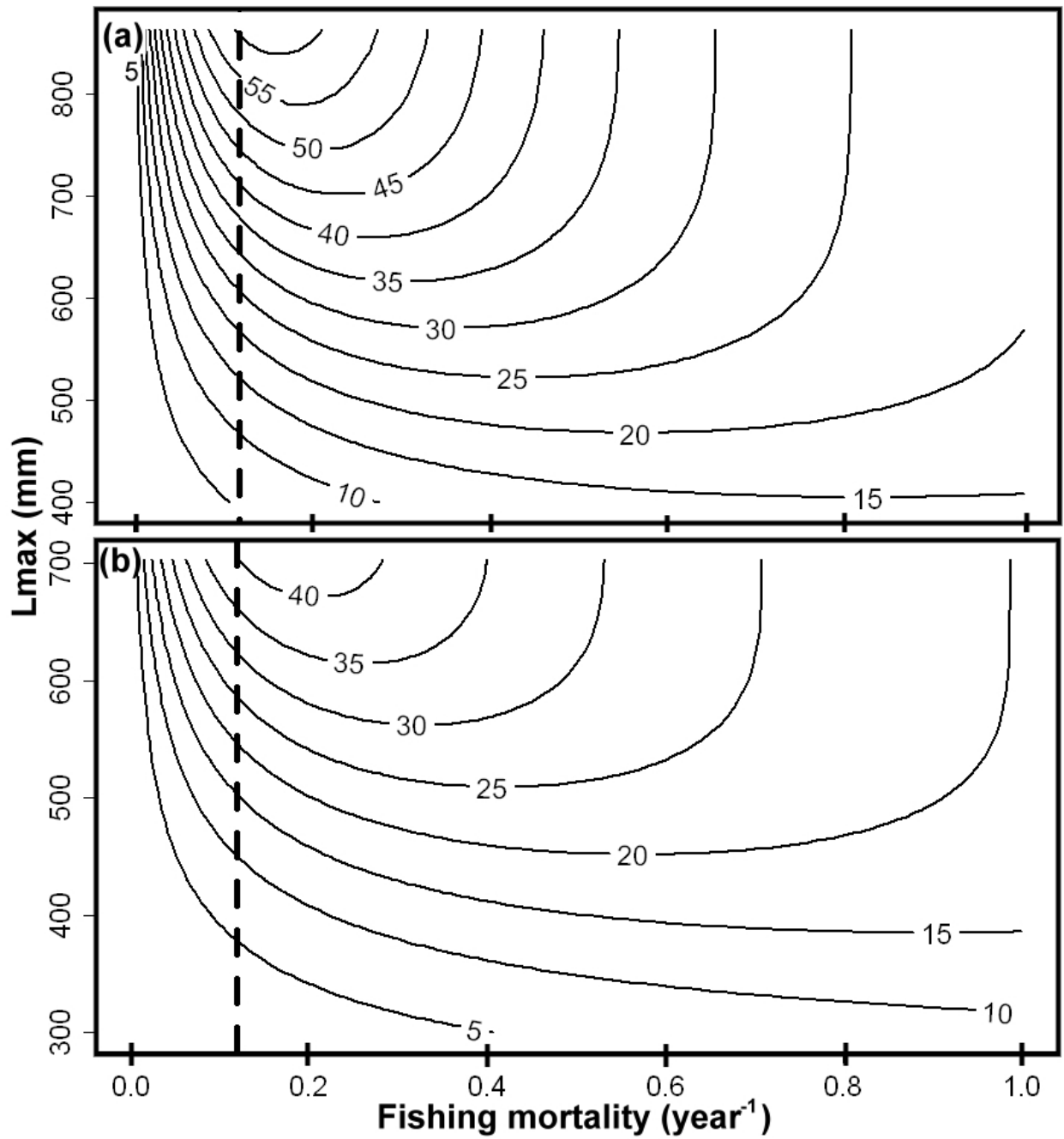


Fig. 25. Isopleths of YPR under different combinations of fishing mortality rates and maximum legal lengths (L_{max}) for (a) females and (b) males.

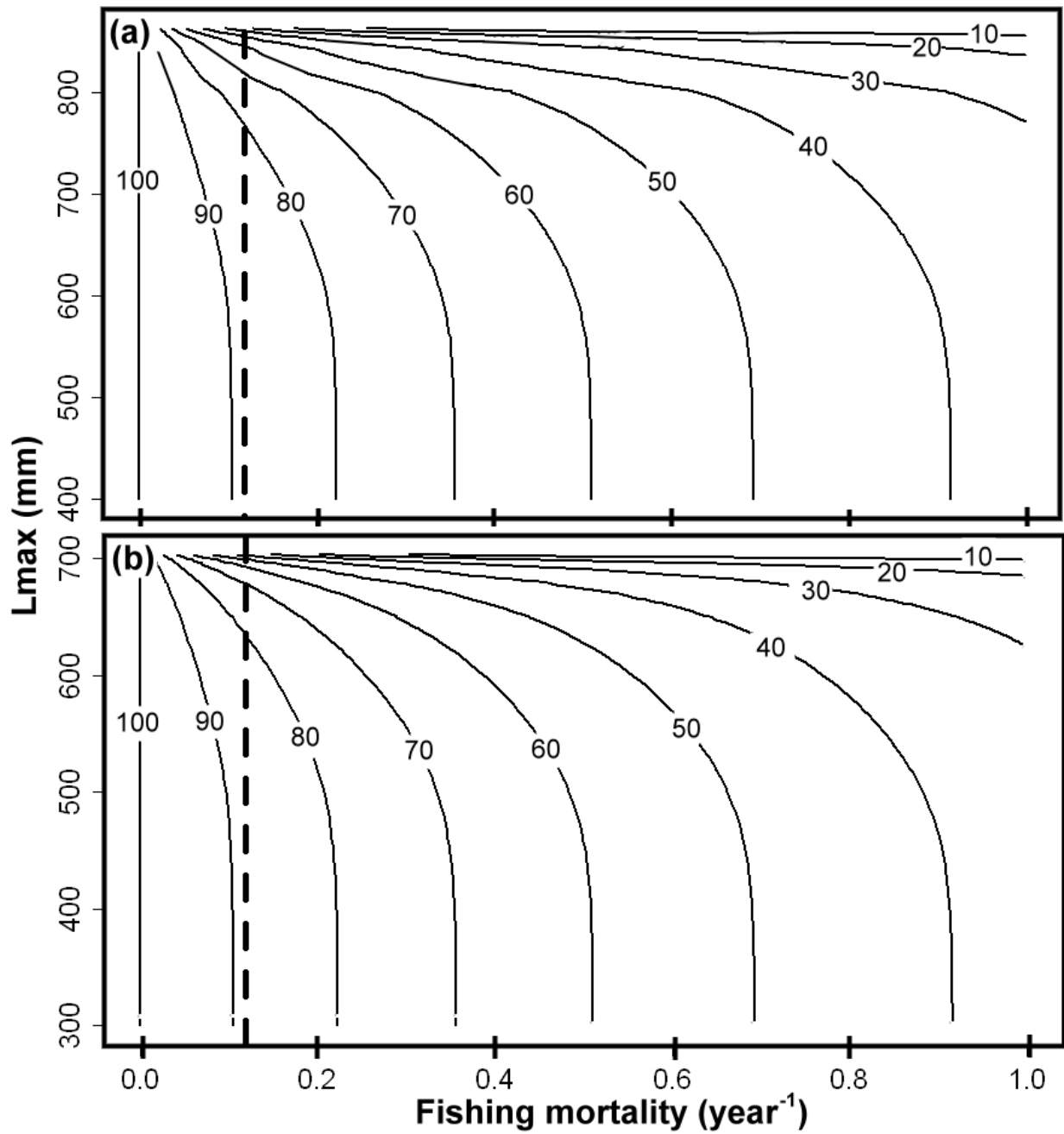
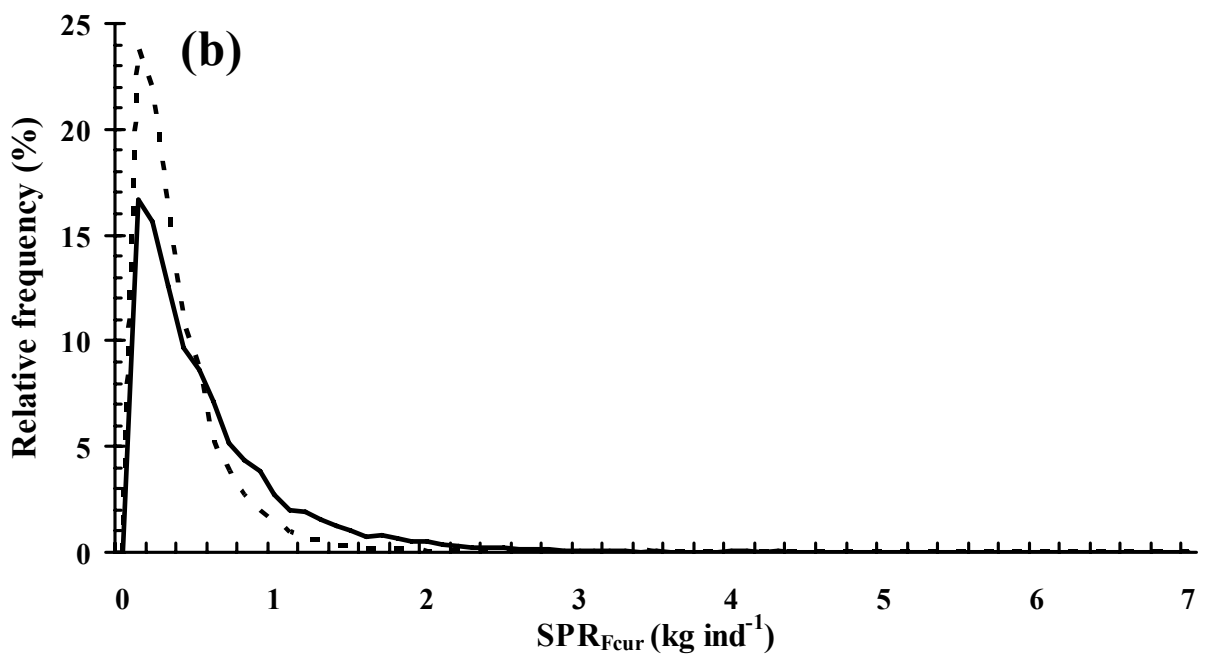
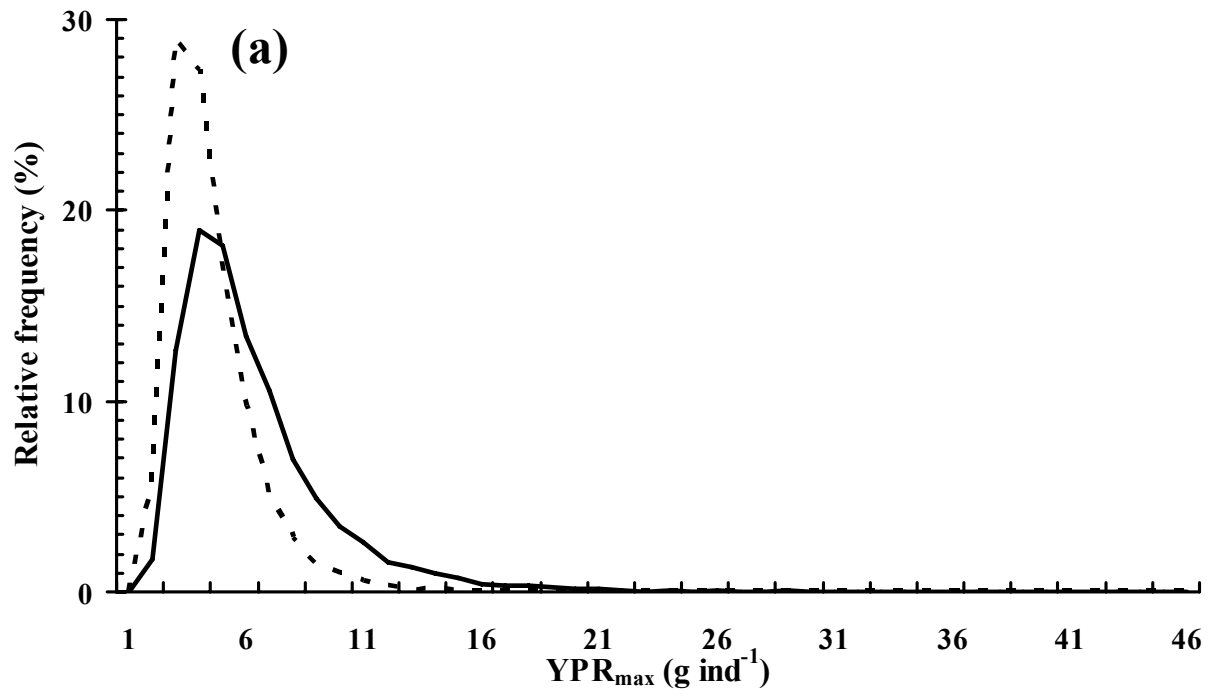


Fig. 26. Isopleths of relative SPR under different combinations of fishing mortality rates and maximum legal lengths (L_{max}) for (a) females and (b) males.



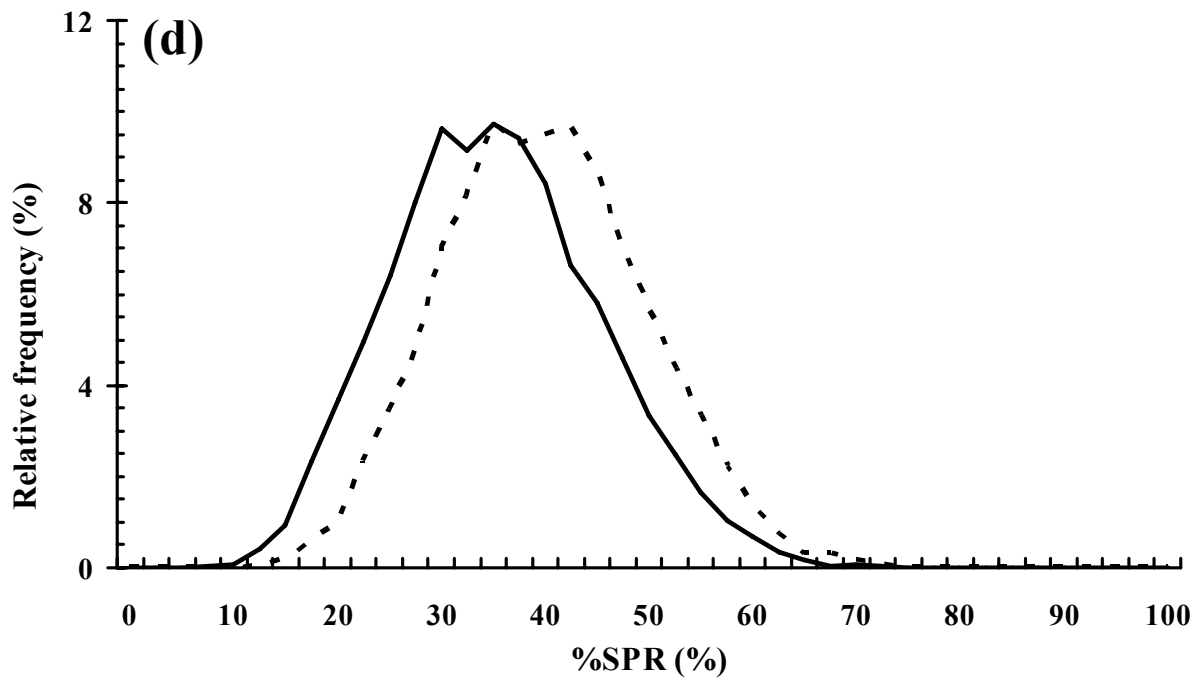
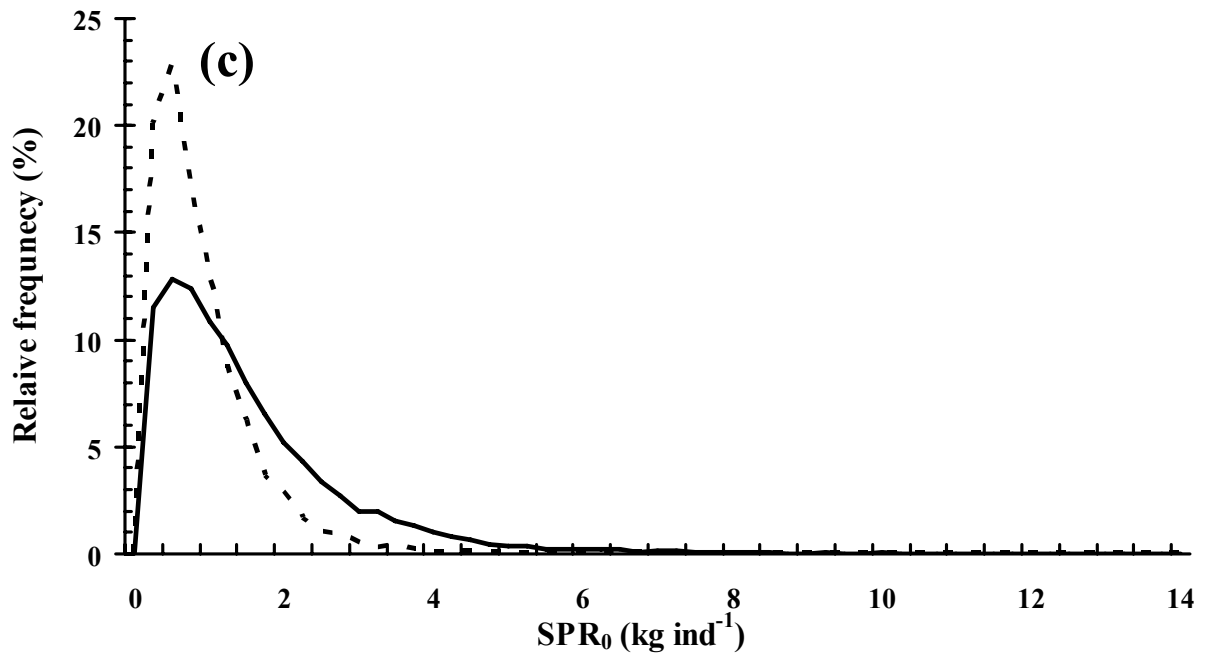
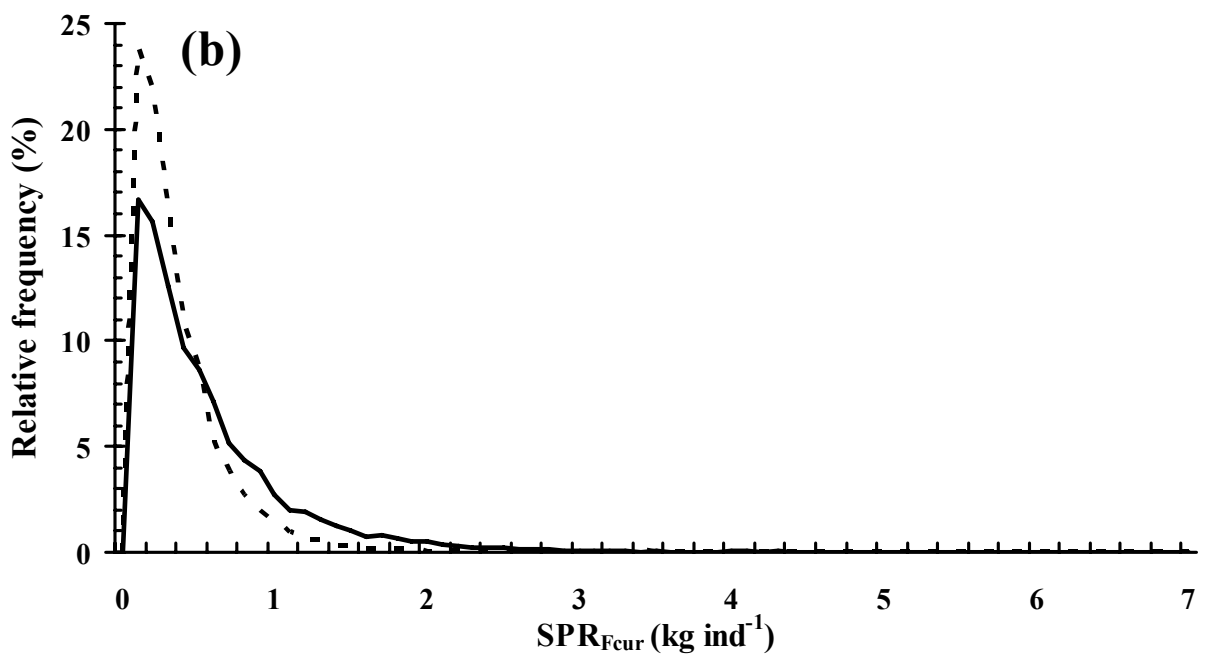
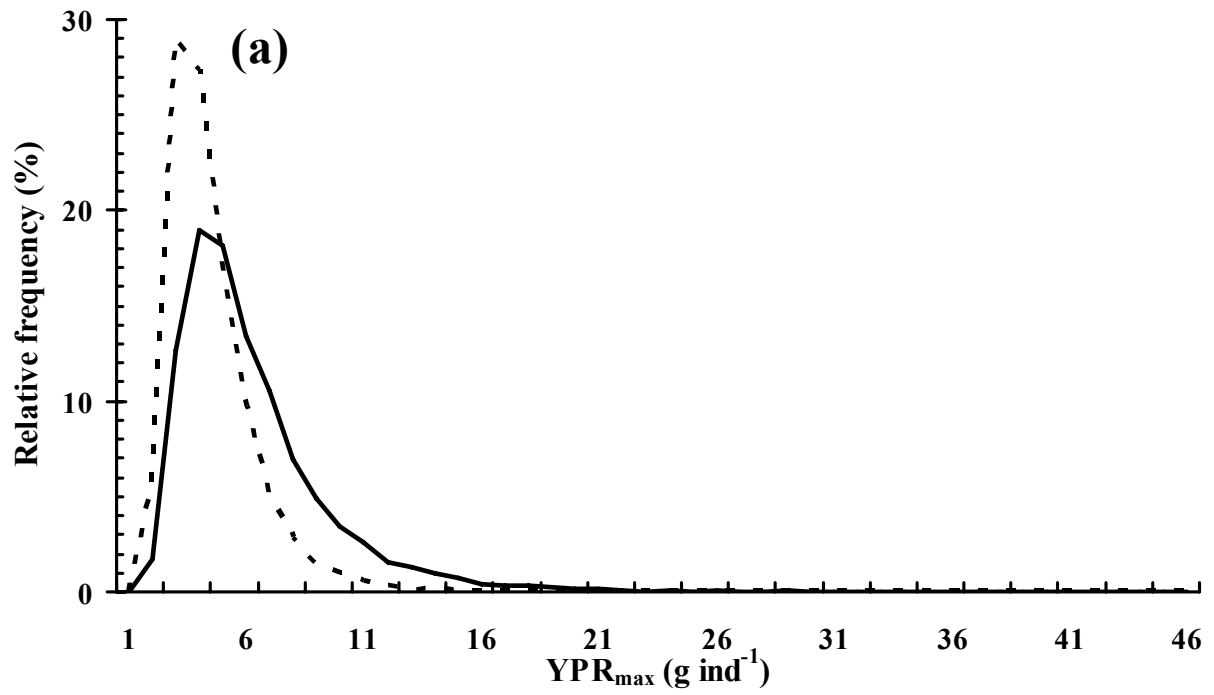


Fig. 27. Distributions of (a) F_{max} , (b) $F_{0.1}$, (c) $F_{40\%}$ and (d) $F_{50\%}$ (year⁻¹) of females (solid line) and males (dotted line) when uncertainties in parameter estimation were incorporated.



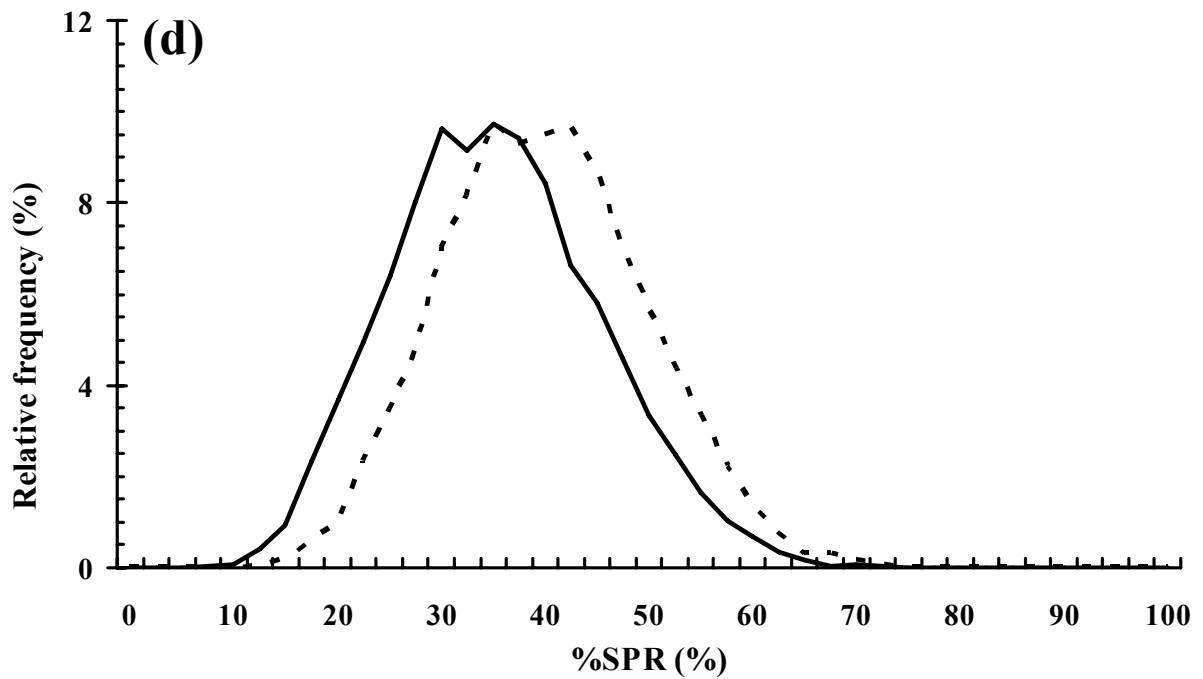
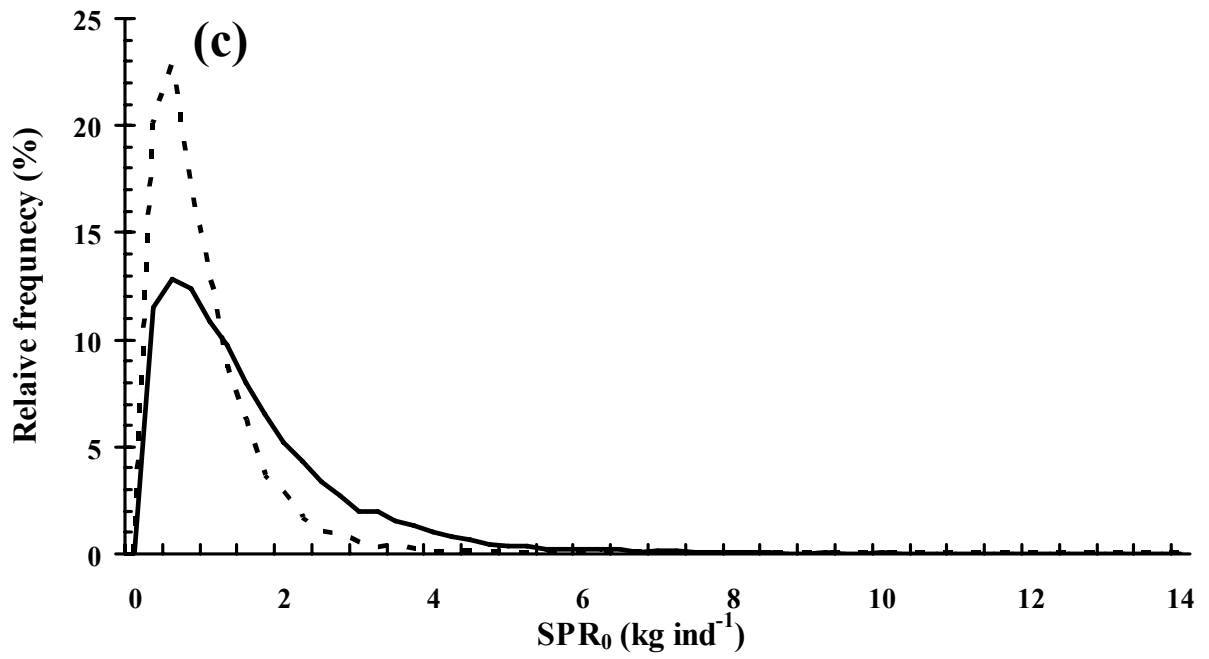
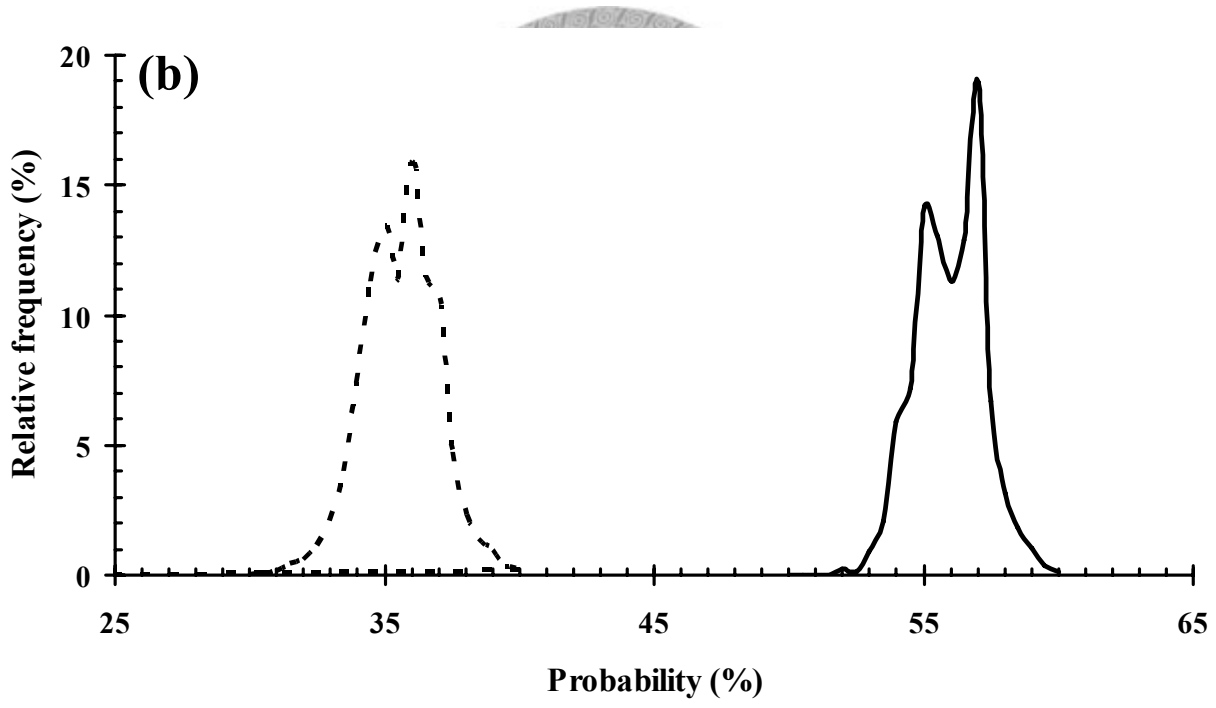
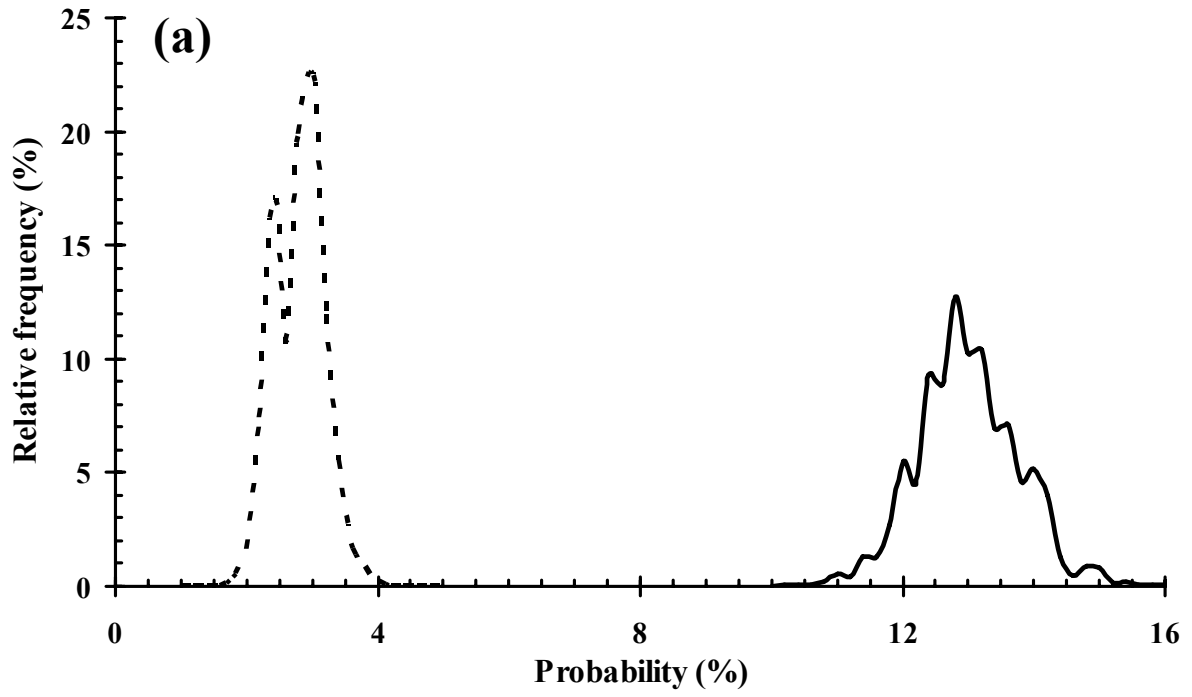


Fig. 28. Distributions of (a) YPR_{max} (g ind⁻¹), (b) SPR_{Fcur} , (c) SPR_0 (kg ind⁻¹) and (d) %SPR (%) of females (solid line) and males (dotted line) when uncertainties in parameter estimation were

5 incorporated.



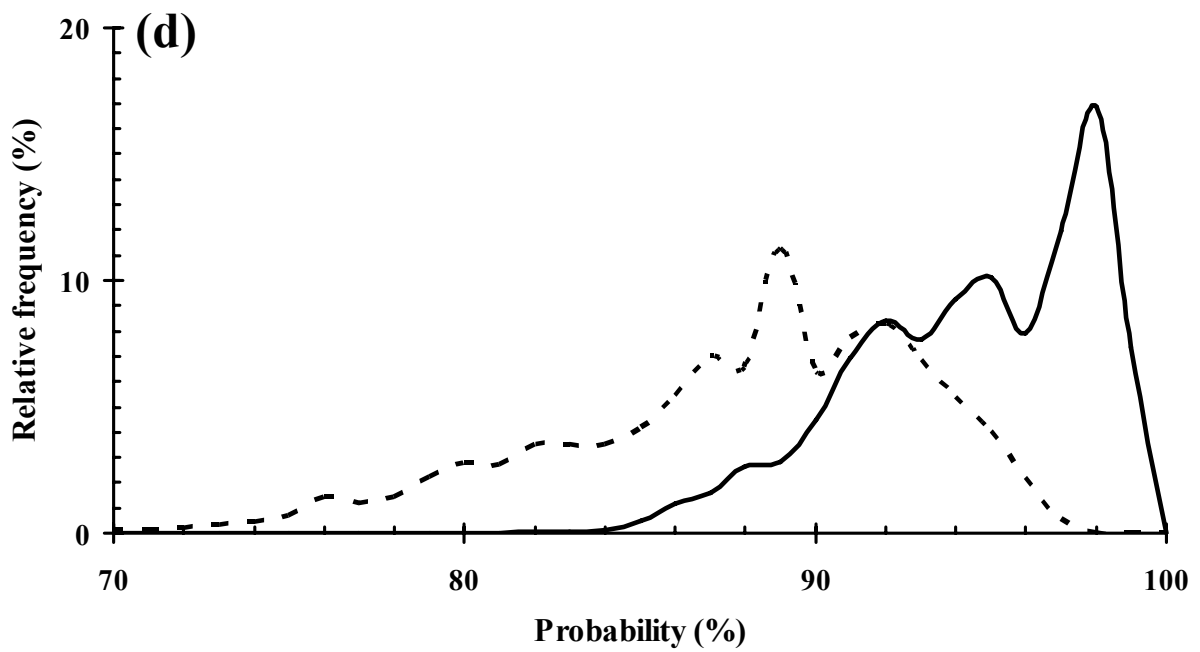
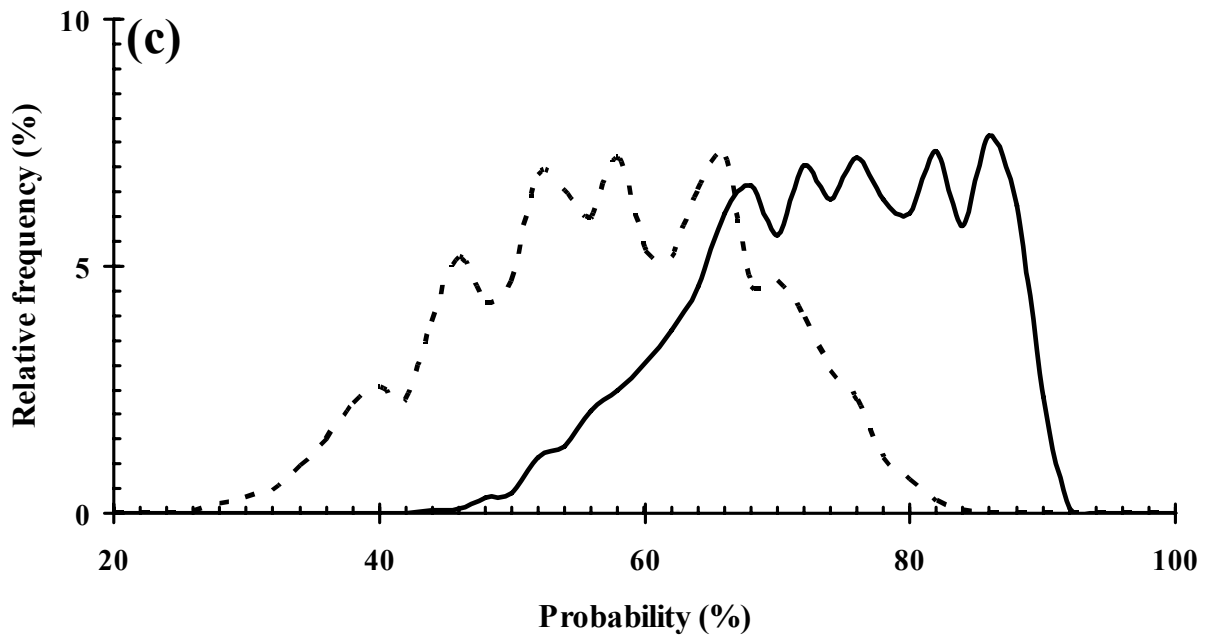


Fig. 29. Distributions of possibilities (%) that F_{cur} was larger than (a) F_{max} , (b) $F_{0.1}$, (c) $F_{40\%}$ and (d) $F_{50\%}$ (year⁻¹) for females (solid line) and males (dotted line).

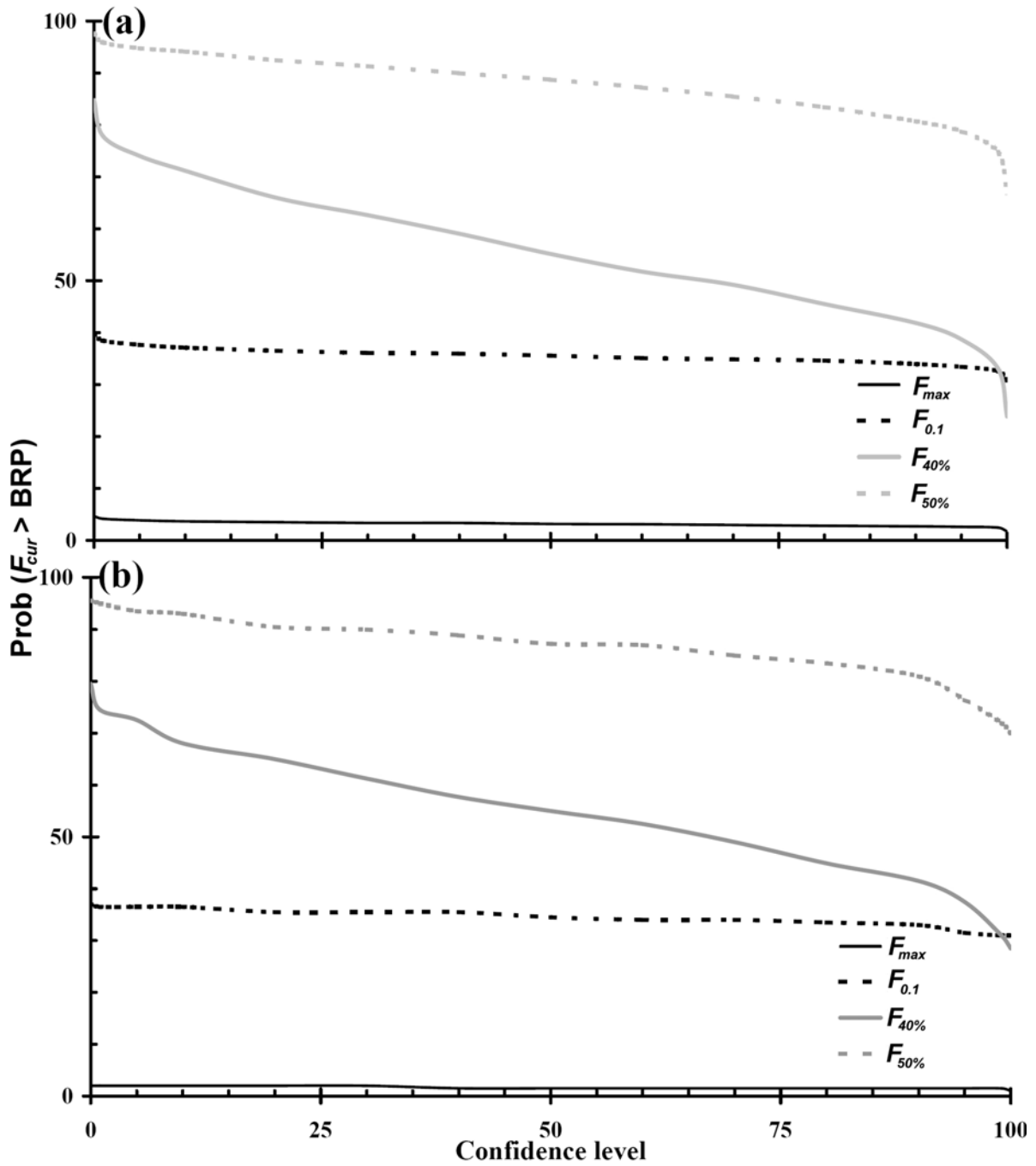


Fig. 30. Probabilities that F_{cur} was larger than a specific BRP (F_{max} , black solid, $F_{0.1}$, black broken, $F_{40\%}$ grey solid, and $F_{50\%}$, grey broken line) for females (a) and males (b) under confidence levels from less than 0.05 % to larger than 99.95 %.

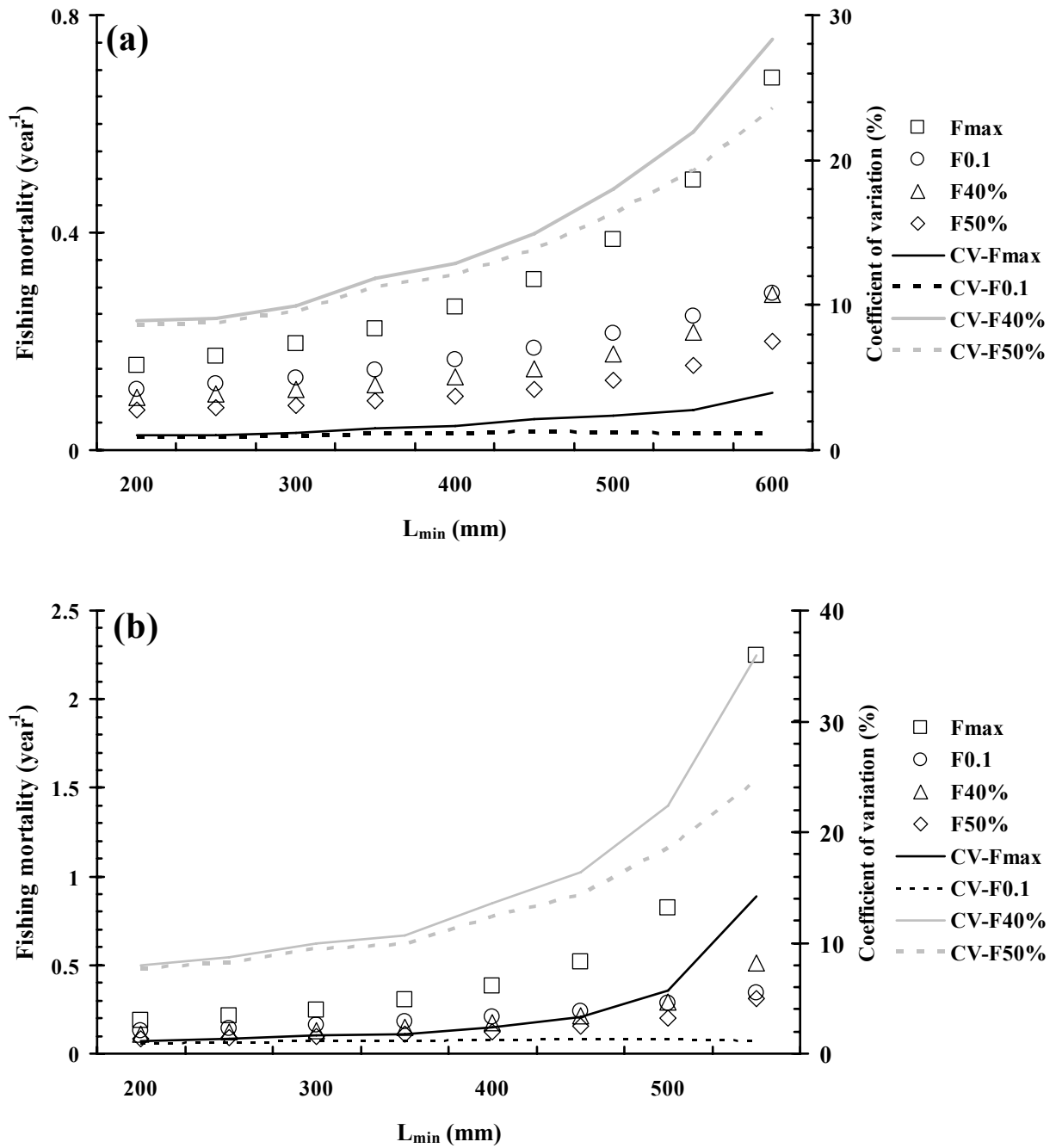


Fig. 31. Mean F_{max} (squares), $F_{0.1}$ (circles), $F_{40\%}$ (triangles) and $F_{50\%}$ (diamonds), and corresponding coefficient of variation (CV, black solid, black broken, grey solid and grey broken line) of for (a) females and (b) males with increasing minimum legal lengths (L_{min}) from 200 to 600 mm. Current L_{min} was equivalent to 200 mm.

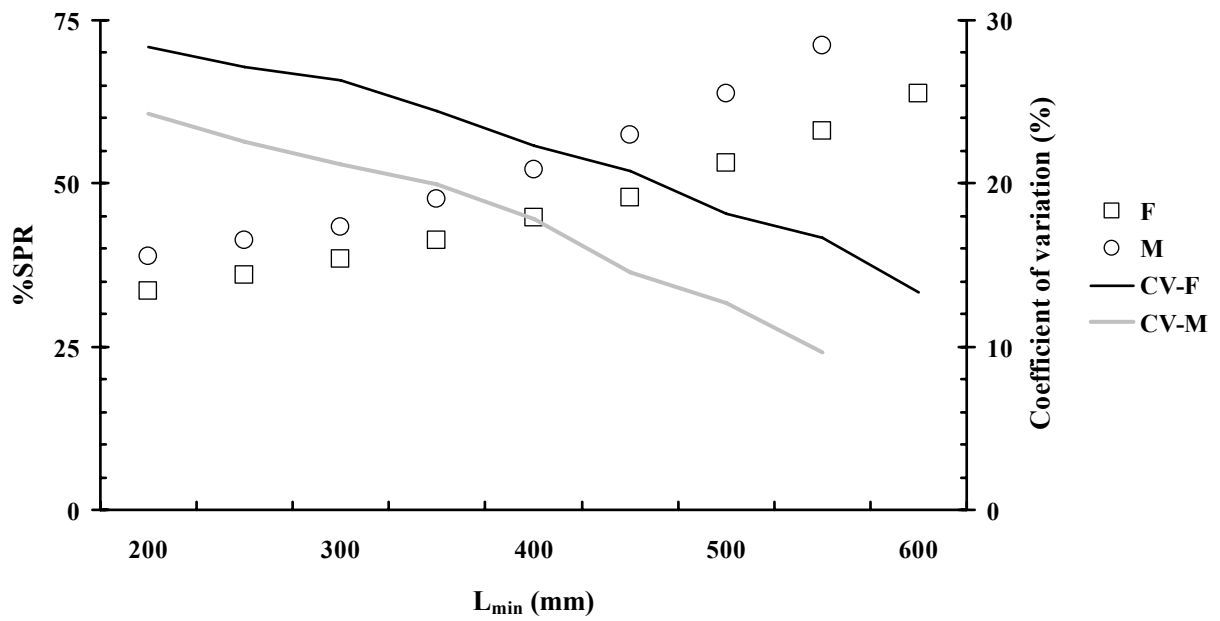


Fig. 32. Mean %SPR and corresponding coefficient of variation (CV, black and grey solid line) of for females (squares) and males (circles) with increasing minimum legal lengths (L_{min}) from 200 to 600 mm.



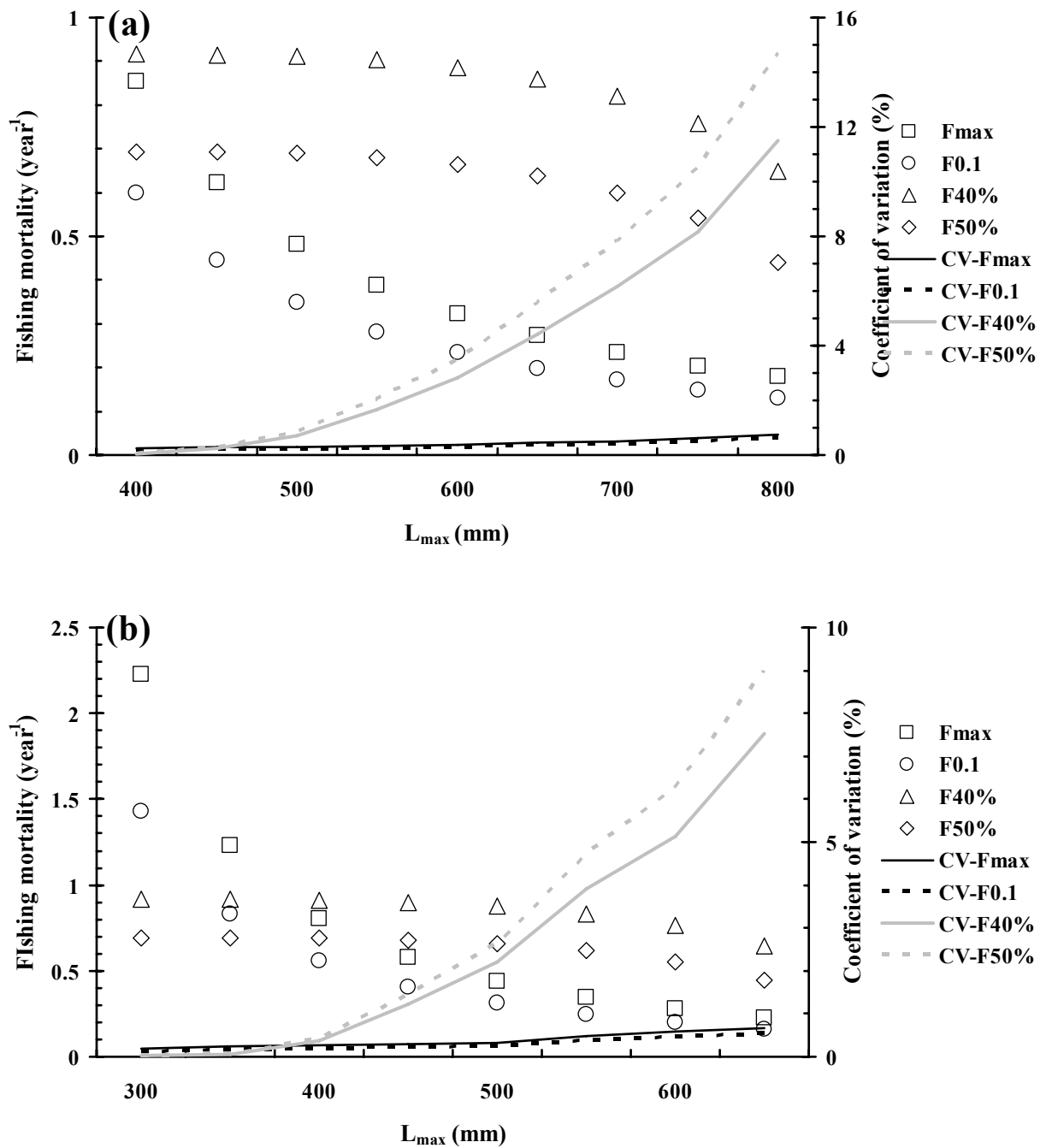


Fig. 33. Mean F_{max} (squares), $F_{0.1}$ (circles), $F_{40\%}$ (triangles) and $F_{50\%}$ (diamonds), and corresponding coefficient of variation (CV, black solid, black broken, grey solid and grey broken line) of for (a) females and (b) males with maximum legal lengths (L_{min}) from 900 to 400 mm for females and from 650 to 300 mm. L_{max} was not enforced in current eel fishery in the lower reach of Kao-Ping River.

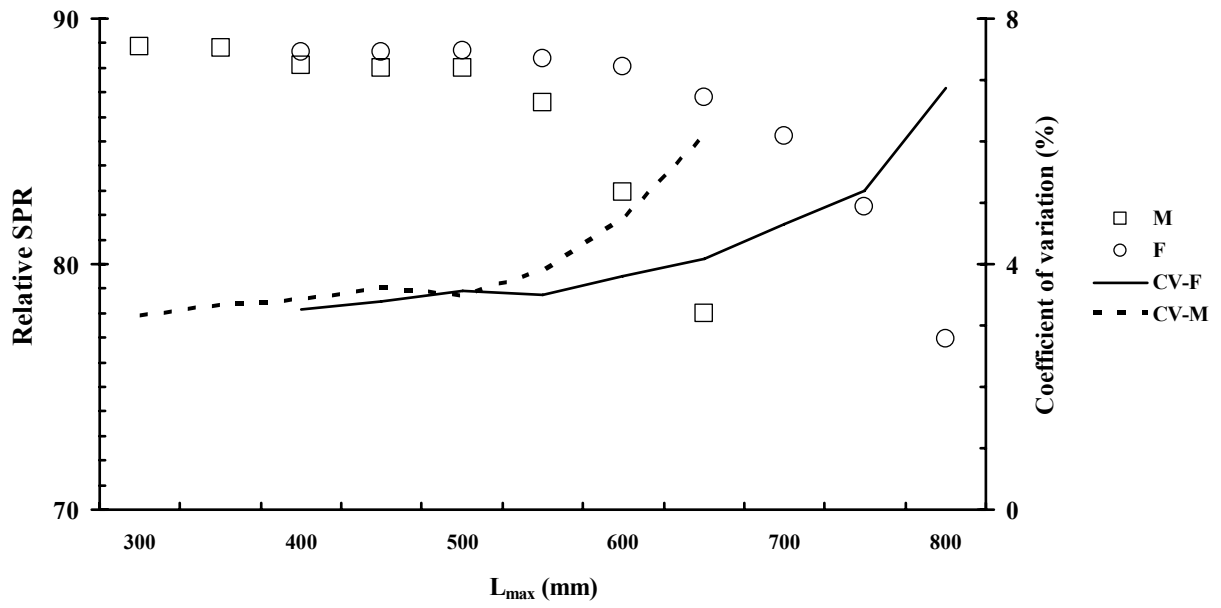
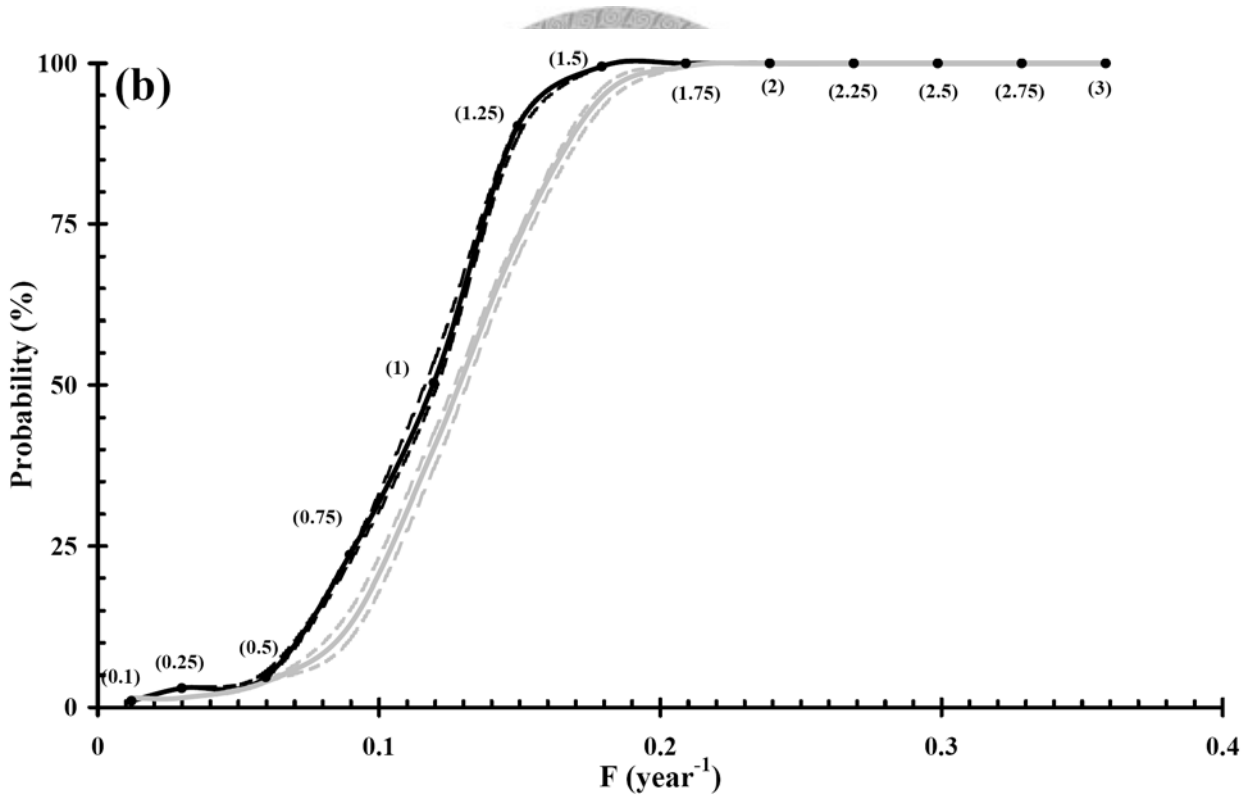
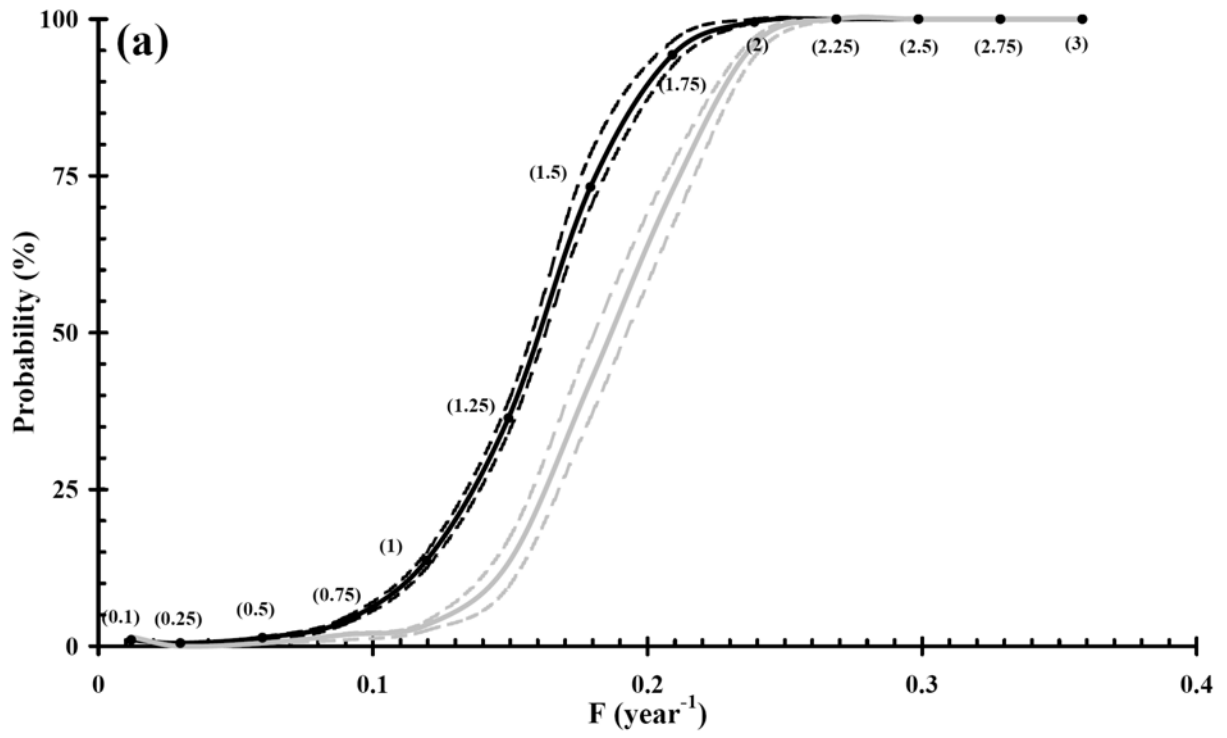


Fig. 34. Mean %SPR and corresponding coefficient of variation (CV, black and grey solid line) of for females (squares) and males (circles) with maximum legal lengths (L_{min}) from 900 to 400 mm for females and from 650 to 300 mm.

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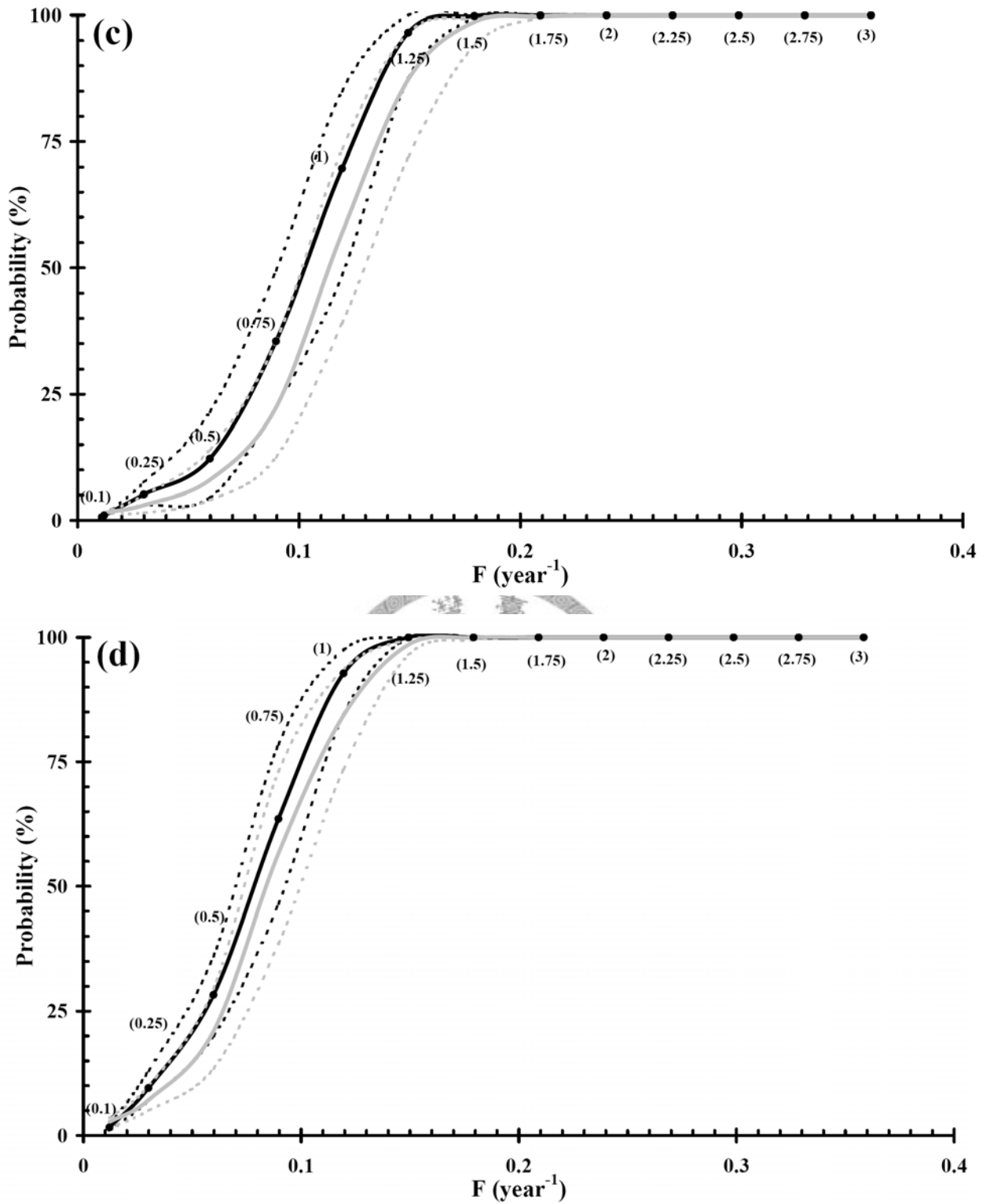
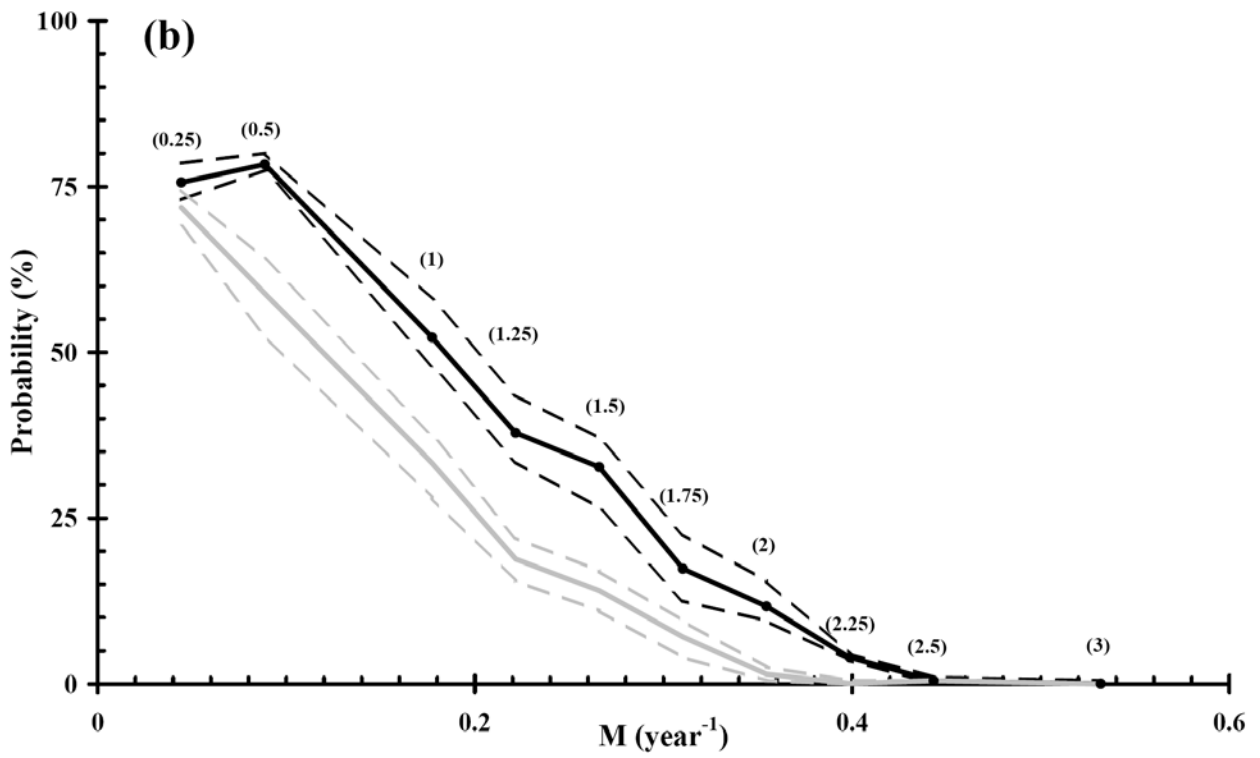
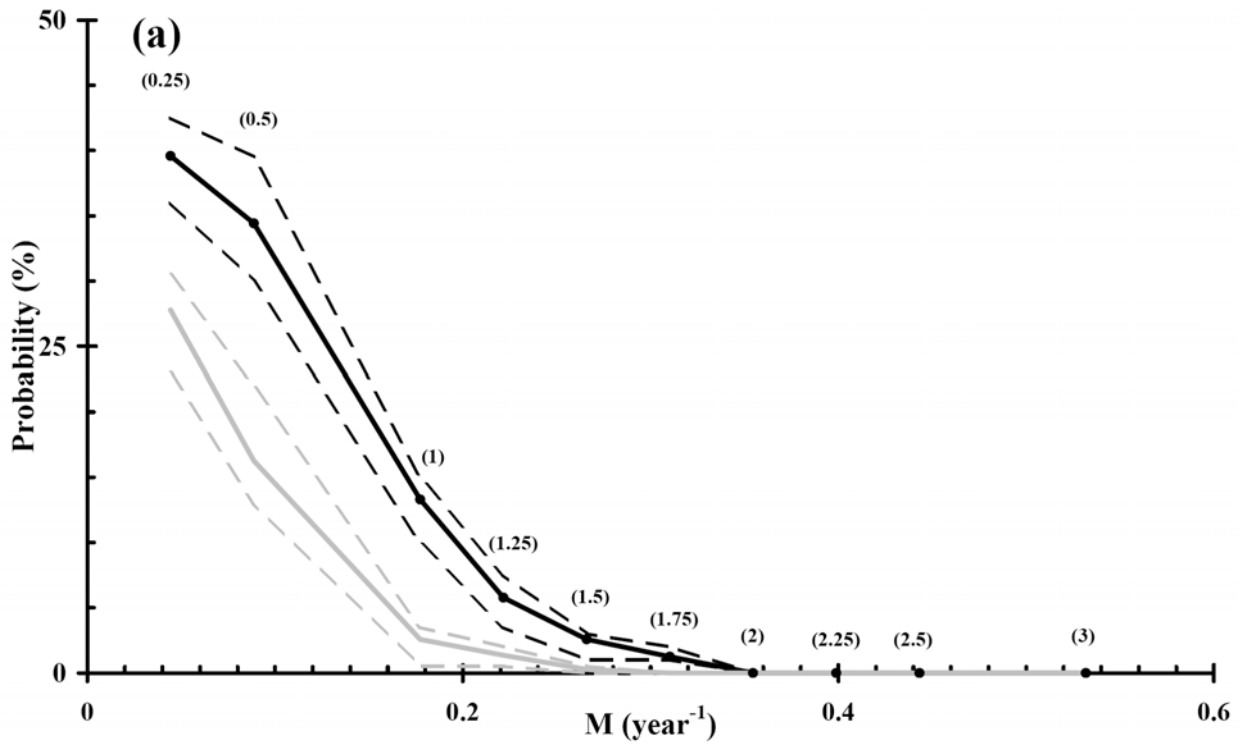


Fig. 35. Mean (solid line) and corresponding 95 %confidence intervals (broken lines) for the probabilities that F_{cur} was larger than (a) F_{max} (b) $F_{0.1}$, (c) $F_{40\%}$ and (d) $F_{50\%}$ under different values of F . Numbers in brackets were the times compared to F_{cur} .

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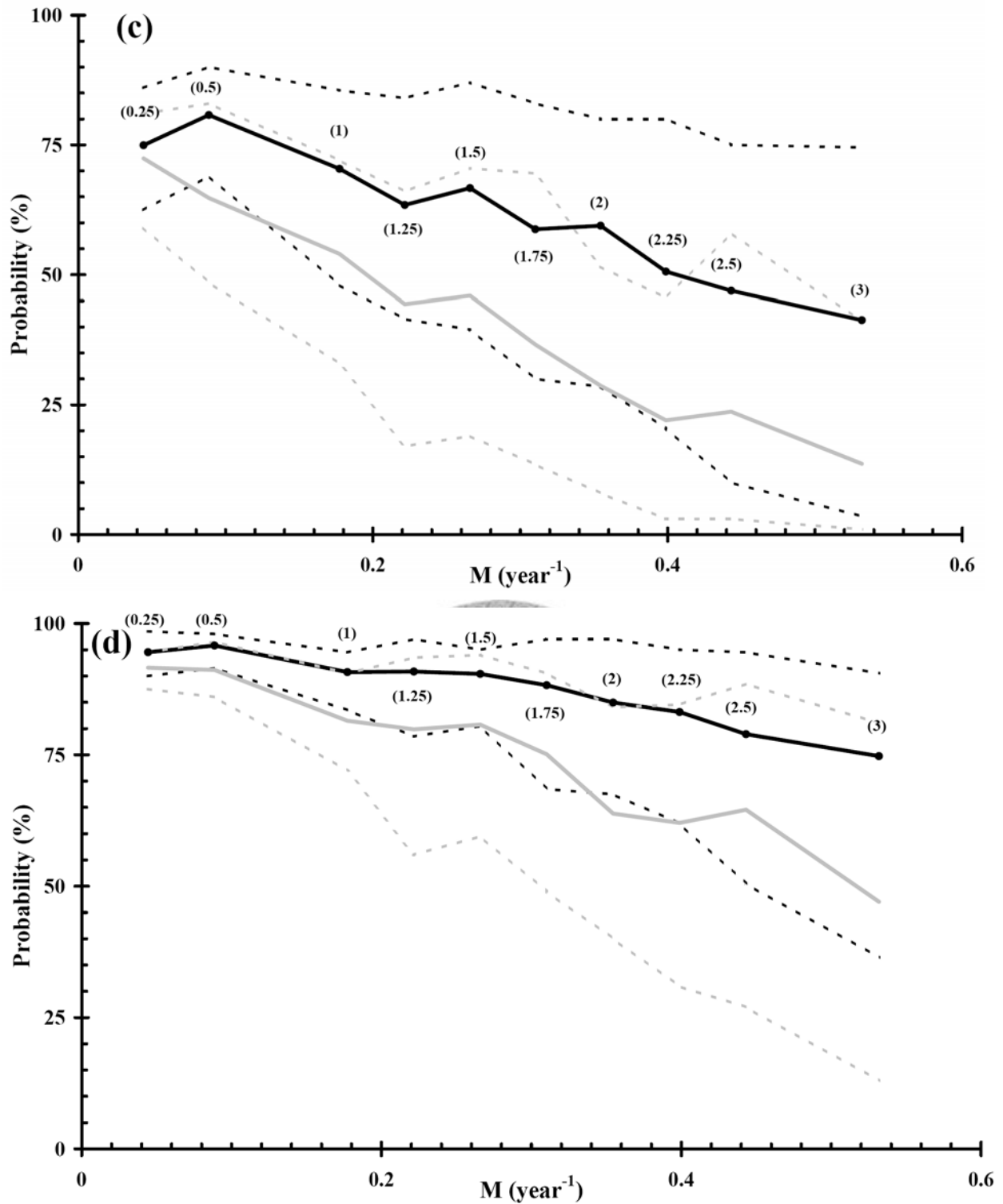


Fig. 36. Mean (solid line) and corresponding 95 %confidence intervals (broken lines) for the probabilities that F_{cur} was larger than (a) F_{max} (b) $F_{0.1}$, (c) $F_{40\%}$ and (d) $F_{50\%}$ under different values of M . Numbers in brackets were the times compared to current M (M_{cur}).

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Tables

Table 1. Sample sizes (N), mean (\pm SD) total lengths (TL, mm) and weights (TW, g) and age (years) of the Japanese eels sampled for evaluation of fishing gears, length-weight relationship, maturation curves, validation of otolith annuli, estimation and selection of growth models by origins, sexes and developmental stages. Numbers in the brackets were the sampling period.*Escaped cultured eels with unknown number were included.

Origins	Wild				Cultured		
	Female		Male		Undifferentiated	F	M
Sex							
Stage	Silver	Yellow	Silver	Yellow	Yellow	Yellow	Yellow
Examination of fishing gears (1999 ~ 2006)*							
N	1996		624		502	Unknown	
TL	446 \pm 105		452 \pm 102		503 \pm 65		
TW	114 \pm 131		176 \pm 78		33 \pm 47		
L-W relationship and maturation curve (1998 ~ 2007)							
N	147	1436	51	97	575	0	0
TL	626 \pm 75	416 \pm 87	552 \pm 67	449 \pm 74	313 \pm 73	-	-
TW	416.2 \pm 178.8	102.6 \pm 103.9	248.2 \pm 100.5	136.8 \pm 78.4	39.0 \pm 56.3		
Validation of otolith annuli (1998 ~ 2003 for wild and 2007 for cultured eels)							
N	45	7	14	19	28	3	28
TL	614 \pm 71	432.1 \pm 59.0	573 \pm 59	468.6 \pm 76.6	348.9 \pm 76.7	502 \pm 58	470 \pm 50
TW	398.5 \pm 155.5	121.0 \pm 56.9	290.4 \pm 75.2	158.1 \pm 94.5	61.4 \pm 59.8	202.5 \pm 100.3	152.2 \pm 69.9
Age	5.2 \pm 0.8	3.7 \pm 0.5	5.1 \pm 0.9	4.2 \pm 1.0	2.8 \pm 1.0	1.7 \pm 0.6	2.0 \pm 0.4
Estimation of growth parameters and model selection (1998 ~ 2003)							
N	55	8	37	20	0	0	0
TL	600 \pm 80	425 \pm 59	544 \pm 71	459 \pm 74	-	-	-

Age

5.6 ± 1.3

3.8 ± 0.5

5.3 ± 1.6

4.1 ± 1.0



Table 2. The summary table of the gears used in the lower reach of Kao-Ping River reported by the 4 cooperating fishermen, including gear types (S = shrimp net and T = eel tube), operation days (D_o), total number of gears used (N_t) in one month and mean (\pm SD) number of daily gears used in that month (N_m) and the overall mean of the number of gears used daily by one fisherman during the study period ($N_{overall}$).

Fisherman	Month	Gear Type	D_o	N_t	N_m	$N_{overall}$
A	05'Sep	S	12	431	36 ± 15.5	66 ± 13.6
	05'Oct	S	25	1000	40 ± 11.2	
	05'Nov	S	30	1800	60 ± 0	
	05'Dec	S	31	2480	80 ± 0	
	06'Jan	S	27	2050	76 ± 5	
	06'Feb	S	24	1680	70 ± 0	
	06'Mar	S	25	1750	70 ± 0	
	06'Apr	S	26	1690	65 ± 0	
	06'May	S	28	1820	65 ± 0	
	06'Jun	S	18	1170	65 ± 0	
B	06'Jul	S	17	1105	65 ± 0	56 ± 11.4
	05'Nov	S	25	1820	73 ± 50.6	
	05'Dec	S	31	1488	48 ± 0	
	06'Jan	S	22	1218	55 ± 3.6	
C	06'Feb	S	19	939	49 ± 3.4	50 ± 0
	05'Dec	S	10	500	50 ± 0	
D	05'Aug	T	5	230	46 ± 2.2	88 ± 53.4
	05'Sep	T	10	770	77 ± 6.3	
	05'Oct	T	5	750	150 ± 0	

Table 3. Estimated values and the estimation errors of the parameters used in yield and spawner per recruit models between sexes. Details of the parameters were defined in Materials and Method. $\rho_{X,Y}$ indicated the correlation between variable X and Y.

Parameter	Female	Male
LW relationship		
a	4.56×10^{-8}	1.61×10^{-7}
b	3.55	3.34
σ_{LW}^2	3.93×10^{-2}	2.74×10^{-2}
Growth		
L_{∞} (mm)	1023.7	758.7
K (year ⁻¹)	0.118	0.169
t_0 (year)	-0.69	-0.5
σ_{GR}^2	3.10×10^{-2}	
Mortality		
F (year ⁻¹)	0.120	
σ_F^2	1.06×10^{-3}	
M (year ⁻¹)	0.177	
σ_M^2	1.98×10^{-5}	
$\rho_{GR,M}$	0.8	
Maturation		
β_0	-13.31	-8.92
β_1 (mm ⁻¹)	2.15×10^{-2}	1.75×10^{-2}
$\sigma_{\beta_0}^2$	1.36	4.08
$\sigma_{\beta_1}^2$	4.04×10^{-6}	1.60×10^{-5}
ρ_{β_0, β_1}	-0.9	
Length and age at recruitment and capture		
L_r (mm)	55	
t_r (year)	0.489	
L_c (mm)	200	

Table 4. Changed parameters in the 19 scenarios for the sensitivity analysis. In each scenario only one parameter was changed while others remained the same to the reference case. Superscript *s* indicated simulated value

Scenarios	Parameter changed	Description
1	Not changed	Reference case
2	Not changed	Degree of random variation
3	$F^s = 2 \times F$	Higher mean F
4	$F^s = 0.5 \times F$	Lower mean F
5	$\sigma_F^2{}^s = 4 \times \sigma_F^2$	Higher variation in F
6	$\sigma_F^2{}^s = 0.25 \times \sigma_F^2$	Lower variation in F
7	$M^s = 2 \times M$	Higher mean M
8	$M^s = 0.5 \times M$	Lower mean M
9	$\sigma_M^2{}^s = 4 \times \sigma_M^2$	Higher variation in M
10	$\sigma_M^2{}^s = 0.25 \times \sigma_M^2$	Lower variation in M
11	$K^s = 2 \times K$	Higher mean K
12	$K^s = 0.5 \times K$	Lower mean K
13	$\sigma_{GR}^2{}^s = 4 \times \sigma_{GR}^2$	Higher variation in K
14	$\sigma_{GR}^2{}^s = 0.25 \times \sigma_{GR}^2$	Lower variation in K
15	$\rho_{GR,M}{}^s = 0$	Independence between K and M
16	$\Delta L_{50} = 100$	Increased length at 50 % maturity
17	$\Delta L_{50} = -100$	Decreased length at 50 % maturity
18	$\Delta slope = 2$	Steep maturation curve
19	$\Delta slope = 0.5$	Mild maturation curve

Table 5. Parameters in length-weight relationship a (g mm^{-1}) and b (no unit), the corresponding R-square and mean sum of square error (MSE) of the female, male and sexually-undifferentiated eels.

Sex	F	M	U
a	1.33×10^{-8}	3.54×10^{-7}	6.85×10^{-8}
b	3.74	3.22	3.46
R^2	0.95	0.92	0.90
MSE	3.94×10^{-2}	3.04×10^{-2}	5.938×10^{-2}

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Table 6. Number of parameters (P), Akaike information criterion corrected for sample size (AIC_c), and corresponding Akaike differences (Δ), Akaike weights (w) and mean sum of squares error (MSE) for female and male Japanese eels. Candidate models were the von Bertalanffy (VB), Gompertz, logistic, power and generalized von Bertalanffy growth model (GVB). The best model fitting the data (i.e. $\Delta = 0$) is in bold.

Model	P	AIC_c	Δ	w	$MSE (10^{-2})$
Female					
VB	4	259822	0.000	0.468	3.065
Gompertz	4	259824	2.184	0.157	3.085
Logistic	4	259830	8.141	0.008	3.139
Power	4	259823	1.749	0.195	3.081
GVB	5	259824	2.013	0.171	3.074
Male					
VB	4	197261	0.000	0.410	3.131
Gompertz	4	197263	1.272	0.222	3.145
Logistic	4	197267	5.433	0.028	3.191
Power	4	197263	1.698	0.179	3.149
GVB	5	197264	2.019	0.153	3.141

Table 7. Number of parameters (P), Akaike information criterion corrected for sample size (AIC_c), and corresponding Akaike differences (Δ), Akaike weights (w) and mean sum of squares error (MSE) for the models in which the sexes (female or male) were pooled or separated. The best model fitting the data is in bold font.

Model	Sex	P	AIC_c	Δ	w	MSE (10^{-2})
VBGF		4	457105	22.396	~ 0	3.229
Gompertz		4	457109	25.494	~ 0	3.245
Logistic	Pooled	4	457118	34.672	~ 0	3.292
Power		4	457109	25.619	~ 0	3.245
GVB		5	457107	24.329	~ 0	3.233
VBGF		7	457083	0.000	0.671	3.095
Gompertz		7	457087	3.457	0.119	3.112
Logistic	Separated	7	457097	13.574	7.57×10^{-4}	3.163
Power		7	457087	3.448	0.120	3.112
GVB		9	457087	4.024	0.090	3.105

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Table 8. Estimates of parameter and corresponding standard errors (SE) between sexes for the growth models with Δ less than 10 in Table 6-3. The model-averaged mean sum of squares error (MSE) was also shown.

Model	Parameter	Female		Male	
		Estimate	SE	Estimate	SE
VBGM	K (year^{-1})	0.118	0.026	0.169	0.032
	L_∞ (mm)	1023.7	146.8	758.7	82.33
	t_0 (year)	-0.69	0.14	-0.50	0.13
Power	b_0 (mm)	6.2	38.4	-63.8	64.4
	b_1 (year^{-1})	178.1	36.4	233.7	62.7
	b_2	0.623	0.080	0.495	0.092
Gompertz	K_2 (year^{-1})	0.319	0.028	0.378	0.035
	L_∞ (mm)	747.9	45.8	618.4	34.1
	t_2 (year)	-1.56	0.41	-0.92	0.35
GVB	K_4 (year^{-1})	0.141	0.108	0.201	0.143
	L_∞ (mm)	958.9	272.8	721.2	153.0
	t_0 (year)	-0.90	1.09	-0.76	1.26
	p	1.138	0.715	1.192	0.989
Averaged	MSE	3.10×10^{-2}			

Table 9. Mean \pm SD, (range in bracket), total length (TL , cm), weight (TW , g), and number of *A. japonica* released ($N_{release}$) 1km upstream of the fishing ground in 2005 and at the fishing ground in 2006. N_{recap} = number of eels recaptured at the fishing ground and T_{Last} = time elapsed from release to the last recapture (days). Eels were from the wild (Wild) or culture ponds (Cultured) and marked by microchip (CHIP) or caudal fin or pectoral fin clip (C-FC or P-FC). NA = data not available.

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Site	1 km upstream in 2005				Fishing ground in 2006			
Origin	Cultured		Wild		Cultured		Wild	
Mark	CHIP	C-FC	CHIP	P-FC	CHIP	FC	CHIP	P-FC
$N_{release}$	349	170	136	62	100	436	100	146
TL	69.3 \pm 4.9 (59.5 ~ 87.5)	NA	57.4 \pm 6.0 (48 ~ 75.5)	41.6 \pm 7.2 (25 ~ 53.5)	74.6 \pm 11.0 (46 ~ 92.5)	65.8 \pm 8.5 (44.5 ~ 90.7)	54.6 \pm 8.8 (40 ~ 86.5)	35.7 \pm 5.9 (21.1 ~ 51.4)
TW	508 \pm 138 (318 ~ 1251)	NA	253 \pm 96 (157 ~ 574)	81 \pm 46 (14 ~ 178)	711 \pm 318 (129 ~ 1326)	425 \pm 240 (127 ~ 1321)	212 \pm 142 (57 ~ 917)	38 \pm 23 (5 ~ 116)
N_{recap}	3	5	5	6	72	310	23	39
T_{Last}	57	40	146	55	57	220	62	14

Table 10. Estimates (95 % CI in brackets) of recapture rates (P_{re} , %) for wild and cultured eels for the experiments in 2005 and 2006.

Year	2005		2006	
Origin	Cultured	Wild	Cultured	Wild
P_{re}	1.54 (0.71 ~ 2.85)	5.55 (2.92 ~ 9.33)	71.27 (67.34 ~ 74.99)	25.20 (20.05 ~ 30.87)

Table 11. Number of parameters (P), $-2 \ln(L)$, Akaike information criterion corrected for sample size (AIC_c), Bayesian information criterion (BIC) and corresponding weights (W_{AIC_c} and W_{BIC} , ~ 0 indicated $< 10^{-5}$) for the estimates of fishing and natural mortality rate by the completed experiment method. Wild + mark indicated that the model parameters for eels with different marks differed for wild eels, but not for cultured eels and vice versa for Culture + mark.

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Model	Parameters	P	$-2\ln(L)$	AIC_c	BIC	W_{AIC_c}	W_{BIC}
1km upstream (2005)							
Full model	$(F, M)_{\text{Origin} \times \text{Mark}}$	8	340.29	356.49	409.09	0.246	~ 0
Wild + mark	$(F, M)_{\text{Wild} + \text{Mark}}$	6	345.30	357.42	396.87	0.156	2.13×10^{-5}
Cultured + mark	$(F, M)_{\text{Cultured} + \text{Mark}}$	6	343.76	355.88	395.33	0.334	4.61×10^{-5}
Origin	$(F, M)_{\text{Origin}}$	4	348.77	356.83	383.13	0.208	0.021
Mark	$(F, M)_{\text{Mark}}$	4	351.88	359.94	386.24	0.044	0.004
Null model	$(F, M)_{\text{Pooled}}$	2	358.24	362.26	375.41	0.014	0.975
At fishing ground (2006)							
Full model	$(F, M)_{\text{Origin} \times \text{Mark}}$	8	3173.05	3189.25	3226.04	0.235	0.003
Wild + mark	$(F, M)_{\text{Wild} + \text{Mark}}$	6	3174.78	3186.89	3214.51	0.765	0.997
Cultured + mark	$(F, M)_{\text{Cultured} + \text{Mark}}$	6	3245.16	3257.27	3284.90	~ 0	~ 0
Origin	$(F, M)_{\text{Origin}}$	4	3246.89	3254.94	3273.38	~ 0	~ 0
Mark	$(F, M)_{\text{Mark}}$	4	3380.28	3388.33	3406.77	~ 0	~ 0
Null model	$(F, M)_{\text{Pooled}}$	2	3404.28	3408.29	3417.52	~ 0	~ 0

Table 12. -2 Log likelihood values, *AIC*, *BIC* and corresponding weights in the estimation of $\mu((F/Z)(1 - e^{-ZT}))$ and survival (*S*) by uncompleted method. UE = unrealistic estimate ($\hat{S} > 1$).

Model	Parameters	<i>P</i>	$-2\ln(L)$	<i>AIC_c</i>	<i>BIC</i>	<i>W_{AICc}</i>	<i>W_{BIC}</i>
1km upstream (2005)							
Full model	$(\mu, S)_{\text{Origin} \times \text{Mark}}$	8	UE	-	-	-	-
Wild + mark	$(\mu, S)_{\text{Wild} + \text{Mark}}$	6	UE	-	-	-	-
Cultured + mark	$(\mu, S)_{\text{Cultured} + \text{Mark}}$	6	UE	-	-	-	-
Origin	$(\mu, S)_{\text{Origin}}$	4	UE	-	-	-	-
Mark	$(\mu, S)_{\text{Mark}}$	4	176.23	184.29	202.53	-	-
Null model	$(\mu, S)_{\text{Pooled}}$	2	184.49	188.51	197.64	-	-
At fishing ground (2006)							
Full model	$(\mu, S)_{\text{Origin} \times \text{Mark}}$	8	2085.45	2101.64	2138.43	0.235	0.003
Wild + mark	$(\mu, S)_{\text{Wild} + \text{Mark}}$	6	2158.73	2099.28	2126.91	0.765	0.997
Cultured + mark	$(\mu, S)_{\text{Cultured} + \text{Mark}}$	6	2087.17	2170.84	2198.47	~ 0	~ 0
Origin	$(\mu, S)_{\text{Origin}}$	4	2160.47	2168.53	2186.96	~ 0	~ 0
Mark	$(\mu, S)_{\text{Mark}}$	4	2293.87	2301.92	2320.37	~ 0	~ 0
Null model	$(\mu, S)_{\text{Pooled}}$	2	2317.87	2321.88	2331.11	~ 0	~ 0

Table 13. Estimates (95 % CI in brackets) of fishing (F) and natural (M) mortality rates (year^{-1}) from the completed method and survival (S , year^{-1}), μ , F and M from the uncompleted method.

Year	2005		2006	
Origin	Pooled	Wild		Cultured
Mark		CHIP	P-FC	Pooled
Completed method				
F	1.45×10^{-3} ($8.86 \sim 22.14$) $\times 10^{-4}$	0.024 (0.015 ~ 0.036)	0.254 (0.177 ~ 0.357)	0.243 (0.207 ~ 0.284)
M	0.053 (0.039 ~ 0.073)	0.079 (0.055 ~ 0.111)	0.698 (0.526 ~ 0.918)	0.098 (0.081 ~ 0.113)
Uncompleted method				
S	0.956 (0.924 ~ 0.984)	0.903 (0.860 ~ 0.936)	0.386 (0.277 ~ 0.505)	0.7106 (0.6859 ~ 0.7346)
μ	0.027 (0.016 ~ 0.040)	0.230 (0.155 ~ 0.319)	0.267 (0.200 ~ 0.3425)	0.713 (0.673 ~ 0.750)
F	1.20×10^{-3}	0.024	0.254	0.243
M	0.044	0.079	0.698	0.098

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Table 14. Estimated values of β_0 (no unit) and β_1 (mm^{-1}), the corresponding standard errors (SE) and negative log likelihood ($-\ln(L)$) of the maturation curves among the female, male eels and sex-pooled model.

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Model	Female	Male	Pooled
β_0	-16.23	-10.80	-13.89
SE	1.1017	1.8294	0.81
β_1	0.027	0.020	0.023
SE	0.0019	0.004	0.0015
$-\ln(L)$	220.79	68.19	323.62

Table 15. Estimated current fishing mortality rate (F_{cur} , year⁻¹), F values resulting in maximal YPR value (F_{max}), at which the increase in YPR is 10% of that when $F = 0$ ($F_{0.1}$), and the values resulting in 40% and 50 % SPR value of that when $F = 0$ ($F_{40\%}$ and $F_{50\%}$). Maximal YPR values (YPR_{max} , g ind⁻¹), SPR values under current fishing mortality ($SPR_{F_{cur}}$) and when $F = 0$ (SPR_0) and relative SPR ($\%SPR = SPR_{F_{cur}} / SPR_0$) were also calculated. Females and males were separated.

	Female	Male
F_{cur}	0.120	
F_{max}	0.156	0.186
$F_{0.1}$	0.111	0.128
$F_{40\%}$	0.097	0.110
$F_{50\%}$	0.073	0.082
YPR_{max}	62.22	42.48
$SPR_{F_{cur}}$	312.68	220.13
SPR_0	957.46	591.34
$\%SPR$	0.327	0.372

Table 16. Mean, coefficient of variation (CV, %) and 95 % confidence intervals of F_{cur} used in simulations, F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$, YPR_{max} , $SPR_{F_{cur}}$, SPR_0 (g ind⁻¹) and $\%SPR$ of females and males when uncertainties in parameter estimation were incorporated.

	Female			Male		
	Mean	CV	95 % CL	Mean	CV	95 % CL
F_{cur}	0.119	27.29	0.064 – 0.190	0.118	26.83	0.065 – 0.180
F_{max}	0.156	1.00	0.153 – 0.159	0.186	1.12	0.182 – 0.190
$F_{0.1}$	0.111	0.83	0.110 – 0.113	0.128	0.90	0.126 – 0.131
$F_{40\%}$	0.097	8.75	0.082 – 0.114	0.111	7.69	0.095 – 0.129
$F_{50\%}$	0.073	8.44	0.062 – 0.085	0.083	7.35	0.071 – 0.095
YPR_{max}	79.1	69.31	18.7 – 223.3	51.2	54.89	15.7 – 123.3
$SPR_{F_{cur}}$	424.7	105.68	12.7 – 1720.5	679.8	78.25	58.8 – 2047.8
SPR_0	1169.1	91.78	52.8 – 3995.9	272.8	88.61	19.1 – 914.0
$\%SPR$	0.343	28.85	0.167 – 0.544	0.384	24.73	0.207 – 0.567

Table 17. Percentage change (PC) for the mean and SD of F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$ and %SPR in different scenarios in the females. Scenarios: 1 = the basic, 2 = randomness, F, VF, M, VM, K, VK, CGM, $L_{50\%}$ and Stp = changes in mean of F , variance of F , mean of M , variance of M , mean of K , variance of K , correlation between natural mortality and growth, length at 50 % maturity and steepness of maturation curve, respectively.

Scenario	Mean(F_{max})	SD(F_{max})	Mean($F_{0.1}$)	SD($F_{0.1}$)	Mean($F_{40\%}$)	SD($F_{40\%}$)	Mean($F_{50\%}$)	SD($F_{50\%}$)
1(Basic)	0	0	0	0	0.00	0.00	0.00	0.00
2(Ran)	-0.03	0.13	-0.03	0.13	0.10	3.85	0.09	3.70
3(F)	-0.03	0.51	-0.03	0.51	-0.69	-4.63	-0.66	-4.48
4(F)	-0.01	0.29	-0.01	0.28	0.50	5.14	0.47	5.21
5(VF)	-0.02	1.19	-0.01	1.18	0.77	-3.05	0.75	-3.16
6(VF)	-0.02	0.79	-0.02	0.79	0.17	-4.81	0.16	-4.86
7(M)	58.01	101.71	45.57	82.51	15.40	48.15	15.12	48.85
8(M)	-16.32	-34.55	-13.88	-31.33	-6.31	-26.12	-6.16	-26.00
9(VM)	-0.03	98.58	-0.03	98.57	0.14	7.31	0.13	7.40
10(VM)	0.02	-49.58	0.02	-49.58	0.31	-4.85	0.30	-4.69
11(K)	36.15	77.62	27.35	59.15	36.52	26.17	34.50	20.48
12(K)	-14.49	-30.78	-12.19	-27.41	-18.92	-63.55	-18.44	-62.62
13(VG)	0.00	-1.37	0.00	-1.38	0.63	44.37	0.50	43.34
14(VG)	0.02	0.52	0.02	0.51	0.27	-42.57	0.31	-42.42
15(CGM)	-0.02	0.87	-0.01	0.87	-0.26	-2.95	-0.25	-3.07
16($L_{50\%}$)	0.04	2.27	0.03	2.25	7.92	-6.36	7.55	-7.73
17($L_{50\%}$)	0.04	0.63	0.04	0.62	-8.14	-9.50	-7.88	-8.44
18(Stp)	0.04	4.13	0.03	4.10	-0.08	25.45	-0.04	25.62
19(Stp)	0.00	2.89	0.00	2.88	4.60	-40.49	4.32	-40.85

Table 18. Percentage change (PC) for the mean and SD of F_{max} , $F_{0.1}$, $F_{40\%}$ and $F_{50\%}$ and %SPR in different scenarios in the males..

Scenario	Mean(F_{max})	SD(F_{max})	Mean($F_{0.1}$)	SD($F_{0.1}$)	Mean($F_{40\%}$)	SD($F_{40\%}$)	Mean($F_{50\%}$)	SD($F_{50\%}$)
1(Basic)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2(Ran)	0.02	1.74	0.02	1.77	-0.31	-2.05	-0.30	-1.94
3(F)	0.07	-11.24	0.06	-11.40	0.44	-3.58	0.41	-3.60
4(F)	0.11	-1.09	0.09	-1.16	0.97	-0.99	0.92	-1.15
5(VF)	-0.08	-5.40	-0.06	-5.42	-0.67	-0.31	-0.64	-0.08
6(VF)	0.05	0.54	0.04	0.54	-0.14	-2.95	-0.14	-2.67
7(M)	68.24	87.00	51.65	67.56	21.68	77.62	21.11	78.35
8(M)	-19.52	-28.79	-16.23	-24.02	-8.57	-30.41	-8.31	-30.22
9(VM)	0.33	131.51	0.26	132.13	0.49	11.84	0.46	11.77
10(VM)	0.01	-47.33	0.01	-47.56	0.20	-3.66	0.20	-3.50
11(K)	52.31	135.57	35.58	97.58	39.08	51.19	36.55	44.05
12(K)	-20.07	-34.50	-16.46	-29.19	-20.58	-49.16	-19.93	-47.94
13(VG)	-0.08	14.06	-0.07	14.22	0.17	49.46	0.06	48.73
14(VG)	0.10	7.06	0.08	7.06	0.18	-38.15	0.21	-38.14
15(CGM)	-0.11	2.41	-0.09	2.43	-0.51	2.45	-0.50	2.43
16(L_{50%})	-0.09	-9.55	-0.07	-9.59	9.31	-18.73	8.77	-20.38
17(L_{50%})	0.01	-1.86	0.01	-1.88	-8.57	-10.04	-8.23	-9.09
18(Stp)	-0.04	6.20	-0.03	6.22	-3.38	34.58	-3.15	35.19
19(Stp)	-0.03	5.78	-0.03	5.81	5.52	-38.50	5.09	-39.31

Table 19. Percentage change (PC) for the mean and SD of YPR_{max} , SPR_{Fcur} , SPR_0 and $\%SPR$ in different scenarios in the females.

Scenario	Mean(YPR_{max})	SD(YPR_{max})	Mean(SPR_{Fcur})	SD(SPR_{Fcur})	Mean(SPR_0)	SD(SPR_0)	Mean($\%SPR$)	SD($\%SPR$)
1(Basic)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2(Ran)	7.37	37.63	16.44	59.33	11.82	45.70	16.44	59.33
3(F)	-1.79	9.50	-64.02	-54.21	-0.03	22.19	-64.02	-54.21
4(F)	4.09	6.58	74.29	72.20	8.02	10.02	74.29	72.20
5(VF)	-1.68	-0.93	10.19	25.36	3.22	8.01	10.19	25.36
6(VF)	-4.39	-1.44	-6.40	-3.66	-1.22	2.09	-6.40	-3.66
7(M)	-65.51	-68.71	-77.75	-75.86	-80.53	-79.04	-77.75	-75.86
8(M)	90.39	78.07	104.92	66.71	123.26	86.58	104.92	66.71
9(VM)	-2.86	-12.01	-0.03	-15.21	-3.22	-14.59	-0.03	-15.21
10(VM)	-3.65	-18.70	-7.75	-32.22	-5.73	-24.64	-7.75	-32.22
11(K)	246.85	241.66	328.46	187.45	230.54	144.50	328.46	187.45
12(K)	-80.26	-82.55	-93.50	-91.33	-91.05	-86.84	-93.50	-91.33
13(VG)	74.45	358.16	117.15	298.38	104.43	371.38	117.15	298.38
14(VG)	-8.83	-58.11	-12.14	-45.81	-9.10	-49.42	-12.14	-45.81
15(CGM)	2.82	15.14	1.30	12.97	3.55	21.43	1.30	12.97
16(L_{50%})	-9.42	5.57	8.94	1.50	5.68	7.02	8.94	1.50
17(L_{50%})	-9.33	-12.10	-39.65	-36.28	-31.19	-19.81	-39.65	-36.28
18(Stp)	-0.99	0.43	2.89	4.50	7.23	12.97	2.89	4.50
19(Stp)	-5.96	-7.17	-14.03	-17.66	-14.07	-14.20	-14.03	-17.66

Table 20. Percentage change (PC) for the mean and SD of YPR_{max} , SPR_{Fcur} , SPR_0 and $\%SPR$ in different scenarios in the males.

Scenario	Mean(YPR_{max})	SD(YPR_{max})	Mean(SPR_{Fcur})	SD(SPR_{Fcur})	Mean(SPR_0)	SD(SPR_0)	Mean($\%SPR$)	SD($\%SPR$)
1(Basic)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2(Ran)	2.95	12.89	-3.11	6.38	-4.80	1.54	-3.11	6.38
3(F)	8.14	-2.12	-51.81	-53.36	8.29	0.87	-51.81	-53.36
4(F)	8.95	16.21	76.35	74.56	11.30	10.67	76.35	74.56
5(VF)	-5.88	-7.60	-5.95	-2.57	-10.77	-14.99	-5.95	-2.57
6(VF)	-5.25	-10.63	-10.89	-24.49	-10.64	-20.17	-10.89	-24.49
7(M)	-54.07	-53.52	-70.86	-70.49	-74.98	-73.89	-70.86	-70.49
8(M)	77.27	55.52	100.54	86.66	116.51	89.73	100.54	86.66
9(VM)	14.96	10.39	11.17	11.32	11.61	9.63	11.17	11.32
10(VM)	10.59	-10.58	14.59	3.73	13.28	-4.00	14.59	3.73
11(K)	228.35	235.10	288.87	238.47	203.62	181.72	288.87	238.47
12(K)	-73.67	-76.14	-86.84	-81.30	-83.18	-75.44	-86.84	-81.30
13(VG)	71.38	286.26	99.95	291.78	89.01	285.22	99.95	291.78
14(VG)	-7.51	-52.38	-12.55	-43.82	-11.27	-49.03	-12.55	-43.82
15(CGM)	-1.58	14.24	-2.03	11.00	-1.13	11.39	-2.03	11.00
16(L_{50%})	1.98	-3.55	27.47	1.41	20.87	-6.68	27.47	1.41
17(L_{50%})	4.78	7.28	-30.40	-2.28	-25.23	-5.34	-30.40	-2.28
18(Stp)	6.83	11.43	2.87	4.11	7.74	4.14	2.87	4.11
19(Stp)	9.56	27.81	1.42	8.39	-0.36	9.20	1.42	8.39

Table 21. The mean and standard deviation (SD) of probabilities (%) that F_{cur} was larger than F_{max} (P_{Grow}), larger than $F_{0.1}$ ($P_{Grow0.1}$), larger than $F_{40\%}$ ($P_{Recruit40}$), and larger than $F_{50\%}$ ($P_{Recruit50}$), probability that %SPR was lower than 50% ($P_{recruit}$) for the females.

Scenario	Mean(P_{Grow})	SD(P_{Grow})	Mean($P_{Grow0.1}$)	SD($P_{Grow0.1}$)	Mean($P_{Recruit40}$)	SD($P_{Recruit40}$)	Mean($P_{Recruit50}$)	SD($P_{Recruit50}$)
1(Ref)	17.19	0.76	55.94	1.64	69.64	11.06	93.13	3.81
2(Ran)	15.03	1.33	54.33	1.29	71.32	9.72	93.57	4.67
3(F)	99.50	0.00	100.00	0.00	100.00	0.00	100.00	0.00
4(F)	1.81	0.36	10.38	0.63	10.05	4.21	28.05	5.42
5(VF)	26.98	1.06	50.47	0.59	50.51	5.51	67.50	4.65
6(VF)	1.50	0.05	71.03	1.73	89.35	9.22	99.34	0.57
7(M)	0.13	0.22	13.06	1.92	58.79	18.15	88.11	7.89
8(M)	31.53	0.72	76.51	1.08	77.39	8.00	95.38	1.66
9(VM)	11.72	0.75	54.44	2.38	70.00	10.03	93.61	4.10
10(VM)	11.31	0.35	54.72	0.64	75.86	10.60	96.08	1.64
11(K)	0.65	0.23	22.27	1.74	27.30	13.24	69.93	8.67
12(K)	36.00	0.90	75.76	1.16	87.37	3.05	98.09	0.40
13(VG)	17.20	1.25	58.18	1.21	67.83	13.13	89.58	6.61
14(VG)	16.06	0.97	58.40	0.75	78.46	5.00	95.17	1.57
15(LGM)	15.26	1.12	54.54	1.85	72.13	10.60	94.27	2.86
16(L50%)	12.44	0.73	55.63	1.06	62.76	10.73	90.28	3.13
17(L50%)	12.82	1.30	54.49	1.41	82.37	7.73	97.31	2.31
18(Stp)	10.93	1.22	57.80	1.12	75.09	11.57	95.14	4.12
19(Stp)	17.17	1.40	56.67	1.30	69.18	7.66	93.94	2.88

Table 22. The mean and standard deviation (SD) of probabilities (%) that F_{cur} was larger than F_{max} (P_{Grow}), larger than $F_{0.1}$ ($P_{Grow0.1}$), larger than $F_{40\%}$ ($P_{Recruit40}$), and larger than $F_{50\%}$ ($P_{Recruit50}$), probability that %SPR was lower than 50% ($P_{recruit}$) for the males.

Scenario	Mean(P_{Grow})	SD(P_{Grow})	Mean($P_{Grow0.1}$)	SD($P_{Grow0.1}$)	Mean($P_{Recruit40}$)	SD($P_{Recruit40}$)	Mean($P_{Recruit50}$)	SD($P_{Recruit50}$)
1(Ref)	4.91	0.36	30.18	1.43	55.08	11.98	87.18	3.89
2(Ran)	3.18	1.42	34.70	1.15	54.63	10.98	86.42	6.41
3(F)	96.27	1.10	100.00	0.00	100.00	0.00	100.00	0.00
4(F)	0.50	0.00	2.50	0.00	6.50	2.70	18.55	2.63
5(VF)	16.15	0.69	36.66	0.75	48.57	6.70	65.71	3.24
6(VF)	0.00	0.00	35.01	2.06	63.40	18.08	98.83	2.14
7(M)	0.00	0.00	0.18	0.24	32.90	16.24	73.40	11.77
8(M)	18.90	0.95	61.70	1.85	67.99	9.07	91.67	2.71
9(VM)	3.19	0.96	32.63	2.72	52.55	9.33	81.76	6.68
10(VM)	3.50	0.00	31.20	0.75	53.61	10.67	88.01	6.19
11(K)	0.00	0.00	7.13	0.47	16.94	7.92	55.27	11.69
12(K)	18.73	1.32	64.53	1.20	85.01	4.28	99.28	0.53
13(VG)	3.95	0.34	41.04	1.60	52.66	16.25	86.19	7.56
14(VG)	7.26	0.49	38.84	1.62	60.05	6.73	86.43	2.09
15(LGM)	5.32	0.81	43.13	1.38	59.39	8.83	89.05	5.57
16(L50%)	1.51	0.07	39.10	0.75	43.39	8.98	80.47	4.76
17(L50%)	1.37	0.44	32.87	1.46	66.69	11.42	92.22	4.28
18(Stp)	3.38	0.75	35.37	1.21	59.84	15.66	90.52	5.89
19(Stp)	3.44	0.98	39.26	0.65	40.58	8.02	81.24	6.12

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