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STAGE-STRUCTURED POPULATION MATRIX MODELS FOR THE FORMOSAN LANDLOCKED SALMON (*ONCORHYNCHUS MASOU FORMOSANUS*) IN TAIWAN

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ABSTRACT. – The Formosan landlocked salmon (*Oncorhynchus masou formosanus*) is an endangered endemic species found only in the basin of the Chichiawan Stream in the mountains of Central Taiwan. Census observations recorded from 1987 to 2004 showed that the regulation of the Formosan salmon population is density-independent, possibly due to the fluctuating environment. In order to better understand and predict the population dynamics, stage-structured population matrix models were constructed for juveniles, subadult and adult stages using the census data. We applied the least-squares solution to determine stage-specific parameters including the growth rates, survival rates and fecundity for the matrix models. The derived population growth rates determined by the matrix models indicated that the Formosan salmon population is declining in the Chichiawan Stream but has been increasing in a tributary, the Kaoshan Stream since 2001, when dams on that stream were demolished. In general, the numbers of each stage of the Formosan salmon could be well predicted by the matrix models. In the Chichiawan Stream, the model performance was better for subadults than for adults or juveniles. The lower predictability of adult numbers across summers might be a result of the low capacity of large-sized adult salmon to seek refuge when typhoons cause floods in the shallow streams. The lower predictability of juvenile numbers from winter to spring suggests that other intrusive factors or interactions with other communities might be involved in determining the fecundity and require further study. Stage-structured population matrix models appear to be a useful tool for the management and conservation of the Formosan salmon.

KEY WORDS. – Chichiawan Stream, Kaoshan Stream, Shei-Pa National Park, dam demolishment, *Oncorhynchus masou formosanus*.

INTRODUCTION

The Formosan landlocked salmon (*Oncorhynchus masou formosanus*) is an endangered endemic species which is distributed only in the basin of the Chichiawan Stream located in Shei-Pa National Park in the high mountains of Central Taiwan. It is known as the Southernmost natural salmon population in the world (Oshima, 1955). The fish has been on the list of endangered species published by the Taiwanese government since the population was found to have declined to only about 200 individuals in 1984 (Lin et al., 1987). Due to the status of its decline and its narrow distribution, the World Conservation Union, IUCN (Kottelat, 1996) listed the species as a critically endangered species in its *Red Data Book*.

In order to conserve this endangered species, the Formosan salmon recovery plan was established. It was the first and most significant wildlife conservation plan in Taiwan (Lin et al., 2004). Although the Formosan salmon population has been monitored since 1987 (Tzeng, 2004), the population dynamics (which would help us better understand and predict the trends in this endangered species) have never been analyzed.

Matrices have been developed by Lewis (1942), Leslie (1945, 1948) and Lefkovitch (1965) to describe the dynamics of age-structured populations. The matrix model has been widely applied in wildlife management to reveal the structure and to estimate the finite rate of change of populations (λ) for the past two decades (Yearsley & Fletcher, 2002). The matrix model is seen to provide a powerful management tool to guide the conservation efforts of a variety of populations (Jensen, 1997; Akcakaya et al., 1999; Charles et al., 2000; Miller et al., 2002; Shultz et al., 2002). Therefore, using the census data obtained from the basin of the Chichiawan Stream over an 18 year period from 1987 to 2004, the objectives of this study were to: 1) determine field stage-specific parameters of the Formosan salmon, including the growth rate, survival rate and fecundity; 2) estimate the finite rate of change in the salmon population; 3) construct stage-structured population matrix models for the main life stages of the salmon population and 4) compare field population parameters of the Formosan salmon before and after 2001 when dams along a tributary, the Kaoshan Stream, were demolished.

MATERIALS AND METHODS

Study site. **–** The Chichiawan Stream, located in Central Taiwan, is an upper tributary of the Tachia River (Fig. 1). The headwaters of Chichiawan Stream originate in Mt. Pingtein (3,536 m), Mt. Chihyu (3,301 m) and Mt. Tao (3,324 m). The Chichiawan Stream together with the tributaries, Kaoshan and Yousheng Streams, form drainage networks in the basin of Chichiawan Stream at elevations above 1,400 m. The Chichiawan Stream is 15.3 km long and ~ 7.1 - 12.3 m wide with a mean gradient of 0.13. The total area of the stream basin is 76 km^2 (Lin et al., 1990). According to the Formosan salmon recovery plan (Tzeng, 2002), four dams along the Kaoshan Stream were demolished in 2001.

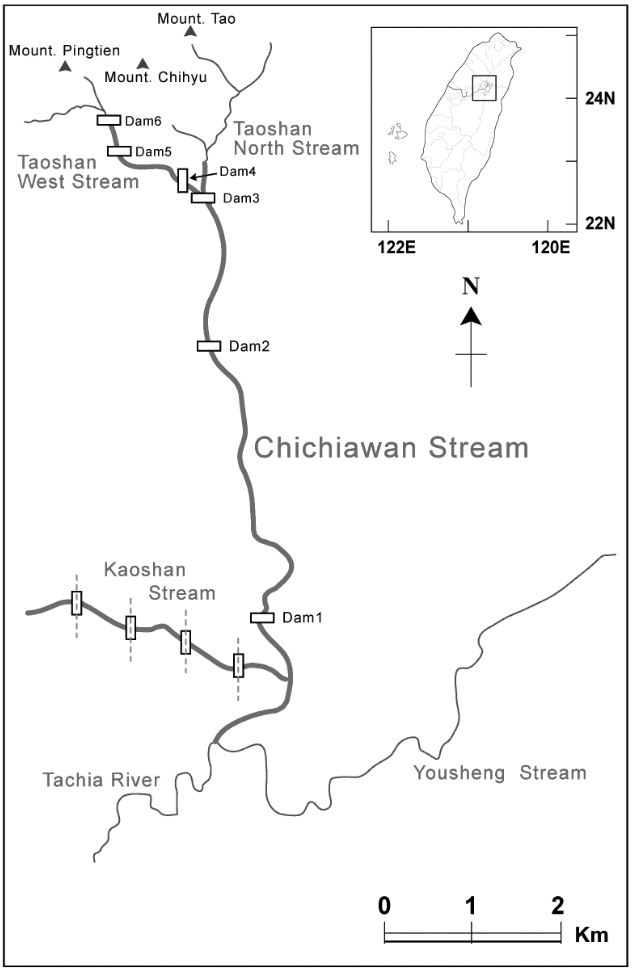

Fig. 1. Study site of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in Taiwan: Inset shows the enlarged area within Taiwan. Four dams along the Kaoshan Stream were demolished in 2001.

Data sources. **–** The three main life stages of the Formosan salmon in the wild were classified according to their total length (Fig. 2): 1) juveniles, ~ 5 - 8 cm in summer and ~ 5 - 15 cm in winter; 2) subadults, ~ 8 - 25 cm in summer and ~ 15 - 25 cm in winter and 3) adults, > 25 cm (Tzeng, 2004). The fish reaches sexual maturity and begins breeding in its second year. Generations of the fish overlap and reproduction occurs in November (winter). In the Chichiawan Stream and Kaoshan Stream, the total number of the Formosan salmon was visually counted during daytime in June (summer) and late October (early winter) before the breeding season. The study was conducted over an 18 year period from 1987 to 2004 (Tzeng, 2004).

The Formosan salmon were counted during the daytime by snorkeling between 1000 and 1700 hours. Water clarity for visual censuses was consistently good in the streams. The streams were divided into sections with dams or abrupt changes in channel gradient forming the upper and lower boundaries of each section. All snorkeling began at the downstream end of each section (~ 300 m long) and was completed in a single upstream pass. During each count, two trained snorkelers, who were parallel to each other, swam slowly upstream the middle of the channel and counted fish outwards and towards the bank nearest to them to avoid double-counting. Snorkelers recorded the fish count data on slates and paused periodically at the end of a section to relay the information to a data recorder on the bank. Fish length estimation was practiced prior to the actual counting on objects of known length lying on the stream bottom. In addition, the underwater slates were marked with a ruler for guidance in size estimation. Each survey of the Chichiawan and Kaoshan Streams was completed within a week. Data on the three main life stages of the Formosan salmon are available from 1996 to 2004. In the Kaoshan Stream, the total number and the proportions of the three main life stages of the Formosan salmon were recorded only over an 8 year period, in the summers of 1997 to 2004.

Modeling approach. **–** In general, four factors that may affect the population size are birth, death, immigration and

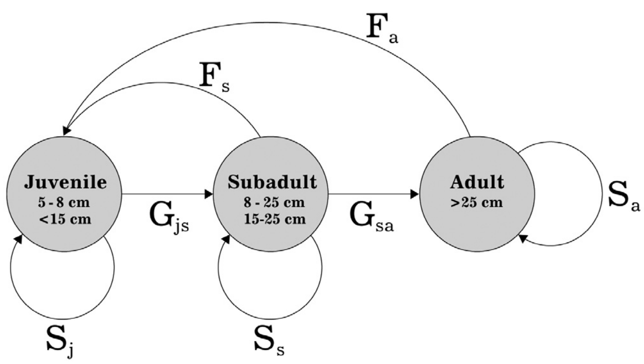

Fig. 2. Life history of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) classified through total length and details of the population parameters. G_{js} = growth rate from juveniles to subadults; G_{sa} = growth rate from subadults to adults; S_j = survival rate of juveniles; S_s = survival rate of subadults; S_a = survival rate of adults; F_s = fecundity of subadults; F_a = fecundity of adults.

emigration. Since the Formosan salmon is a landlocked species, it was assumed that it is a closed population. Immigration and emigration were therefore excluded as factors. It was also assumed that the stage-specific fecundity and survival parameter values are density-independent and constant from year to year. In order to examine whether the population is density-independent, the summer and winter population counts were respectively used to regress (N_{t+1}/N_t) against N_t, where N_t and N_{t+1} are the total population numbers at time t and t+1 years, respectively (Torres-Sorando et al., 2003).

There are six population parameters for the life history of the Formosan salmon (Fig. 2). The growth rates from juvenile to subadult and subadult to adult are G_{js} and G_{sa} respectively. The survival rates of subadults and adults are S_s and S_a respectively, while F_s and F_a are the fecundity of subadults and adults respectively (Caswell, 1996; Oli, 2003).

We adopted the model selection approach in which several competing hypotheses are simultaneously confronted with data as compared to the traditional null hypothesis test approach (Johnson & Omland, 2004). In order to better understand and predict the population dynamics, we applied the approach of Lewis (1942), Leslie (1945, 1948) and Lefkovitch (1965) to construct a population projection matrix for the life history of the Formosan salmon in the following matrix form:

$$\mathrm{M} = \begin{bmatrix} 0 & F_s & F_a \\ G_{js} & S_s & 0 \\ 0 & G_{sa} & S_a \end{bmatrix} \qquad (1)$$

The relationship between the summer and winter population numbers in year t and the summer population numbers in year t+1 can then be described by equations (2) and (3):

$$N(t+1) = MN(t) + \xi N(t) \qquad (2)$$

$$\begin{bmatrix} n_j(t+1) \\ n_s(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & F_s & F_a \\ G_{js} & S_s & 0 \\ 0 & G_{sa} & S_a \end{bmatrix} \begin{bmatrix} n_j(t) \\ n_s(t) \\ n_a(t) \end{bmatrix} \qquad (3)$$

Where N is the population structure vector or stage distribution vector, $\boldsymbol{M}$ is the Leslie and Lefkovitch matrix (Lewis, 1942; Leslie, 1945; Lefkovitch, 1965; Caswell, 2001) which is often referred to as the population projection matrix and $N(t)$ represents a column vector of the numbers of juveniles, subadults and adults in year t. An environmental stochastic term ξ was assumed to be a normally-distributed random variable. The mean of ξ is zero and its standard deviation is 0.1 (Miller et al., 2002).

Since the breeding season of the Formosan salmon is in November, the relationship between the summer population number (June) and the winter population number (late October) in the same year can be expressed by the following equation:

$$\begin{bmatrix} n_j(t+1) \\ n_s(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} S_j & 0 & 0 \\ G_{js} & S_s & 0 \\ 0 & G_{sa} & S_a \end{bmatrix} \begin{bmatrix} n_j(t) \\ n_s(t) \\ n_a(t) \end{bmatrix} \qquad (4)$$

The relationship between the winter population number in year t and the summer population numbers in year t+1 can be expressed by the following equation:

$$\begin{bmatrix} n_j(t+1) \\ n_s(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & F_s & F_a \\ G_{js} & S_s & 0 \\ 0 & G_{sa} & S_a \end{bmatrix} \begin{bmatrix} n_j(t) \\ n_s(t) \\ n_a(t) \end{bmatrix} \qquad (5)$$

The following combined equations (6) were derived from equation (3) using the census data of the stage-structured Formosan salmon population numbers from 1997 to 2004:

$$\begin{cases} n_j(1997) = F_s \cdot n_s(1996) + F_a \cdot n_a(1996) \\ n_s(1997) = G_{js} \cdot n_j(1996) + S_s \cdot n_s(1996) \\ n_a(1997) = G_{sa} \cdot n_s(1996) + S_a \cdot n_a(1996) \end{cases}$$

$$\begin{cases} n_j(1998) = F_s \cdot n_s(1997) + F_a \cdot n_a(1997) \\ n_s(1998) = G_{js} \cdot n_j(1997) + S_s \cdot n_s(1997) \\ n_a(1998) = G_{sa} \cdot n_s(1997) + S_a \cdot n_a(1997) \end{cases}$$

$$\begin{cases} n_j(2004) = F_s \cdot n_s(2003) + F_a \cdot n_a(2003) \\ n_s(2004) = G_{js} \cdot n_j(2003) + S_s \cdot n_s(2003) \\ n_a(2004) = G_{sa} \cdot n_s(2003) + S_a \cdot n_a(2003) \end{cases} \qquad (6)$$

In order to determine the field fecundity parameters, F_s and F_a, we rearranged equation (6) to form the following matrix:

$$\begin{bmatrix} n_j(1997) \\ n_j(1998) \\ | \\ n_j(2004) \end{bmatrix} = \begin{bmatrix} n_s(1996) & n_a(1996) \\ n_s(1997) & n_a(1997) \\ | & | \\ n_s(2003) & n_a(2003) \end{bmatrix} \begin{bmatrix} F_s \\ F_a \end{bmatrix} \qquad (7)$$

Equation (7) can then be simplified as follows:

$$N_j(t+1)_{(8\times1)} = N_{sa}(t)_{(8\times2)} F_{sa(2\times1)} + \varepsilon(t)_{(8\times1)} \qquad (8)$$

The $N_j(t+1)_{(8\times1)}$ vector consists of population numbers of juveniles from 1997 through 2004, while the $N_{sa}(t)_{(8\times2)}$ matrix consists of population numbers of subadults and adults from 1996 through 2003, while the $F_{sa(2\times1)}$ vector is the fecundity of subadults and adults. $\varepsilon(t)$ is a normally-distributed random variable. The mean of $\varepsilon(t)$ is zero, its variance is constant and $\varepsilon(t)$, $\varepsilon(t+1)$ and $\varepsilon(t+2)$ are independent.

Parameterization. – In this study, we had eight equations for the two variables of each matrix model, suggesting that we would be unable to obtain the exact solution for the combined equations. We applied the least-squares solution for fitting the data to each matrix model with the minimum squared difference between each equation (8). We then determined the fecundity vector using the following equation:

$$F_{sa} = \begin{bmatrix} F_s \\ F_a \end{bmatrix} = (N_{sa}^T N_{sa})^{-1} N_{sa}^T N_j \qquad (9)$$

Vectors $[G_{js}\ S_s]^T$ and $[G_{sa}\ S_a]^T$ can be determined based on a similar algorithm. When the six field parameters of each

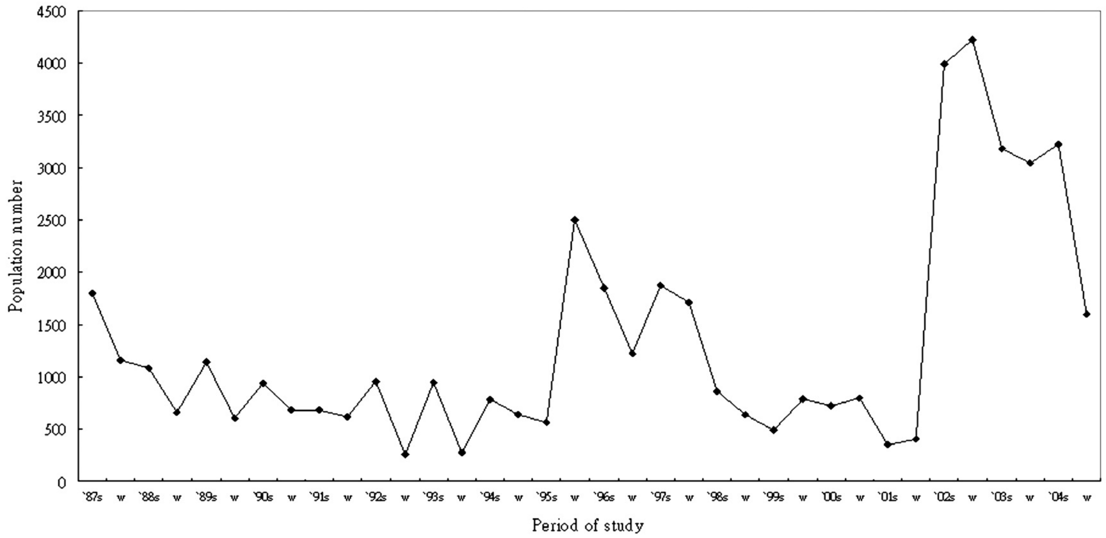

Fig. 3. Total number of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) recorded in the Chichiawan Stream from 1987 to 2004. s = summer; w = winter.

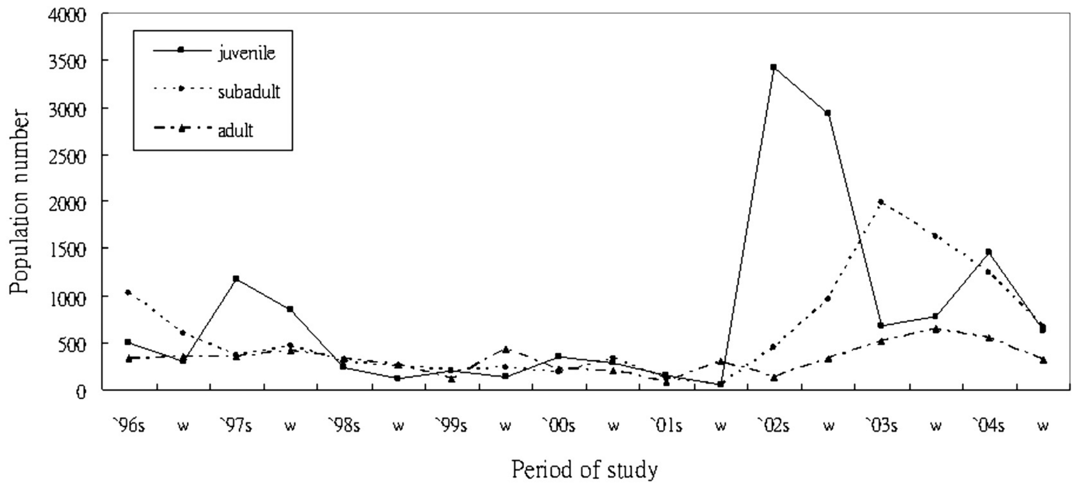

Fig. 4. Population number of the three main life stages of the Formosan salmon (*Oncorhynchus masou formosanus*) recorded in the Chichiawan Stream from 1996 to 2004. s = summer; w = winter.

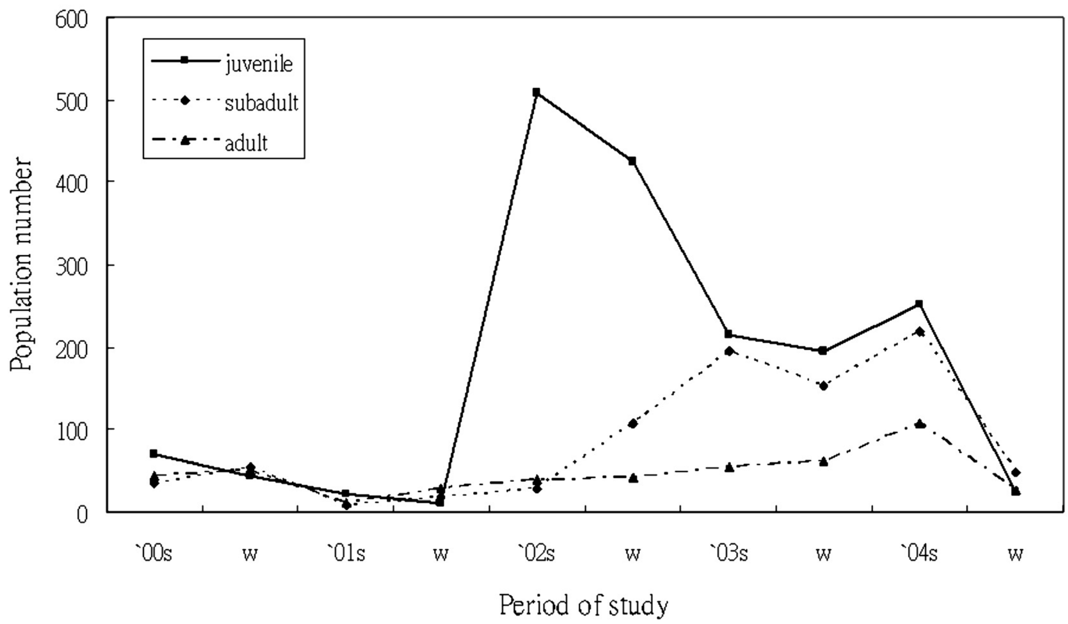

Fig. 5. Population number of the three main life stages of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) recorded in the Kaoshan Stream from 2000 to 2004. s = summer; w = winter.

Table 1. Population parameters determined by the matrix models using different pairs of census data collected from the Chichiawan and Kaoshan Streams.

Location and Period	G_{js}	G_{sa}	S_j	S_s	S_a	F_s	F_a	λ
Chichiawan Stream								
Summer and the following summer	0.49	0.18	0.00	0.37	0.52	0.55	1.16	0.93
Summer and winter	0.17	0.09	0.79	0.63	0.79	0.00	0.00	n/a
Winter and the following summer	0.49	0.26	0.00	0.47	0.37	-0.76	3.72	0.94
Kaoshan Stream								
Summer and the following summer (~ 2001 - 2004)	0.34	0.40	0.00	0.72	0.55	0.20	3.88	1.30
Summer and the following summer (~ 1997 - 2001)	-0.11	0.47	0.00	0.83	-0.09	-0.14	1.11	0.77

G_{js} = growth rate from juveniles to subadults; G_{sa} = growth rate from subadults to adults; S_j = survival rate of juveniles; S_s = survival rate of subadults; S_a = survival rate of adults; F_s = fecundity of subadults; F_a = fecundity of adults; λ = population growth rate; n/a = the population growth rate was not available because it was not the breeding season.

matrix model were respectively determined by the least-squares solution using the census data from 1996 to 2004, the population projection matrix (**M**) can be replaced by the single value of the population growth rate (λ) which is the dominant eigenvalue of the matrix model (Caswell, 1996; Case, 2000). In equation (10), the eigenvector (**w**) is the stable stage-structured population:

$$\mathbf{M} \times \mathbf{w} = \lambda \times \mathbf{w} \qquad (10)$$

Dominant eigenvalue, λ, can be expressed as equation (11), where r is the intrinsic population growth rate of the Formosan salmon:

$$\lambda = e^r \qquad (11)$$

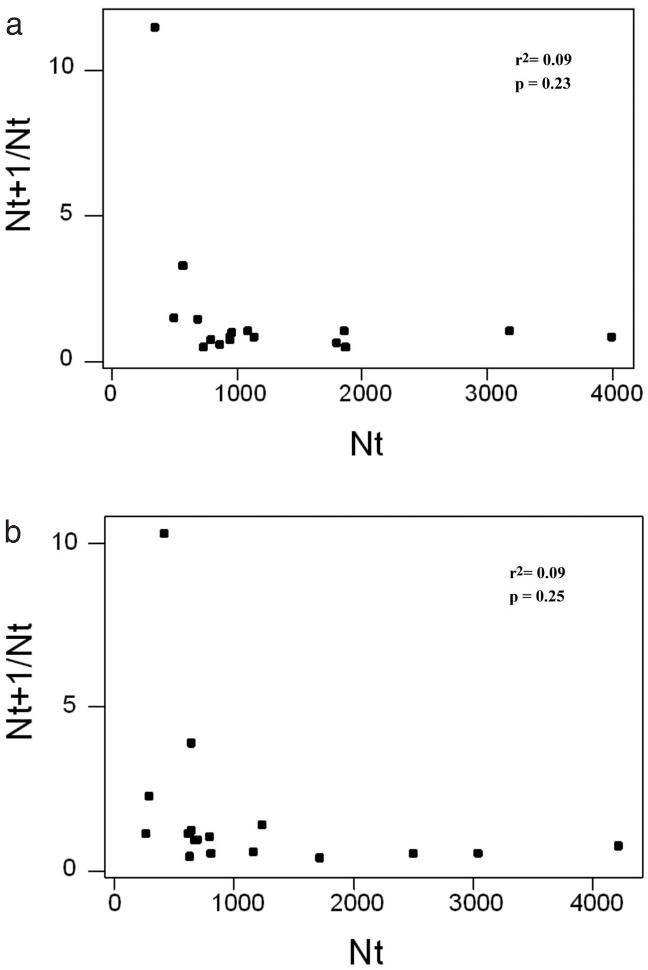

Fig. 6. Scatter plots of (Nt+1/Nt) against Nt for census observations of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) population recorded from 1987 to 2004. a) summer, b) winter.

RESULTS

The census observations (Tzeng, 2003, 2004) obtained from the Chichiawan Stream over an 18 year period from 1987 to 2004 showed remarkable fluctuations in total population of the Formosan salmon (Fig. 3). The numbers ranged from 253 to 4,221 individuals, with a mean of 1,343 individuals. There were two peaks in the total numbers, with one occurring in the summer of 1996 and the other occurring in the summer of 2002. The 2002 summer peak could be attributed to the large increase in the number of juveniles (Fig. 4). The number of subadults, therefore reached a peak the following summer. Similarly, in the tributary Kaoshan Stream, the number of juveniles also reached a peak in the summer of 2002 (Fig. 5).

One critical assumption of the population projection matrix of the life history of the Formosan salmon is that the population is regulated in a density-independent manner. If the regulation of a population is density-dependent, the linear regression of (N_{t+1} / N_t) against N_t is significantly negative (Case, 2000). In the Chichiawan Stream, however, the linear regressions for the summer (Fig. 6a, r^2 = 0.09 and p = 0.23) and winter populations (Fig. 6b, r^2 = 0.09 and p = 0.25) of the Formosan salmon recorded from 1987 to 2004 were not significant. As with the total numbers, the linear regressions for the numbers of the three stages were also not significant (Fig. 7a to 7c). These non-linear relationships between (N_{t+1} / N_t) and N_t reveal that the regulation of the Formosan salmon population is likely density-independent, regardless of seasons and the growth stages.

Population parameters of the Formosan salmon determined by each matrix model differed, depending on the location and season of the census data (Table 1). In general, values of S_s, S_a, G_{js} and G_{sa} determined by the matrix models using the census data collected across winters were more consistent than across summers within the same year. In the Chichiawan Stream, the population growth rates (λ) derived from the matrix models were less than one, which indicates that the Formosan salmon population is declining and in the population is experiencing negative growth.

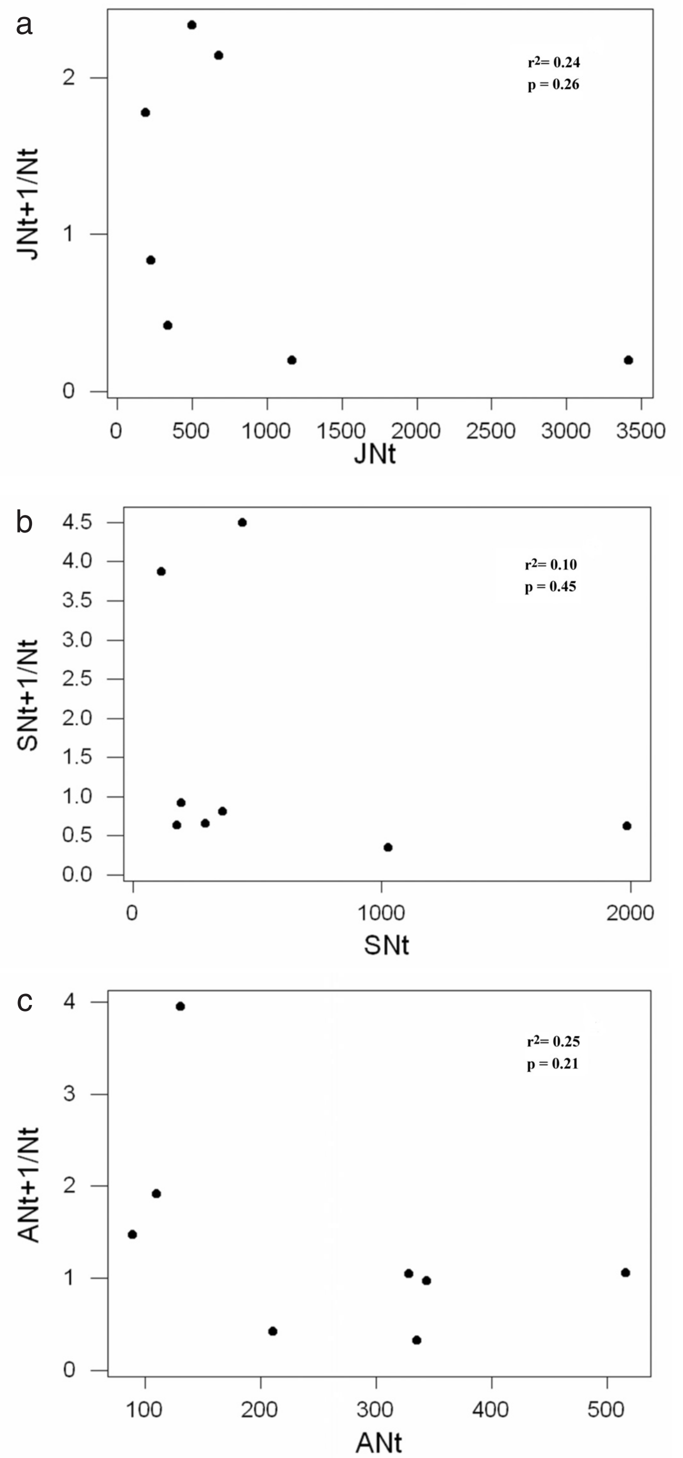

Fig. 7. Scatter plot of (Nt+1/Nt) and Nt for census observations of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) recorded in the summer from 1996 to 2004. a) juveniles (J), b) subadults (S), c) adults (A).

In the Kaoshan Stream, the population growth rates determined by the matrix model were also less than one before 2001 (Table 1). However, the population growth rate rose to 1.30 after 2001, when dams along the stream were demolished according to the Formosan salmon recovery plan. This indicates that the Formosan salmon population is increasing and its population growth rate is positive. There were increasing trends in both the numbers observed during field observations and model predictions of all three growth stages of the Formosan salmon in the Kaoshan Stream after 2001 when the dams were demolished (Fig.8a to 8c). Also, in 2003 to 2004, the numbers from field observations fit the predictions of the stage-structured matrix model particularly well.

DISCUSSION

Visual counts invariably underestimate fish numbers (Sale & Sharp, 1983). This is seen in the study of Thurow & Schill

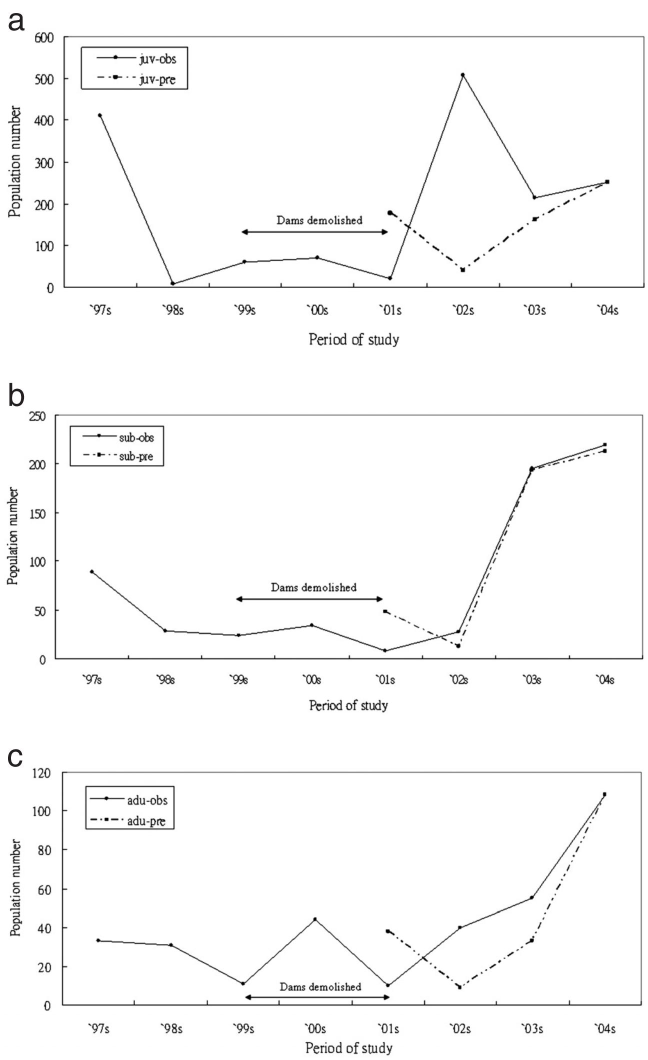

Fig. 8. Census observations of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in the Kaoshan Stream in summer from 1997 to 2004 compared with the predictions of the stage-structured matrix model based on census data collected in the summer from 2001 to 2004. a) juveniles, b) subadults, c) adults. juv = juvenile; sub = subadult; adu = adult; obs = observation; pre = prediction; s = summer.

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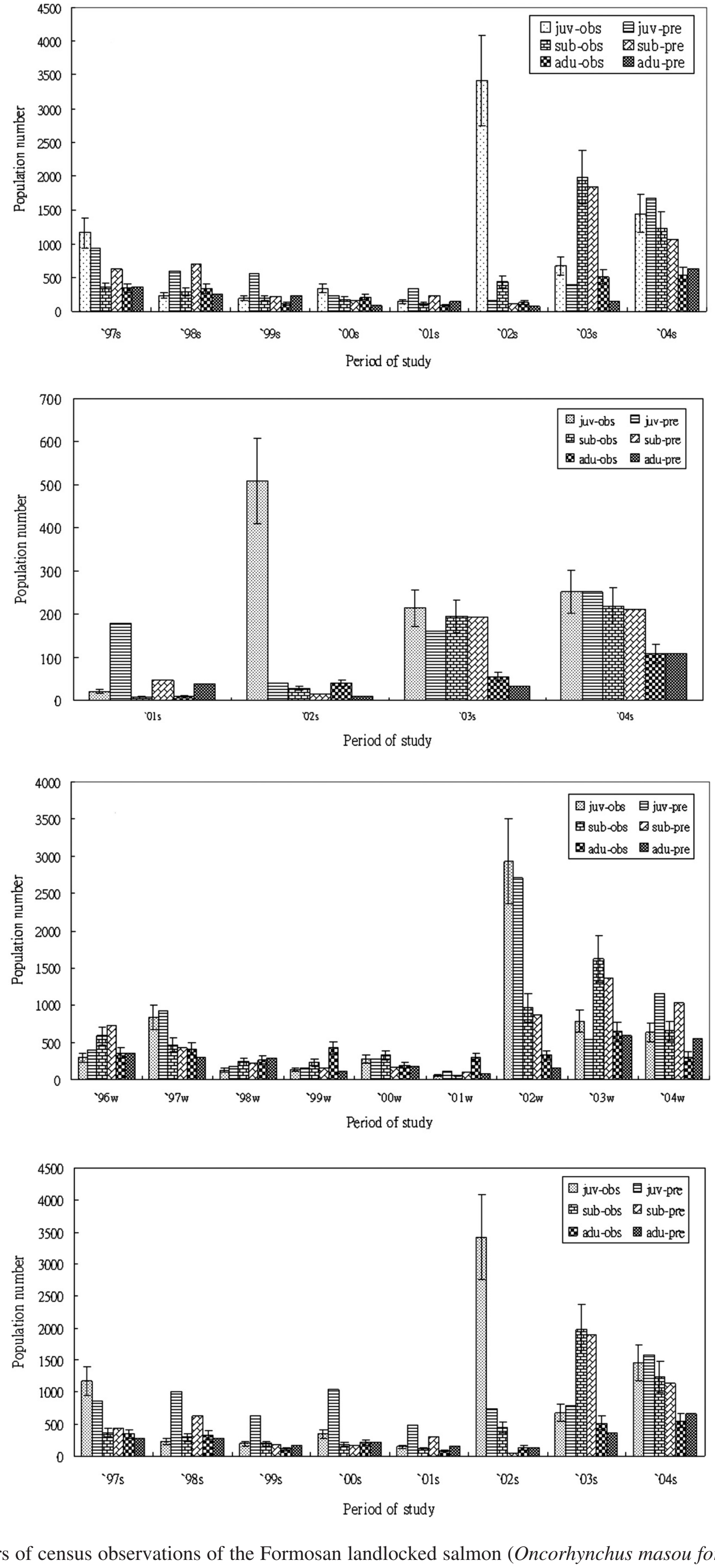

Fig. 9. Histograms of pairs of census observations of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) compared with the predictions of the stage-structured matrix model. a) summer to the following summer in the Chichiawan Stream, b) summer to the following summer in the Kaoshan Stream, c) summer to winter in the Chichiawan Stream, d) winter to the following summer in the Chichiawan Stream. juv = juvenile; sub = subadult; adu = adult; obs = observation; pre = prediction; s = summer; w = winter.

(1996) where daytime snorkeling counts accounted for only 75% of the bull trout, *Salvelinus confluentus*, collected by electrofishing (Thurow & Schill, 1996). However, it was found that these two sampling techniques yielded similar estimates of the size structure of the fish population. Since underwater observation is non-destructive and has minimal impact on fish populations and environments, Thurow et al. (2006) suggested that it is well-adapted for sampling sensitive species that are federally listed under the Endangered Species Act like the Formosan salmon.

In the Chichiawan Stream, the value of S_a determined by the matrix model using the census data collected from every two consecutive summers from 1996 to 2004, was very close to the independent field estimate (Tzeng, 2000). The determined values of S_s and S_a were higher than Tzeng (2000) when using the census data collected within the same year. Similarly, the determined values of G_{js} and G_{sa} were higher than Tzeng (2000) when using the data collected across winters. This indicates the importance of spring for the growth of the Formosan salmon when there is a bloom in their main food source of aquatic insects (authors' personal observations). In the Kaoshan Stream, the population growth rates (λ) derived from the matrix models were greater than one, indicating that the Formosan salmon population is increasing. Our results are consistent with independent field observations by Tzeng (2003).

The overall performance of the matrix models can be accessed by comparing predictions for each stage of the Formosan salmon with histograms of pairs of observed numbers (Ruesink, 1997; Hoffmann, 1999). In general, the numbers of each stage of the Formosan salmon population were well predicted by the stage-structured matrix models. For example, in Chichiawan Stream, the observed numbers of subadults in the following summer generally match the predictions by the matrix model using the census data collected in summers over the period from 1997 to 2004 (Fig. 9a). In the Kaoshan Stream, the performance of the matrix models was better after the first two years when the dams were demolished for the

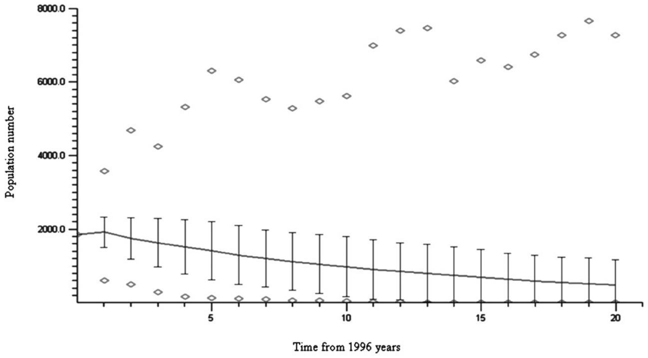

Fig. 10. A sensitivity analysis of the effects of environmental factors on the total numbers of Formosan landlocked salmon (*Oncorhynchus masou formosanus*) by adding an environmental stochastic term ξ to the stage-structured matrix model and running 1,000 simulations every year from 1996 for 20 years (RAMAS EcoLab 2.0: Akcakaya, 1999). The line indicates the mean value and the bars represent the 95% confidence intervals. ✧ = denotes the simulated maximum and minimum values.

three growth stages (Fig. 9b). This suggests the suitability of the stage-structured matrix model for the Formosan salmon population.

The performance of the matrix models in Chichiawan Stream was better for subadults than for adults or juveniles, regardless of which pairs of census data were used. Specifically, the model's performance using the census data collected in the summer to predict the numbers in the winter of the same year for juveniles and subadults was better than that for adults (Fig. 9c). The lower predictability of adults across summers might have resulted from the low capacity of the large-sized adult salmon to seek refuge in summer when typhoons cause floods in the shallow streams. However, the model's performance using census data collected in the winter to predict the numbers in the following summer for subadults and adults was better than that for juveniles (Fig. 9d). Moreover, the model's performance using the census data in the summer to predict the numbers in the winter within the same year was better than that using data collected in the summer or winter to predict numbers across years. The lower predictability of juveniles across years might have resulted from their higher vulnerability. It is clear that other intrusive factors such as climate and environmental factors or interactions with other communities occurring in winter and spring might be involved in determining the fecundity. This was reflected by the high variation in fecundity using the census data collected in the summer or winter to predict the population number the following summer (Table 1). The high variation in the fecundity of the Formosan salmon illustrates concerns that require further study.

The non-linear relationships between observed (N_{t+1}/N_t) and N_t in different seasons and growth stages (Figs. 6 & 7) reveal that the regulation of the Formosan salmon population is likely density-independent and this is likely because of the small water volumes and limited habitats such as the Chichiawan and Kaoshan Streams. A sensitivity analysis was run with 1,000 simulations (*RAMAS Ecolab 2.0*: Akcakaya et al., 1999) to examine effects of environmental fluctuations on the total numbers of the Formosan salmon in the Chichiawan Stream over a 20-year period from 1996 by adding an environmental stochastic term ξ to the stage-structured matrix model (Fig. 10). There were decreasing trends in total numbers of the Formosan salmon as predicted by the population growth rates (λ) determined by the matrix models. The considerably large ranges between the maximum and minimum values suggest that environmental fluctuations exert significant influence on Formosan salmon population dynamics.

Density-independent regulation of the Formosan salmon is also evident in the remarkable fluctuations of the long-term census observations over an 18-year period in Chichiawan Stream (Fig. 3). On average, 3.7 typhoons hit Taiwan each year (http://61.56.13.9/data.php). However, the Wulin area of Northern Taiwan was not directly hit by typhoons in 1996 and 2002. Consequently, total numbers of the Formosan salmon showed two peaks: one reaching 2,500 individuals in 1996 and the other reaching 4,221 individuals in 2002. In the tributary of the Kaoshan Stream, the total number also reached a peak in 2002 (Fig. 5). Obviously, floods caused by typhoons might have had a great impact on the Formosan salmon population dynamics. Although the total number of Formosan salmon in Chichiawan Stream averaged 1,343 individuals, the total numbers often remained below 1,000 individuals during the census period (Fig. 3). Assuming the carrying capacity of Formosan salmon in the Chichiawan Stream was 3,350 individuals (estimated by averaging the two peaks of the long-term census observations), then the total numbers were often only 30% of the carrying capacity. In addition, trophic models of the Chichiawan Stream showed that the abundance of the main food source (aquatic insects) available for the Formosan salmon was much higher than the amount consumed by the salmon (Lin et al., unpublished data). It is likely that floods caused by typhoons overshadowed the density-dependent processes of the Formosan salmon to reach their carrying capacity.

Despite a lack of data on the Formosan salmon, there was generally good agreement between census observations and predictions of the stage-structured matrix models. In the Chichiawan Stream, the population growth rates determined by the matrix models indicate that the Formosan salmon population is declining. However, the matrix model showed the Formosan salmon population in the tributary of the Kaoshan Stream to be increasing since 2001 when the dams were demolished. Stage-structured matrix models appear to be a useful tool for management and conservation of endangered species.

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