Accelerating population decline of Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*)

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ABSTRACT

The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) is now the only cetacean species in the Yangtze River following the probable extinction of the baiji (*Lipotes vexillifer*). However, population abundance estimates and genetic diversity studies both indicate that the porpoise population is declining and may also become extinct in the wild in the near future. We used data from 279 stranded porpoises that were collected along the middle and lower reaches of the Yangtze River since 1978 to construct life tables for the porpoise population before and after 1993. Demographic rate estimates reveal an accelerating decline of the Yangtze porpoise population according to the instantaneous rate of increase ($\bar{r}$), from $\bar{r} = -0.0159$ (SD = 0.0135) to $\bar{r} = -0.0625$ (SD = 0.0169). Using an individual-based Leslie matrix model, there is a high probability of extinction (86.06%) within the next 100 years. Effective conservation measures must be enacted immediately. The pattern of cetacean decline and extinction in the Yangtze provides a startling demonstration of how rapid economic development without adequate environmental control leads to deterioration of natural habitats and threatens native species extremely rapid. This research also emphasizes the need for precautionary conservation action in other riverine systems containing freshwater cetacean species.

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1. Introduction

The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) is a subspecies of the narrow-ridged finless porpoise (*N. asiaeorientalis*), it is endemic to the middle and lower reaches of the Yangtze River, and is the only freshwater porpoise (Gao and Zhou, 1993; Zhao et al., 2008; Committee on Taxonomy, 2009). Following the probable extinction of the Yangtze River dolphin or baiji (*Lipotes vexillifer*) in the first decade of the twenty-first century (Turvey et al., 2007), the Yangtze finless porpoise has become the only cetacean species to be found in the Yangtze River. However, progressive declines in the number of porpoises observed during boat surveys (Zhang et al., 1993; Wei et al., 2002; Zhao et al., 2008), drastic loss of suitable habitats resulting in apparent distribution gaps in the formerly contiguous population (Wang et al., 2000; Zhao et al., 2008; Wang, 2009), and low levels of genetic diversity (Yang et al., 2002, 2008b; Xia et al., 2005; Zheng et al., 2005) all suggest that the Yangtze finless porpoise

may follow the baiji and also become extinct in the wild in the near future. The apparent decline of the porpoise population in the Yangtze mainstem, from more than 2550 animals in 1991 (Zhang et al., 1993) to fewer than 1225 animals in 2006 (Zhao et al., 2008), raises an important question: how many years do we have left to reverse the decline of this cetacean?

The answer to this question depends on the actual rate of porpoise decline. This decline is being driven by high levels of mortality resulting from anthropogenic impacts such as incidental by-catch in legal and illegal fishing gear, ship collisions, widespread sand dredging, pollution, and water development projects along the middle and lower reaches of the Yangtze River (Wang et al., 2000, 2005; Yang et al., 2002, 2008a; Xia et al., 2005; Zheng et al., 2005; Zhao et al., 2008; Wang, 2009). The Yangtze is known as the "golden channel" of central China, and supports the livelihoods of hundreds of millions of people through agriculture, aquaculture and industrial activities. The status of cetaceans and other megafaunal taxa (e.g. acipenseriform fishes) inhabiting the Yangtze River has deteriorated continuously since the early 1990s, when economic growth began to escalate in China and led to increasing environmental degradation. Understanding the severity of anthropogenic threats to the surviving finless porpoise population in the Yangtze system is a necessary step before appropriate conservation

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interventions can be developed and implemented. This key question can be informed by understanding the rate of porpoise population decline.

Cetacean population decline rates can be estimated directly by using historical abundance estimates (Stevick et al., 2003; George, 2004; Zerbini et al., 2006; Zhao et al., 2008), or by demographic approaches (Fujiwara and Caswell, 2001; Stolen and Barlow, 2003; Moore and Read, 2008; Currey et al., 2009a,b; Huang et al., 2012b) such as life table analysis (Caswell et al., 1998; Dans et al., 2003; Stolen and Barlow, 2003; Moore and Read, 2008; Huang et al., 2012b). However, direct detection of population trends, either increases or declines, usually requires decades of field investigations, and the target population may have declined substantially before a change in abundance is detectable (Gerrodette, 1987; Taylor and Gerrodette, 1993; Thompson et al., 2000; Taylor et al., 2007; Wilson et al., 2011; Huang et al., 2012a). Conversely, demographic approaches also provide quantitative predictions of future population trends and extinction risk that can inform precautionary management (Harwood, 2000; Lacy, 1993; Thompson et al., 2000; Fujiwara and Caswell, 2001). Comparative study of rate of decline or risk of extinction between different scenarios of anthropogenic impact using a demographic framework (Moore and Read, 2008; Currey et al., 2009b) can also quantify how uncontrolled environment deterioration may impact long-term survival of threatened populations.

In this study, we constructed life tables for the Yangtze finless porpoise before and after 1993 using data from stranded animals. An individual-based Leslie matrix model was used to predict the porpoise population trend and its risk of extinction over the next 100 years. Our research shows how rapidly the current porpoise population is likely to decline to extinction, and highlights the urgency of implementing robust conservation measures.

2. Methods

2.1. Specimen collection and age estimation

All age-at-death data (n = 279 animals) used in this analysis came from porpoises that were opportunistically collected along the middle and lower reaches of the Yangtze River from 1978 onwards (Fig. 1). In 66 of these cases (reported in Yang et al., 1998) no body length was recorded, and age was estimated by counting dentinal growth layer groups (GLGs) in tooth sections (Myrck et al., 1983; Hohn et al., 1989; Stolen and Barlow, 2003). In the other 213 cases, no teeth were collected or preserved, but other biological information, including sex and body length, was recorded. Zhang (1992) used 68 samples (31 males and 37 females) aged by GLGs to estimate age–length curves. The relationship between age x and body length (in cm) of male (L_m) and female (L_f) Yangtze finless porpoises can be expressed by:

$$L_m = 114.4458 \times x^{0.1410}$$

and :   (1)

$$L_f = 116.2519 \times x^{0.0947}$$

We therefore estimated the age of these additional 213 animals using the above equations.

2.2. Life tables and demography

Life table parameters of the Yangtze finless porpoise population before and after 1993 (Pre93 and Post93), including the number of animals alive at age x (n_x), the proportion surviving from birth to age x (l_x), and the mortality rate at age x (q_x), were calculated using the traditional method summarized by Krebs (1989). Biased demographic estimates may arise from departure from the assumption of stable age distribution in this method (Caughley, 1966; Gaillard et al., 1998); however, the life history pattern of cetacean species, including relatively long interbirth interval, long life expectancy of females and high adult survival rates, usually reduces such bias (Stolen and Barlow, 2003). Furthermore, the age-at-death data in our study span more than 10 years, reducing the likelihood of potential deviations in any single year (Stolen and Barlow, 2003). This method has previously been employed for bottlenose dolphins (*Tursiops truncatus*) (Stolen and Barlow, 2003), harbor porpoises (*Phocoena phocoena*) (Moore and Read, 2008), and humpback dolphins (*Sousa chinensis*) from the Pearl River Estuary (Huang et al., 2012b), as well as for several terrestrial mammals (Barlow and Boveng, 1991).

A break point of 1993 was defined because this date represents the start of rapid economic development in China under the country's economic reform policy launched in 1992 by Deng Xiaoping. Since then, economic and industrial activities along the Yangtze
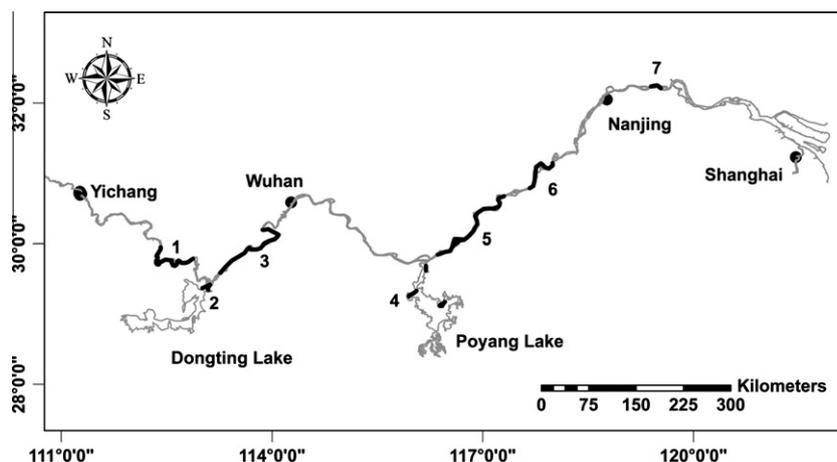
Fig. 1. Map of the middle-lower Yangtze River drainage from Yichang to Shanghai, showing the region where all 279 Yangtze finless porpoise specimens were collected (gray area), and the location of the seven *in situ* cetacean reserves along the Yangtze River mainstem, Poyang Lake and Dongting Lake. Legend: 1, Shishou Tian'e-Zhou reserve; 2, East Dongting Lake reserve; 3, Honghu reserve; 4, Poyang Lake reserve; 5, Tongling reserve; 6, Anqing reserve; 7, Zhenjiang reserve. 1, 3 and 5 are national nature reserves, 4 and 7 are provincial reserves, and 2 and 6 are local (city) reserves. Poyang Lake reserve (8600 ha) is divided into three independent protective areas in Duchang, Xingzi and Hukou.

Table 1
Life history parameters for the Yangtze finless porpoise that were used for demographic rate estimates and predicting population trends.

Life history parameters	Ranges	Sources
Age at maturation (years)	4.5–5.5	Zhang (1992), Gao and Zhou (1993), and Hao et al. (2007)
Calving interval (years)	1.41–1.43	Zhang (1992) and Zhang and Wang (1999)
Life span (years)	18–21	Gao and Zhou (1993) and Huang et al. (2008)

River have grown exponentially, and have been accompanied by large-scale environmental development programmes such as dam construction and land reclamation. Systematic range-wide abundance estimates for the Yangtze finless porpoise were also first published in 1993 (Zhang et al., 1993), and the previously published life table for the Yangtze finless porpoise population constructed by Yang et al. (1998) was based on data collected up to 1993.

Because of uncertainty over parameter values resulting from the range of relevant life history parameters that were used (Table 1), we did not apply these calculated values directly to make demographic rate estimates and population trend predictions. Instead, we applied Siler's competing-risk model of survivorship (Siler, 1979) to the values of l_x derived from empirical data for constructing a modelled life table (Stolen and Barlow, 2003), and this was further used to estimate demographic rates and population trends. Siler's model was used because it accurately describes mammalian survivorship and mortality schedules (Siler, 1979; Barlow and Boveng, 1991; Stolen and Barlow, 2003; Moore and Read, 2008). In Siler's model, age-specific survivorship $l(x)$ is determined by three components:

$$l(x) = l_j(x) \times l_c(x) \times l_s,$$
(2)

including (i) an exponentially decreasing risk of mortality due to juvenile risk factors:

$$l_j(x) = \exp\left(-\frac{a_1}{b_1} \times (1 - \exp(-b_1 \times x))\right),$$

(ii) a constant risk experienced by all age classes:

$$l_c(x) = \exp(-a_2 \times x),$$

and (iii) an exponentially increasing risk due to senescent risk factors:

$$l_s(x) = \exp\left(\frac{a_3}{b_3} \times (1 - \exp(b_3 \times x))\right).$$

The five Siler's parameters (hazard weight, a_1, a_2, and a_3; adjustment constant, b_1 and b_3) were regressed by the least-squares method. Life table parameters of the Pre93 and Post93 porpoise populations were fitted to Siler's model separately.

Demographic rates, including net reproductive rate (R_0), generation time (T_0), and instantaneous rate of increase (r), were calculated using the standard methods described by Krebs (1989):

$$R_0 = \sum l(x) \times m(x)$$
(3)

and:

$$T_0 = \frac{\sum x \times l(x) \times m(x)}{\sum l(x) \times m(x)}$$
(4)

where $m(x)$ is the age-specific reproduction rate. Because detailed data for $m(x)$ are still unavailable for the Yangtze finless porpoise, we estimated $m(x)$ by the following method:

$$m(x) = 0 \quad \text{when } 0 \leqslant x < Am,$$
and
$$m(x) = \frac{\rho}{CI} \quad \text{when } Am \leqslant x < Ax$$
(5)

where Am, Ax, CI and ρ were age at maturation (female), life span (female), calving interval, and expected proportion of female calves respectively (Huang et al., 2008). The value of r was then estimated by:

$$r = \frac{\ln R_0}{T_0}$$
(6)

In order to include the effect of parameter uncertainty into demographic rate estimates and subsequent population trend simulation, we re-sampled relevant life history parameters ($LHP(i)$, where i = the ith iteration) between their upper (LHP_u) and lower (LHP_l) limits (Table 1) randomly according to the equation:

$$LHP(i) = LHP_l + (LHP_u - LHP_l) \times \sigma$$
(7)

where σ was a random number (0–1) generated using the MATLAB function (rand) of MATLAB 7.0 (Mathworks, 2005). As we re-sampled a value of Ax between plausible upper and lower bounds in this study (Table 1) rather than using a fixed Ax estimate, as is often conducted in other population viability analyses, we calculated the "relative porpoise age":

$$xr = x \times \frac{A_\infty}{Ax(i)}$$
(8)

in order to unify the survivorship curves at different re-sampled levels of $Ax(i)$ (Barlow and Boveng, 1991). A_∞ represents the maximum determined age for stranded animals. Re-sampling and estimation of demographic rates were repeated for 5000 iterations, and the mean and SD of T_0 and r were calculated.

2.3. Population trend modelling and status assessment

We simulated future changes of abundance for the Yangtze finless porpoise population, $N(t)$, at year t using an individual-based Leslie matrix model that also factors the effects of demographic stochasticity and parameter uncertainty (Slooten et al., 2000; Currey et al., 2009a; Huang et al., 2012b). In this approach, $N(t)$ was modelled by the following process:

1. An individual survived from age x at year t to age $x + 1$ at year $t + 1$ whenever the random number σ (range = 0–1) exceeded the mortality rate at age x, $q(x) = 1 - l(x+1)/l(x)$ (Stolen and Barlow, 2003; Moore and Read, 2008). When $\sigma \leqslant q(x)$, the individual porpoise was considered to have died, otherwise it survived. Uncertainty in age-specific mortality was incorporated by including the SD of modeled $q(x)$.
2. A female that survived into year $t + 1$ was determined to have given birth by comparing σ with $\frac{1}{CI_i}$, with a birth occurring when $\sigma \leqslant \frac{1}{CI_i}$.
3. The sex of the newborn was male when σ exceeded the sex ratio ρ (default = 0.50), otherwise the calf was a female.
4. For each of the above simulations, a new random number σ was generated using the MATLAB 7.0 function (Mathworks, 2005).

The starting population abundance (N_0) was defined as 1225 porpoises with an estimated CV of 13.26%, based on the most recent porpoise population estimate for the Yangtze mainstem using survey data from Zhao et al. (2008). The length of future population projection was defined as two, three, and five generations or 100 years under Criterion A, C1 and E of the IUCN Red List Categories and Criteria Version 3.1 (IUCN, 2001). Two simulation scenarios were tested, using modelled survivorships ($l(x)$) from the

Post93 and Pre93 populations. Each simulation ran 200 replications, and each replication ran 5000 iterations. For each replication, the probability of extinction (PE) within a given time was estimated by the frequency of only one sex, either male or female, remaining in the population over 5000 iterations; the time (calendar date) of extinction (TE) was also recorded. The mean (±SD) for our PE and TE estimates was calculated from 200 replications. We then applied the five criteria of the IUCN Red List Categories and Criteria Version 3.1 (IUCN, 2001) to known (abundance and occurrence) and projected (rate of decline and PE) population information for the Yangtze finless porpoise (see Currey et al., 2009a).

3. Results

3.1. Life table and demography rate estimates

Age-at-death data included 183 animals from the Pre93 population (including data up to and including 1993) and 96 animals from the Post93 population. The ages of all individuals from the Post93 population were estimated from body length using Eq. (1), while age data for the Pre93 population were based on both GLG counts (66 animals) and estimation from body length (117 animals). Life table parameters, including number of animals (n_x) and survivorship (l_x) for each age class, are listed in Table 2. For the Pre93 population, the difference of n_x based on different methods of age estimation was not statistically significant ($\chi^2 = 13.94$, $p = 0.604$). However, the difference of n_x between the Pre93 and Post93 populations was significant ($\chi^2 = 36.91$, $p < 0.01$). We therefore combined data on age-at-death determined using both GLG counts and body length for the Pre93 population. Male and female data were treated separately for both the Pre93 and Post93 populations; estimates of the five Siler's parameters for males and females in both populations are listed in Table 3. The fitted curves of modelled survivorship $l(x)$ and mortality rate $q(x)$ from the Pre93 population (Fig. 2a and b) and the Post93 population (Fig. 2c and d) were then used to calculate estimates of demographic rate and projected population trends (see below).

Estimates of demographic rate show a negative trend for both the Pre93 and Post93 populations ($\bar{r} = -0.0159$, SD = 0.0135 and $\bar{r} = -0.0625$, SD = 0.0169 respectively; Table 4). The Yangtze finless porpoise population has therefore been declining since before 1993, but this decline has accelerated substantially since 1993. The mean of T_0 for Pre93 and Post93 life tables was 8.96 (SD = 0.430) and 7.93 (SD = 0.413) years respectively. The length of future projection required for simulating percentage population decline under IUCN Criteria A4 and C1 and percentage probability of extinction under IUCN Criterion E (IUCN, 2001) was calculated using the Post93 life table as 8 years (one generation), 16 years (two generations), 24 years (three generations), 40 years (five generations), and 100 years.

3.2. Population trend modelling and status classification

The change of simulated abundance, $N(t)$, under Pre93 and Post93 population scenarios is shown in Fig. 3. Neither scenario supports a stable or increasing population trend (Fig. 3a). Furthermore, the Post93 model shows a more drastic decline than the Pre93 model. The modelled estimates (mean, SD) of probability of extinction (PE) within 100 years, expected date of extinction (TE years), and percentage of abundance decline within one, two and three generations are listed in Table 5. In the Post93 model, there is an 86.06% probability (SD = 6.60%) of total extinction of the porpoise population within 100 years; the mean TE occurs at 62.7 years (SD = 18.8 years) (Fig. 3b). In the Pre93 model, $N(t)$ declines more slowly, but there is greater uncertainty over the fate of the population (Fig. 3c). The PE within 100 years and TE estimates averaged 19.05% (SD = 1.00%) and 133 (SD = 58.3) years respectively.

The distribution of percentage decline within three and two generations for all simulations under the Post93 model is shown in Figs. 4a and 5a respectively. Within three generations, 75.4% of iterations (SD = 2.41% in 200 repeats) predicted an abundance decline greater than 80% (Fig. 4b), meeting the criteria for CR status under Criterion A4 (IUCN, 2001). Within two generations, 99.2% of iterations (SD = 3.53 in 200 repeats) predicted an abundance decline greater than 50% (Fig. 5b). As the estimated population size is greater than 250 adults but less than 2500 adults, this decline meets the criteria to classify the porpoise as EN under Criterion C1 (Fig. 5b). Estimates of PE within three generations (CR), five generations (EN) and 100 years (VU) were 0, 5.75% (SD = 0.65%) and 86.1% (SD = 6.60%) respectively, meeting the criteria for VU status under Criterion E (Fig. 6). Incorporation of further recent

Table 2
Life table parameters, including number (n_x) and survivorship (l_x) at age x, for the Yangtze finless porpoise population up to 1993 (Pre93) and after 1993 (Post93). Pre93 data are based on both GLG counts (a) and age–length relationships (b) (Zhang, 1992), whereas all Post93 data are based on age–length relationships.

Age	n_x						l_x					
	Pre93				Post93		Pre93				Post93	
	Male		Female		Male	Female	Male		Female		Male	Female
	(a)	(b)	(a)	(b)	(a)	(a)	(a)	(b)	(a)	(b)	(a)	(a)
0	6	14	7	14	11	13	1.000	1.000	1.000	1.000	1.000	1.000
1	1	8	5	9	2	3	0.818	0.754	0.788	0.767	0.723	0.776
2	1	5	2	2	3	3	0.788	0.614	0.636	0.617	0.660	0.735
3	6	1	1	4	4	7	0.758	0.526	0.576	0.583	0.596	0.673
4	1	3	4	3	4	3	0.576	0.509	0.545	0.517	0.447	0.592
5	3	3	3	5	4	2	0.545	0.456	0.424	0.467	0.383	0.510
6	2	2	2	0	5	4	0.455	0.404	0.333	0.383	0.340	0.429
7	2	2	1	4	2	3	0.394	0.368	0.273	0.383	0.255	0.327
8	2	3	1	3	2	0	0.333	0.333	0.242	0.317	0.191	0.286
9	3	3	0	1	3	0	0.273	0.281	0.212	0.267	0.191	0.245
10	0	4	2	3	4	0	0.182	0.228	0.212	0.250	0.191	0.184
11	1	2	0	4	3	5	0.182	0.158	0.152	0.200	0.191	0.102
12	1	3	1	0	0	2	0.152	0.123	0.152	0.133	0.085	0.041
13	0	1	0	0	0	1	0.121	0.070	0.121	0.133	0.043	0.041
14	0	0	2	0	0	0	0.121	0.053	0.121	0.133	0.021	0.041
15	0	0	0	2	0	0	0.121	0.053	0.061	0.133	0.021	0.041
16	4	3	2	6	2	1	0.121	0.053	0.061	0.100	0.021	0.041

Table 3
Siler's parameter (a_1, b_1, a_2, a_3 and b_3) estimates for life table parameters from the Pre93 and Post93 porpoise models, calculated using the least-squares method.

Parameters	a_1	b_1	a_2	a_3	b_3	r^2
Pre93						
Male	0.1890	0.2253	0.0000	0.0219	0.2032	0.9930
Female	0.2269	0.2229	0.0000	0.0194	0.1853	0.9890
Post93						
Male	0.1458	0.2258	0.0000	0.0261	0.2534	0.9950
Female	0.2307	0.2220	0.0000	0.0293	0.1955	0.9930

Table 4
Demographic rate estimates (mean, SD) for the Yangtze finless porpoise population up to 1993 (Pre93) and after 1993 (Post93), using life history parameters listed in Table 1, and modelled survivorship from Siler's model (Fig. 2). T_0 = generation time; r = instantaneous rate of increase.

	T_0	r
Pre93	8.96 (SD 0.430)	−0.0159 (SD 0.0135)
Post93	7.93 (SD 0.413)	−0.0625 (SD 0.0169)

population information (Zhao et al., 2008) also allows the Yangtze finless porpoise to meet the criteria for EN or VU under Criterion B1 or D1 respectively (Table 6).

4. Discussion

### 4.1. Uncertainties of predicted risk

The accurate prediction of rate of decline and future extinction date depends upon the accuracy of demographic parameter values and the number and magnitude of different impacts that are included in a population model. In this analysis, most porpoise individuals (213/279) were aged using length–age relationships (Zhang, 1992) rather than standard GLG counts from teeth sections. However, the comparison of Pre93 l_x based on different aging methods does not show any statistical difference. Moreover, the Pre93 $\bar{r}$ estimate ($\bar{r} = -0.0159$, SD = 0.0135) is similar to the estimate by Yang et al. (1998) of $\bar{r} = -0.0165$ (no SD calculated),

which was only based on GLGs counts. The decline in porpoise abundance from more than 2550 individuals to fewer than 1225 individuals between 1991 and 2006 in the Yangtze mainstem (Zhang et al., 1993; Zhao et al., 2008) corresponds to a 51.96% reduction within 15 years, which falls within the range of the Post93 $\bar{r}$ estimate (Fig. 5a). Recent analysis of published and unpublished porpoise survey data shows an average abundance decline of 6.4% per annum between 1990 and 2007 (Zhao Xiujiang, unpublished data), which is comparable to the value of Post93 $\bar{r}$ estimate. These comparisons strongly suggest that our estimates of $\bar{r}$ based on life table data are likely to be valid. Although there is relatively wide variation in these $\bar{r}$ estimates (84.90% and 29.20% for the Pre93 and Post93 models respectively), this does not affect general trend projections or status assessment.

The population model we used here may be too "simple" to plausibly estimate the exact risk of decline and future extinction, as demographic consequences on mortality and reproductive rates resulting from factors such as habitat degradation/fragmentation, catastrophic events or inbreeding depression are not incorporated. The intensity of anthropogenic impacts across the Yangtze region
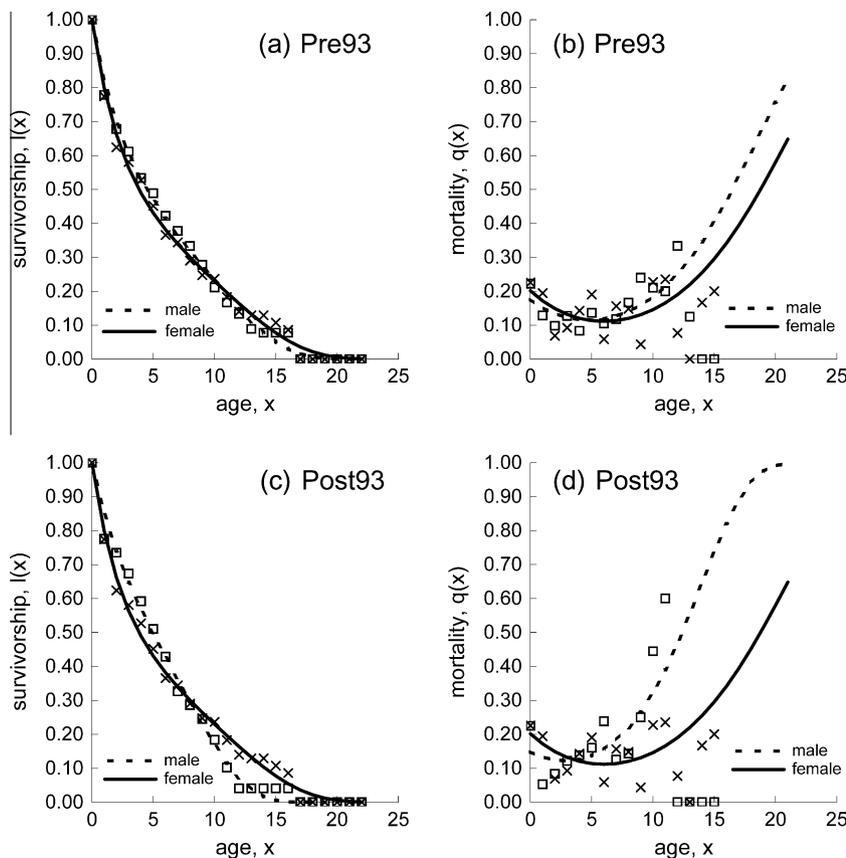
Fig. 2. Age-specific survivorship and mortality rates of the Yangtze finless porpoise population up to 1993 (Pre93: a and b) and after 1993 (Post93: c and d), showing a substantial increase in mortality after age at maturation (between 4 and 5 years old). Figure legend: points = estimates using the standard method of Krebs (1989) (cross = female, block = male), lines = smoothed estimates using Siler's model (solid: female, dashed: male).
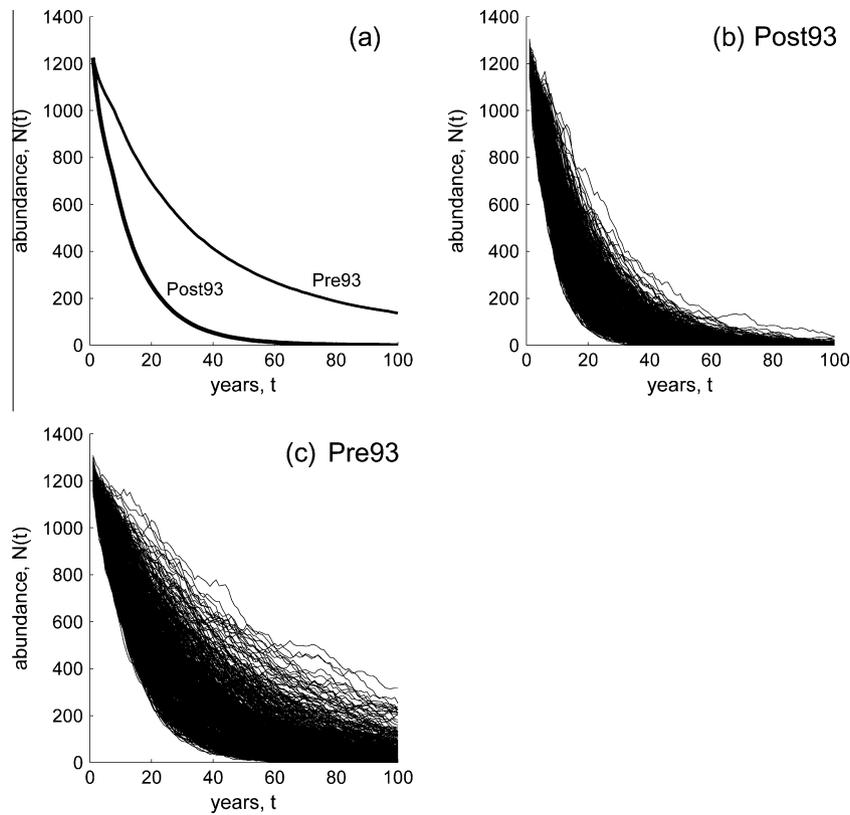
Fig. 3. Fluctuation of abundance, $N(t)$, of the Yangtze finless porpoise population over 100 years, predicted using the life history parameters from Table 1 and modelled survivorships from Fig. 2. (a) Median values of all iterations (200 replications × 5000 iterations for each replication). (b) Trends of $N(t)$ predicted under the Post93 population model, showing rapid declines with a narrow range of uncertainty. (c) Trends of $N(t)$ predicted under the Pre93 population model, showing slow declines on average (dark cloud area) with a wide range of uncertainty and stochastic fluctuation.

Table 5
Model estimates (mean, SD) of probability of extinction (PE) within 100 years, expected date of extinction (TE, years after start of simulation), and percentage of abundance decline within one, two and three generations ($\%_{T0}$, $\%_{2T0}$, $\%_{3T0}$ respectively) under the Pre93 and Post93 population models.

|	Pre93 (mean, SD)	Post93 (mean, SD)
PE	19.05% (1.00%)	86.06% (6.60%)
TE	133 (58.3)	62.7 (18.8)
$\%_{T0}$	25.65% (9.26%)	49.70% (7.23%)
$\%_{2T0}$	47.15% (14.01%)	75.65% (7.22%)
$\%_{3T0}$	61.57% (15.42%)	87.85% (5.47%)

is also highly likely to continue to increase in the future rather than being constant over time. Indeed, an even faster rate of decline (7.3% abundance per annum) has been reported in some porpoise "hotspots" in the Yangtze (Wei et al., 2002). One of the difficulties in constructing a more complicated model is that the quantitative relationship between demographic consequences and human impacts is not clearly understood for the Yangtze finless porpoise, as is also the case for many other cetacean species. However, even this "simplest" model has predicted the very urgent situation that the Yangtze finless porpoise is very likely to become extinct within a matter of decades. The current rate of decline meets the criterion to classify the Yangtze finless porpoise as CR under Criterion A4 (IUCN, 2001). The predicted PE will be even greater and extinction
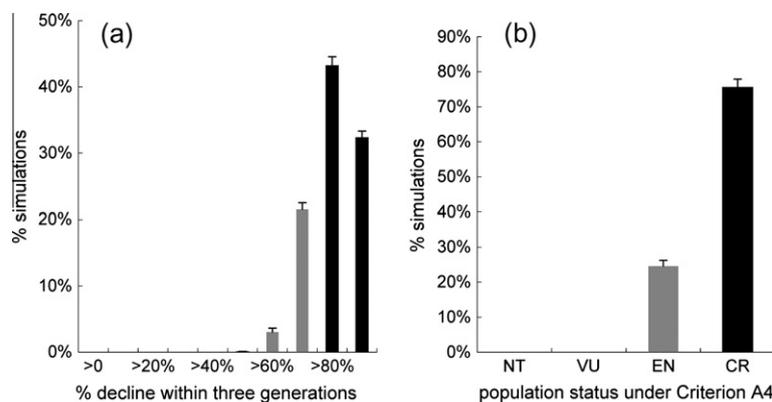
Fig. 4. Frequency distribution (% simulations) of percentage of abundance for the Yangtze finless porpoise based on the current rate of decline from the Post93 population model after three generations (a), and the resultant frequency of status classification for the Yangtze finless porpoise under IUCN Criterion A4 (b).
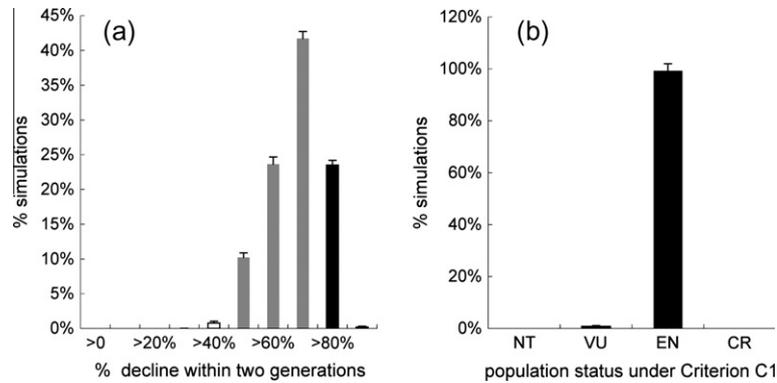
Fig. 5. Frequency distribution (% simulations) of percentage of abundance for the Yangtze finless porpoise based on the current rate of decline from the Post93 population model after two generations (a), and the resultant frequency of status classification for the Yangtze finless porpoise under IUCN Criterion C1 (b).
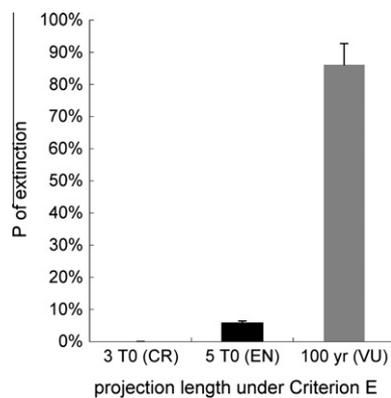
Fig. 6. Probability (% simulations) of extinction for the Yangtze finless porpoise, based on the current rate of decline from the Post93 population model, within three generations (CR), five generations (EN) and 100 years (VU), according to IUCN Criterion E.

will occur even more rapidly if the demographic consequences of unquantified anthropogenic impacts were further included into the model (Huang et al., 2012a). However, considerable further research is required to collect sufficient data to model these additional anthropogenic impacts, which does not represent a priority for Yangtze finless porpoise conservation under its current critical situation.

The risk of stochastic extinction may become more significant if the drastic levels of environmental deterioration along the Yangtze River lead to separation of the Yangtze finless porpoise population into discrete subpopulations. Zhao et al. (2008) reported that no porpoises were encountered during the 2006 boat-based survey between Yueyang and Shishou (Fig. 1), a region where sightings were previously frequent. If the Yangtze finless porpoise no longer occurs in a single continuous population, the effective value of abundance for each subpopulation could be far less than 1225

animals and extinction may take place substantially sooner due to stochastic processes (Soulé and Simberloff, 1986; Lacy, 1993; Lande, 1993; Reed et al., 2003).

The inevitable uncertainty around our model outputs therefore does not alter our conclusions about the highly threatened status of the Yangtze finless porpoise. We consider that the most important concern is now to immediately identify and implement appropriate and more proactive conservation responses to reduce or reverse the accelerating decline of the porpoise population in the Yangtze, rather than continue to collect data to improve precision over the exact level of estimated risk to the population (Rojas-Bracho et al., 2006; Jaramillo-Legorreta et al., 2007).

4.2. Immediate acts for conservation

The Yangtze finless porpoise was classified as Endangered in 1996 under the IUCN 1994 Red List Categories and Criteria (Baillie and Groombridge, 1996), and is currently listed as Vulnerable under the wider assessment for the narrow-ridged finless porpoise (*N. asiaeorientalis*), with no subspecies-specific assessment currently available (Wang and Reeves, 2011). However, our analysis indicates that this endemic subspecies is facing a risk of extinction higher than previously evaluated. The major threats to this subspecies have escalated over the last two decades, and there is no evidence to suggest that these threats will be neutralized or minimized in the near future. The current rate of porpoise decline exceeds the threshold for CR status (loss of 80% of abundance or higher within three generations) under Criterion A4 of the IUCN Red List Categories and Criteria Version 3.1 (IUCN, 2001). We therefore recommended reclassifying the status of the Yangtze finless porpoise to CR (Table 5).

Immediate threats to the continued survival of the Yangtze finless porpoise include by-catch and ship strikes, the accumulative effect of pollutants, reduction of prey resources, and habitat degradation by large-scale land reclamation and damming (Wang et al.,

Table 6
Status assessment for the Yangtze finless porpoise based on the current rate of decline from the Post93 population model, under the five criteria of the IUCN Red List Categories and Criteria Version 3.1 (IUCN, 2001).

Criterion	Current status	Source	Classification
A4	$\frac{\Delta N}{N_0} > 80\%$ within three generations	This study	CR
B1	Extent of occurrence <5000 km^2, declining trend	Zhao et al. (2008)	EN
C1	Number of adults <2500, $\frac{\Delta N}{N_0} > 50\%$ within two generations	Zhao et al. (2008) and this study	EN
D	Number of adults <1000 but >250	Zhao et al. (2008)	VU
E	Probability of extinction = 5.75% within five generations (<20%, EN) and = 86.1% within 100 years (>10%, VU)	This study	VU

2005; Wang, 2009). Implementing effective measures that can neutralize or minimize this wide range of threats is the key to counteracting the porpoise's current population decline. A series of cetacean reserves have been established along the Yangtze mainstem since the 1990s (Fig. 1) in an attempt to reduce anthropogenic threats. However, these measures have so far not been very effective in reducing the effect of escalating anthropogenic impacts, as demonstrated by the recent probable extinction of the baiji, the other cetacean formerly found in the Yangtze drainage, as well as other large sympatric vertebrates such as the Yangtze paddlefish (*Psephurus gladius*) (Turvey et al., 2007, 2010). A wider-scale, co-ordinated and proactive framework of conservation activities is urgently needed across the entire middle-lower Yangtze River system to ensure the long-term persistence of the last cetacean species in the Yangtze. Conservation actions should include stricter regulation both for legal and illegal fisheries practices and for ship traffic and sand-dredging activities, higher effluent water quality standards, regulation of point and non-point pollutant sources, development of large-scale sewage treatment facilities, and stricter rules for peripheral development programmes. Ultimate success in finless porpoise conservation will not be simple and the cost will not be low. Nevertheless, improved environmental management of the Yangtze drainage is essential not only for finless porpoise conservation but also for the hundreds of millions of people that rely on the Yangtze's resources for livelihoods, food security and ecosystem services.

The Yangtze finless porpoise and the baiji are not the only cetacean species that inhabit riverine ecosystems. Other freshwater cetacean species, including the Indus and Ganges River dolphins (*Platanista* spp.), the Amazon River dolphin (*Inia geoffrensis*), the Irrawaddy dolphin (*Orcaella brevirostris*) and the tucuxi (*Sotalia fluviatilis*), also face comparable challenges of long-term survival (Reeves et al., 1991; Reeves and Chaudhry, 1998; Smith and Smith, 1998; Smith et al., 2001; Martin et al., 2004; Braulik, 2006), but demographic data for these species are still extremely limited. Although specific threats facing these freshwater cetaceans may vary geographically in their importance, common threats include substantial loss of effective habitat (Reeves et al., 1991; Braulik, 2006), increasing concentrations of persistent organic pollutants in cetacean tissue (Senthilkumar et al., 1999), and incidental fisheries by-catch (Martin et al., 2004). The drastic decline of the Yangtze finless porpoise in two decades as a result of rapid industrial and economic growth reveals how uncontrolled environmental deterioration threatens the future of freshwater cetaceans despite the potential for the massive scale of the Yangtze system to buffer anthropogenic impacts. Our study presents a quantitative comparison between porpoise population trends in low-development and high-development environments at different time periods, and provides a cautionary warning for the conservation of other freshwater cetacean species.

Acknowledgments

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