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Population trends and vulnerability of humpback dolphins *Sousa chinensis* off the west coast of Taiwan

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ABSTRACT: Predictive modeling of population trends can indicate the rate of population decline and risk of extinction, providing quantitative means of assessing conservation status and threats. Our study tests the rate of population change and risk of extinction of the Indo-Pacific humpback dolphin *Sousa chinensis* off the west coast of Taiwan, the only humpback dolphin population classified as Critically Endangered (CR) by the IUCN Red List of Threatened Species. Under the most optimistic assumptions, almost 60% of simulations (out of 250 replications × 5000 iterations) predicted that population decline will exceed 80% within 3 generations, while the mean estimate of population decline within 1 generation was >50% of the current population numbers. Status classification performed using IUCN Red List Categories and Criteria Version 3.1 supported previous CR classification, while risk assessment models that factored in anthropogenic impacts further increased the estimated extinction risk. At an adult survival rate of 0.95, a modeled increment of annual bycatch rate by 1% of population size increased the probability of extinction within 100 yr by 7.5%; this increase was lower at a higher adult survival rate. The estimated extinction risk was greatest under the impact of habitat loss, reaching a hazardous level when habitat carrying capacity dropped to less than 50%, indicating that habitat fragmentation and alteration of coastal environments pose the greatest threats to this population, even if the cumulative sum of fragmented patches of habitat may superficially appear to be large.

KEY WORDS: *Sousa chinensis* · Demographic analyses · Individual-based model · Status assessment · Bycatch · Habitat degradation

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INTRODUCTION

The Indo-Pacific humpback dolphin *Sousa chinensis* inhabits coastal waters of the Indian and western Pacific Oceans (Jefferson & Karczmarski 2001, Reeves et al. 2008) and is found predominantly close inshore in waters less than 20 m deep (Karczmarski 1999, 2000, Karczmarski et al. 2000, Jefferson & Karczmarski 2001, Reeves et al. 2008, Ross et al. 2010, Mendez et al. 2013). This restricted inshore distribution exposes humpback dolphins to various anthropogenic impacts, such as incidental mortality in fishing gear (bycatch), vessel collisions, resource depletion, bioaccumulation of harmful pollutants and habitat destruction through direct human activities (Jefferson & Karczmarski 2001, Reeves et al. 2008, Jefferson et al. 2009, Ross et al. 2010, Huang et al. 2013, Slooten et al. 2013). The long-term survival of humpback dolphin populations has received remarkable conservation attention in recent years, especially in areas neighboring intense human urbanization, industrialization and coastal land exploitation (Reeves et al. 2008, Jefferson et al. 2009, Ross et al. 2010, Huang et al. 2012b, 2013). The current IUCN Red List of Threatened Species classifies humpback dolphins globally as Near Threatened (NT) (Reeves et al. 2008). However, adequate evidence of the rate of population decline and risk of extinction relevant

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to population status assessment under Criteria A, C and E of the IUCN Red List Categories and Criteria version 3.1 (IUCN 2001) remains rare across the species range (Huang et al. 2012b, Huang & Karczmarski 2014), leaving relevant impact assessments under various anthropogenic threats to qualitative rather than quantitative means. The effectiveness of management policies based on qualitative assessments can be easily compromised or, even worse, the policies themselves may be misguided and focus on the mitigation of the apparent threats but overlook other, indirect but sometime powerful impacts, as indicated by the recent history of the extinction of the baiji *Lipotes vexillifer* (Turvey et al. 2007, 2013) and the currently accelerating decline of the Yangtze finless porpoise *Neophocaena asiaeorientalis asiaeorientalis* (Mei et al. 2012, 2014).

A common management approach for ensuring population viability in cetacean species is to define a tolerable threshold of incidental removal, termed potential biological removal (PBR) (Wade 1998, Slooten et al. 2006), to mitigate or minimize anthropogenic threats. In practice, the causes of incidental mortality are often generalized to fishery bycatch (Caswell et al. 1998, Read & Wade 2000, Dans et al. 2003, Lennert-Cody et al. 2004, Moore & Read 2008). The PBR calculation for cetaceans is based on an intrinsic population growth rate that is usually set as 0.04 when demographic data are not available (Wade 1998). However, for species and/or populations classified under the IUCN Red List of Threatened Species as NT or higher, such as Vulnerable (VU), Endangered (EN) or Critically Endangered (CR), that have been declining (as is the case with humpback dolphins) the PBR calculation based on an assumed value of the rate of increase, 0.04, may need to be viewed with caution. The strategy of keeping bycatch under the hypothetically calculated PBR may not facilitate long-term survival of endangered and declining populations. Such risk has not yet been quantitatively addressed for humpback dolphins.

Impact of fishery bycatch is only one of many anthropogenic threats that endanger the long-term viability of coastal cetaceans. Other impacts, such as resource depletion through overharvesting of local fish stocks (Bearzi et al. 2006, 2008, 2010, Piroddi et al. 2011), harmful levels of pollutant and pathogen accumulation (Tanaka 2003, Parsons 2004, Reeves et al. 2008), and habitat degradation due to land reclamation and coastal development (Huang et al. 2013), can severely affect population viability through slow but irreversible processes. Such processes usually deteriorate habitat quality and, in turn, decrease the habitat carrying capacity (Thomas et al. 2001, Clausen & York 2008, Griffen & Drake 2008) that defines the upper limit of fluctuation in population numbers (Lacy 1993, Lande 1993, Huang et al. 2012a). Consequently, the decline of habitat carrying capacity fundamentally reduces the capability of a population to resist environmental and anthropogenic impacts (Lacy 1993, Doak 1995, Hilderbrand 2003, Griffen & Drake 2008). As a considerable proportion of the coastal waters inhabited by humpback dolphins off southeast Asia is increasingly degraded as a result of industrial and economic development and human population growth (Mackinnon et al. 2012, Huang et al. 2013, Huang & Karczmarski 2014), an assessment of such impacts on dolphin survival becomes increasingly important and urgent.

Of the known humpback dolphin populations, the animals off the Taiwan west coast (TWC) represent the only population currently classified as CR under Criteria C2 and D (Reeves et al. 2008). In the past decades, the west coast of Taiwan, including both terrestrial and aqueous zones, has experienced rapid human population growth and urbanization that has eliminated native coastal and estuarine landscape with no adequate conservation consideration or environmental mitigation measures (Huang et al. 2013). This large-scale degradation or even destruction of coastal and estuarine ecosystems has likely affected the quality of the habitat vital to the long-term viability of TWC humpback dolphins. In this study, we model the rate of decline and extinction probability of TWC humpback dolphins within 1 to 5 generations (Criteria A, C and E; IUCN 2001) using demographic parameters estimated from the available data. Subsequently, we quantify the risk of extinction contributed by mortality through bycatch and habitat degradation. The results of this study provide a preliminary quantitative risk assessment of the population viability of TWC humpback dolphins and offer insights into population processes that can function as a useful case study for other populations or subpopulations of this species where baseline demographic data are not available and precautionary measures have to be applied.

MATERIALS AND METHODS

Demographic rates

Demographic rates of TWC humpback dolphins, including instantaneous rate of increase (r) and generation time (T_0), were calculated using the traditional method with the following equations (summarized in Krebs 1989):

$$T_0 = \frac{\sum x \times l(x) \times m(x)}{\sum l(x) \times m(x)} \quad (1)$$

and

$$r = \frac{\ln(\sum l(x) \times m(x))}{T_0} \quad (2)$$

where $l(x)$ and $m(x)$ are age-specific survivorship and mortality rate at age x, respectively. For humpback dolphins, as well as many other cetacean species, the detailed age-specific $m(x)$ is not available and therefore was defined by:

$$m(x) = \begin{cases} 0, \ 0 \le x < A_m \\ \frac{\rho}{\mathrm{RI}}, \ A_m \le x < A_x \end{cases} \quad (3)$$

where RI, A_m and A_x represent reproductive interval (in years), age at maturity (in years) and expected lifespan (in years) of females, respectively (Huang et al. 2012a,b, Mei et al. 2012). The ratio of daughters, ρ, was assumed to be 0.50.

For most cetaceans, $l(x)$, is usually estimated using data collected from stranded or bycaught animals (Stolen & Barlow 2003, Moore & Read 2008, Huang et al. 2012b, Mei et al. 2012). Given the small population size (Wang et al. 2007, 2012, Yu et al. 2010) and short time span of previous research in Taiwan, the currently available number of collected specimens was insufficient to build a representative life-history table for TWC humpback dolphins that could facilitate the construction of the $l(x)$ model. Therefore, we applied an alternative approach where the $l(x)$ model is built as follows (Huang et al. 2012a):

$$l(x) = S_c \times S_a^{x-1} \quad (4)$$

where S_c and S_a are the survival rates of calf ($x \ge 1$) and non-calf dolphins, respectively. The value of S_c was defined as 0.62 (± 0.15 SD) based on recent photo-ID analysis (Chang 2011). A precise estimate of S_a, however, is not yet available for the TWC humpback dolphins, despite recent work by Wang et al. (2012) where the S_a estimate (0.985) is accompanied by an extremely wide variation (CI = 0.832 – 0.998). Therefore we use here the range of S_a between 0.832 and 0.998 reported by Wang et al. (2012), rather than a fixed value (0.985). To include uncertainty as a precautionary measure when calculating demographic parameters and running population trend projection, S_a was randomly and repeatedly re-sampled between 0.832 and 0.998.

The 3 life history parameters that relate to demographic parameter calculation and population trend projection, A_m, RI and A_X, were re-sampled within their plausible lower ($\mathrm{LHP_l}$) and upper ($\mathrm{LHP_u}$) bounds (Table 1) by the following equation (Huang et al. 2012a,b, Mei et al. 2012):

$$\mathrm{LHP}(i) = \mathrm{LHP_l} + (\mathrm{LHP_u} - \mathrm{LHP_l}) \times \sigma \quad (5)$$

where σ is a random number between 0 and 1 generated by MATLAB function 'rand' (MathWorks). By re-sampling these parameters, the effect of parameter uncertainty could be included in both the demographic parameter estimates and predictions of population trends. The calculation of r and T_0 was repeated using 5000 iterations, and mean (±SD, CI) estimates were calculated.

Population trend projection

The population change of TWC humpback dolphins, $N(t)$, was simulated using an individual-based model that factors in the effects of parameter uncertainty and demographic stochasticity (Slooten et al. 2000, Currey et al. 2009a, Huang et al. 2012a,b, Mei et al. 2012). In this model, the population change was simulated by the following processes:

(1) An individual survived from age x at year t to age $x + 1$ at year $t + 1$ whenever the random number

Table 1. Range of life-history parameters, including age at maturity (A_m), reproductive interval (RI) and expected lifespan (A_x), of female humpback dolphins *Sousa chinensis*

Parameter	Range	Reference
A_m (yr)	9–11[a]	Jefferson (2000), Jefferson & Hung (2004), Jefferson et al. (2012)
RI (yr)	2.19–2.48	Chang (2011)
A_x (yr)	25[b]–43[a]	Jefferson (2000), Jefferson et al. (2012), Huang et al. (2012b)

[a] Values from the Pearl River Estuary population

[b] The largest number of growth layer groups counted in specimens held at the National Museum of Nature and Science, Taiwan (provided by C. J. Yao). GLGs indicate the age and are obtained through sectioning of teeth and counting annual layers of incremental growth of cementum and dentine

σ (between 0 and 1) exceeded the mortality rate (q) at age x, as per the following equation: $q(x) = 1 - S$, where S is the survival rate, either S_c (for $x \le 1$) or S_a (for $x > 1$). In cases when $\sigma \le q(x)$, the individual dolphin was considered a victim of mortality, otherwise it survived.

(2) A female that survived to the next year was determined to give birth by comparing σ with $\frac{1}{RI_i}$, with the presence of newborn when $\sigma \le \frac{1}{RI_i}$, where i represents the ith iteration in simulation.

(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.

The initial abundance (N_0) was defined as between 54 and 74, according to Wang et al. (2012). This range, however, may be an underestimate (compared with Yu et al. 2010), as Wang et al. (2012) apparently overlooked the humpback dolphins inhabiting the southern TWC waters (Chou & Lee 2010, Ross et al. 2010). At least 20 individually distinctive animals inhabit this region and have never been reported further north in the area studied by Wang and colleagues (Chang 2011, Yeh 2011).

The length of population trend projection in our study was defined at 5 generations or 100 yr, whichever is longer (IUCN, 2001). Each simulation ran 250 replications and each replication repeatedly ran 5000 iterations. As the population trend might fluctuate upward at high S_a value (for example, S_a = 0.985), we introduced a density-dependent effect on population change using

$$r' = r \times \left(1 - \frac{N(t)}{K_0}\right) \tag{6}$$

(Lacy 1993, Huang et al. 2012a), where r' is a density-adjusted r when $N(t)$ exceeds the ceiling K_0. The value of K_0 was defined as 99 animals because it is the earliest abundance estimate (Wang et al. 2007) and so far the highest; none of the subsequent estimates (Yu et al. 2010, Wang et al. 2012) exceeded this value. Furthermore, recent analyses of satellite imagery of the Taiwan west coast indicate a substantial loss of humpback dolphin habitat to land reclamation (Huang et al. 2013), suggesting that population numbers above this previously estimated ceiling are unlikely.

For each iteration, we estimated the percentage of abundance decline, $\frac{\Delta N(t)}{N_0}$ within 1 and 3 generations according to Criteria A3b and C1 in the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2001, Currey et al. 2009a, Wilson et al. 2011, Huang et al. 2012b, Mei et al. 2012). For each replication, we estimated the probabilities of extinction (PE) within 100 yr (PE_{100}), 3 generations (PE_{3T_0}) and 5 generations (PE_{5T_0}) based on Criterion E (IUCN 2001). The condition of population extinction was defined as having occurred whenever only one sex, either male or female, remained in the population.

Status classification

We calculated the probabilities of the percentage abundance decline within 1 generation and 3 generations meeting the standards for classification as VU, EN or CR under Criteria A3b (in 3 generations) and C1 (in 1 generation). Under Criterion B1b (iii, v) (IUCN 2001), the population status is classified by its geographic range and population decline (r). As current habitat area is obviously larger than 100 km^2 but smaller than 5000 km^2 (Wang et al. 2007, 2012, Ross et al. 2010), which are the size thresholds for classification as CR ($\le$100 km^2) and EN ($\le$5000 km^2), we estimated the probability for the condition when $r < 0$ as the probability of meeting the classification of EN under Criterion B1bv. The PE_{3T_0}, PE_{5T_0} and PE_{100} estimates were used to classify the population as VU, EN or CR under Criterion E (IUCN 2001).

Sensitivity test for adult survival rate

Besides projecting r and the population trend based on a dynamic range of S_a (0.832–0.998), we estimated $\bar{r}$ and PE_{100} values of the TWC humpback dolphin at different fixed S_a. In this process, the value of S_a increased from 0.832 to 0.998. Means (±SD) of $\bar{r}$ and PE_{100} at each S_a value were calculated.

Vulnerability test for anthropogenic impacts

The influence of anthropogenic impacts on population trends and the probability of extinction were assessed as 2 categories: those directly causing incidental mortality (e.g. bycatch and vessel collisions) were categorized as 'bycatch impact', while indirect impacts that could potentially decrease the availability and quality of habitat (e.g. land reclamation, resource depletion and habitat degradation) were categorized as 'habitat loss impact'. The range of bycatch impact was tested from 0 to 5% $N(t)$ per annum. The extent of habitat loss impact, in contrast, was defined between 0 and 90% K_0, where K_0 was defined as 99 animals (Wang et al. 2007) by introducing a previously described density-dependent effect. This ceiling was defined because the availability and quality of potential habitat for humpback dolphins off the Taiwan west coast is unlikely to increase in the future due to substantial recent alteration of habitat and environmental change (Huang et al. 2013). As the S_a initially used has a very wide range that could likely interfere with the assessment of impacts, we adopted fixed S_a values in this test. The S_a were defined as 0.985 (Wang et al. 2012) and 0.95 (Karczmarski 2000, Jefferson & Karczmarski 2001, Taylor et al. 2007) and tested separately. The latter value was selected because it appears close to the S_a estimate for an 'undisturbed' population of cetaceans (Taylor et al. 2007), such as the bottlenose dolphin (*Tursiops truncatus*) ($\bar{S}_a = 0.951$: Small & Demaster 1995). Means (±SD) of PE_{100} under these 2 impact scenarios were estimated. Table 2 summarizes the simulation environment of trend projections for status assessment and sensitivity of decline at different S_a values and under different anthropogenic impacts.

RESULTS

Demographic rates and population trend

Demographic rate estimates for the TWC humpback dolphins are summarized in Table 3. The $\bar{r}$ estimate of −0.0278 indicates a moderate population decline at 2.74% (1 − exp[−0.0278]) per annum. However, the CI of the estimate is large, ranging from −0.113 (rapidly downward) to 0.0317 (moderately upward). The generation time $\overline{T_0}$ is estimated at 21.28 yr (SD = 3.76 yr, CI = 16.20 − 28.80 yr). Thus, the temporal length for status classification under Criteria A3b, C1 and E was chosen as 22, 64 and 100 yr for 1, 3 and 5 generations, respectively.

Table 3. Estimates of the demographic parameters generation time (T_0) and instantaneous rate of increase (r) for humpback dolphins off the west coast of Taiwan

Parameter	Mean	SD	CI
T_0	21.28	3.76	16.20 to 28.80
r	−0.0278	0.0434	−0.113 to 0.0317

The population change $N(t)$ projected by the individual-based model is shown in Fig. 1. The indeterministic plot shows the stochasticity of simulations and indicates a wide uncertainty and the difficulty of reaching a determinate conclusion (Fig. 1A). Although 43% (SD = 1.54%) of simulations (250 replications × 5000 iterations) suggested a 'stable' population, almost 54% (SD = 1.52%) of simulations predicted population extinction within 100 yr. The direction of the deterministic population trend was most affected by the value of S_a (Fig. 1B). With S_a = 0.985, the dolphin population was projected to slowly increase, while with S_a = 0.95 it was projected to decline at a slow but continuous rate (Fig. 1B).

Mean probability of extinction estimates, using S_a = 0.832 − 0.998, were 47.30% (SD = 1.51%), 64.13% (SD = 1.62%) and 53.93% (SD = 1.52%) of simulations for PE_{3T_0}, PE_{5T_0} and PE_{100}, respectively (Fig. 2). A total of 69.4% of simulations (SD = 8.71%) predicted a population decline greater than 25% within 1 generation (22 yr), with the mean estimate suggesting that population numbers would diminish by an average of 50.48% (SD = 50.79%) (Fig. 3A). The population loss reached an average of 66.09% (SD = 58.23%) decline in 3 generations (64 yr), while 59% (SD = 3.23%) of simulations indicated that the population decline over 3 generations could exceed 80% (Fig. 3B).

Table 2. Definition of parameters used for projecting population trends and risk of extinction. K_0: initial habitat carrying capacity

Parameter	Value or range	Reference
Initial abundance, N_0	54–74	Wang et al. (2012)
Survival rate (yr^{-1})		
Calf (age ≤ 1)	0.62	Chang (2011)
Non-calf (age > 1)	0.832–0.998	Wang et al. (2012)
Ratio of daughters	0.5	Present study
Length of projection	100 yr or 5 generations, whichever is longer	IUCN (2001)
Anthropogenic impacts		
Bycatch	0–5% $N(t)$	Present study
Habitat degradation	0–90% K_0	Present study

Status classification

The status classification of the TWC humpback dolphins under Criteria A–E is summarized in Table 4. For all population trend projections (250 replications × 5000 iterations), 59% (SD = 3.23%) of simulations meet the conditions for classification as CR under Criterion A3b (Fig. 3B), although the mean population decline estimates meet the conditions for classification as EN, defined as the percent-

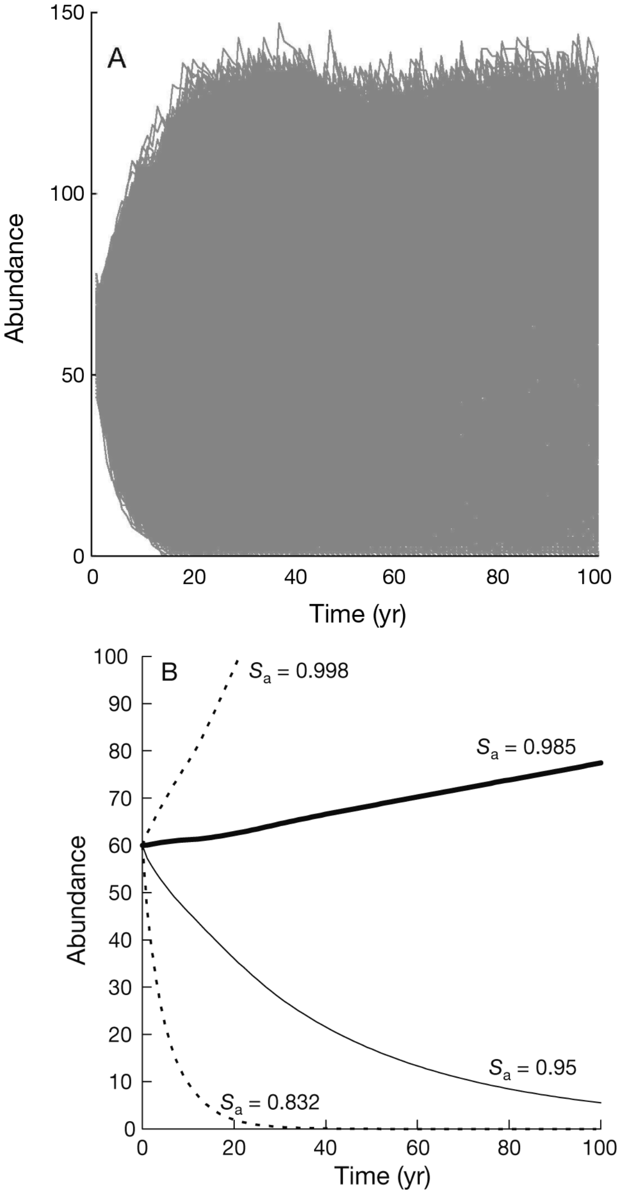

Fig. 1. Population trend projections for humpback dolphins *Sousa chinensis* off the Taiwan west coast run by individual-based model. (A) Stochastic result of projections, showing a highly indeterministic trend primarily due to the wide range of the non-calf survival rate, $S_a = 0.832 - 0.998$ (Wang et al. 2012). Each line represents one simulation iteration. (B) Deterministic plot of population trends at different S_a values: 0.832, 0.95, 0.985 and 0.998

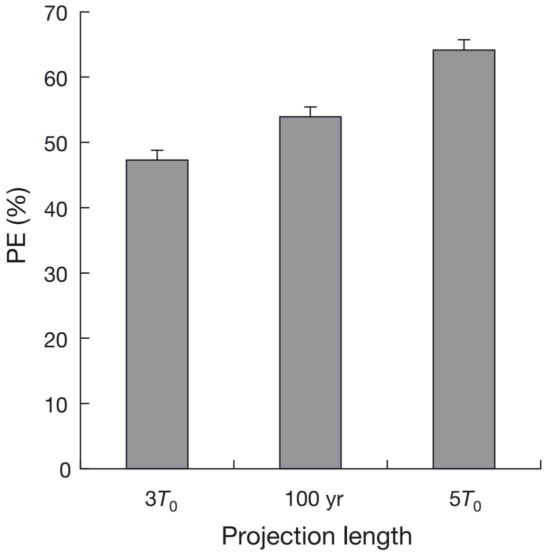

Fig. 2. Probability of extinction (PE; mean + SD) of the Taiwan west coast humpback dolphin *Sousa chinensis* within the lifespan of 3 generations ($3T_0$), 5 generations ($5\ T_0$) and 100 yr using an individual-based model ($T_0 = 21.28$ yr)

age decline higher than 50% but lower than 80% within 3 generations. Applying the precautionary principle, the CR classification under Criterion A3b seems appropriate, although EN classification is also plausible. Under Criterion C1, as the current population has fewer than 250 adults and the estimated percentage decline within 1 generation is higher than 25%, the TWC humpback dolphins can be classified as CR. The PE estimates meet the conditions for classification as EN under Criterion E, defined as PE > 20% within 5 generations but <50% within 3 generations.

Sensitivity of population survival under anthropogenic impacts

The estimate of the instantaneous rate of increase $\bar{r}$ within the range of non-calf survival rates of 0.832 to 0.998 is shown in Fig. 4A, which can be approximated by:

$$\bar{r} \approx 1.0714 \times S_a - 1.0263,\ R^2 = 0.995 \qquad (6)$$

Although a stationary trend ($\bar{r} \approx 0$) can be reached at $S_a = 0.958$, PE_{100} does not decrease ($\overline{PE}_{100} \leq 5\%$) until $S_a \geq 0.963$ (Fig. 4B), primarily due to high demographic stochasticity in a small population. However, as soon as the S_a estimate decreases below 0.913, the probability of extinction within 100 yr becomes more evident: $\overline{PE}_{100} \geq 95\%$ (Fig. 4B).

The impact of bycatch on population survival was most affected by the value of S_a. Generally, PE_{100} increased with the percentage of bycatch (Fig. 5) and the extent of habitat loss (Fig. 6). With $\bar{S}_a = 0.985$ (after Wang et al. 2012), the PE_{100} was generally low (Fig. 5A), but with $\bar{S}_a = 0.95$ ('undisturbed' survival

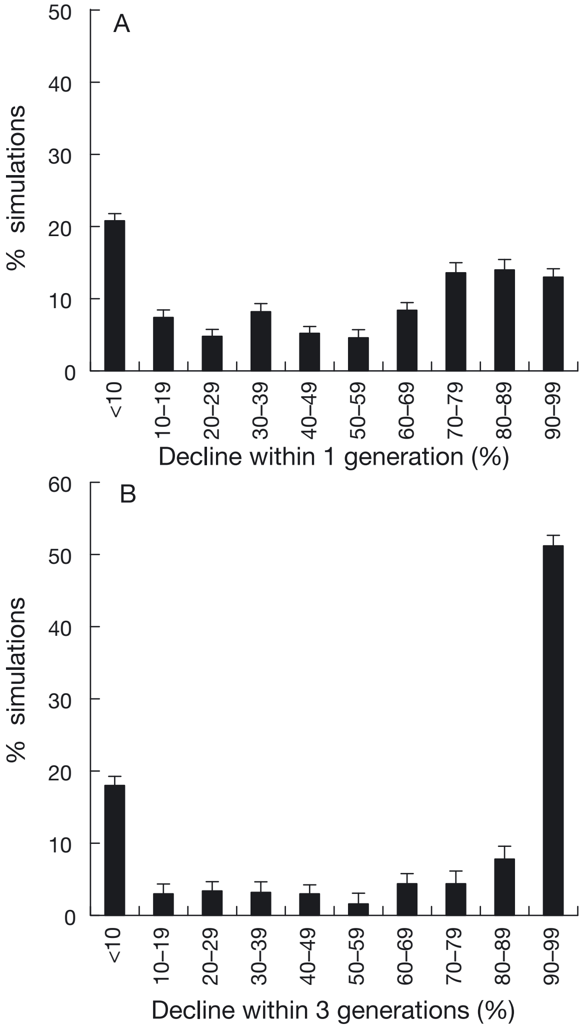

Fig. 3. Estimates of the percentage of *Sousa chinensis* population decline in a lifespan of (A) 1 and (B) 3 generations with respect to Criteria C1 and A3b of the IUCN Red List Categories and Criteria: Version 3.1 (IUCN 2001)

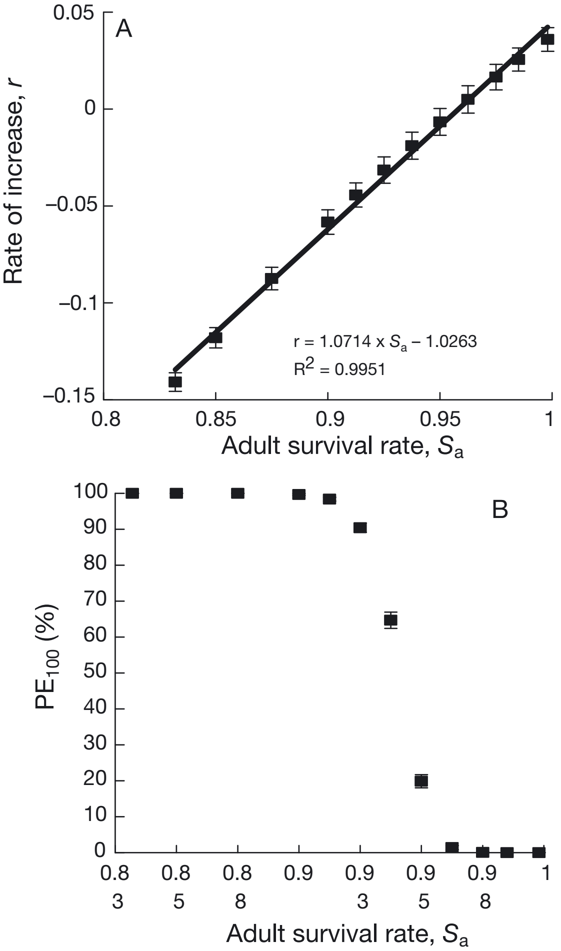

Fig. 4. Mean (±SD) values of (A) the instantaneous rate of increase (r) and (B) probabilities of extinction in the next 100 yr (PE_{100}) of Taiwan west coast humpback dolphin *Sousa chinensis* at different values of adult survival rates (S_a)

Table 4. Results of population trend predictions and status classification of Taiwan west coast humpback dolphins under Criteria A–E (IUCN 2001) based on currently available baselines. T_0: generation time; ΔN: change in population size calculated as $(N_t–N_0)/N_0$ where N_t: population size at time t and N_0: initial (current) population size; r: instantaneous rate of increase; PE: probability of extinction; CR: Critically Endangered; EN: Endangered. Note that under criterion A3b, average decline indicates EN status, but 59% simulations suggest CR

Criterion no.	Details of criterion	Results of population viability analyses	Status
A3b	50% ≤ $\Delta N < 80\%$ within $3T_0$	59.00% (SD = 3.23%) simulations predicted $\Delta N \geq 80\%$ (Fig. 3B) $\overline{\Delta N}$ 66.09% (SD 58.23%)	EN (CR)
B1b (iii,v)	100 km^2 ≤ extent of occurrence < 5000 km^2 ^{iii}Continuing decline of habitat area $^{v}r < 0$	Current extent of occurrence <1000 km^2 (Wang et al. 2007, Ross et al. 2010) Substantial habitat loss and/or deterioration (Huang et al. 2013) $r = -0.0278$ (Present study)	EN
C1	No. of adults ≤ 250 $\Delta N \geq 25\%$ within T_0	N_0 = 54–75 (Wang et al. 2012) $\overline{\Delta N}$ = 50.48% (SD = 50.79%) (Fig. 3A)	CR
D	No. of adults ≤ 50	N_0 = 99, no. of adults < 50 (Wang et al. 2007),	CR
E	EN: PE_{5T_0} but PE_{3T_0} CR: PE_{5T_0}	PE_{5T_0} = 64.13% (SD = 1.62%) PE_{3T_0} = 47.30% (SD = 1.51%) (Fig. 2)	EN

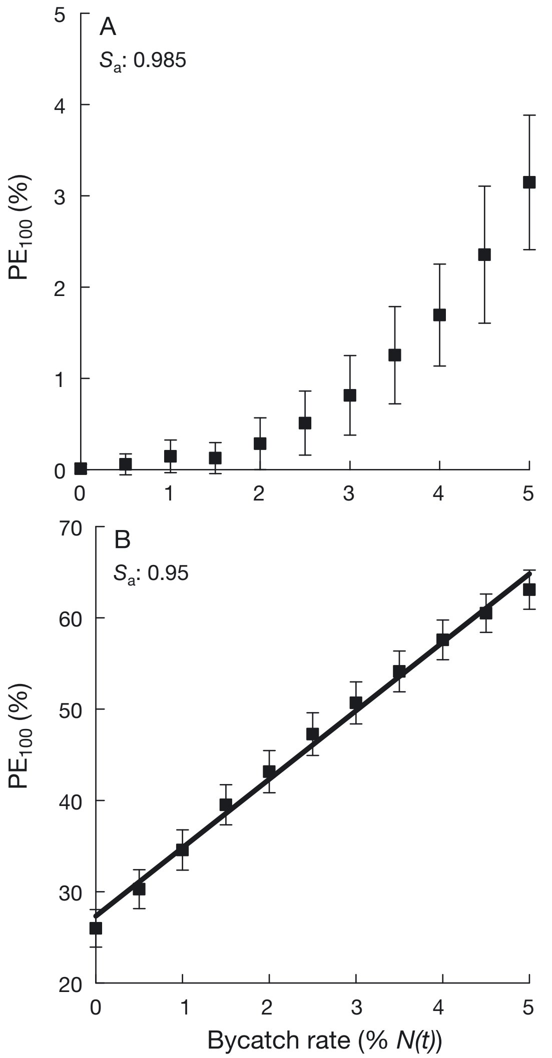

Fig. 5. Sensitivity test of *Sousa chinensis* population survival (measured using the probability of extinction in 100 yr, PE_{100}) impacted by varied intensities of bycatch (represented by % $N(t)$, where $N(t)$ is initial population size) at (A) S_a = 0.985 (Wang et al. 2012) and (B) S_a = 0.95 (undisturbed value assumed for most toothed cetaceans; Taylor et al. 2007)

rate for most toothed cetaceans; Taylor et al. 2007), a 1% increment of bycatch per annum raised PE_{100} by 7.5% (Fig. 5B).

The impact of habitat loss, represented by the percentage K_0 loss, affected population survival in a nonlinear pattern. At a low level of habitat loss, PE_{100} slowly increased for both $\bar{S}_a$ = 0.985 (Fig. 6A) and $\bar{S}_a$ = 0.95 (Fig. 6B). When the extent of habitat loss exceeded 50% K_0 loss, PE_{100} escalated rapidly and reached a hazardous level even at $\bar{S}_a$ = 0.985 (Fig. 6A).

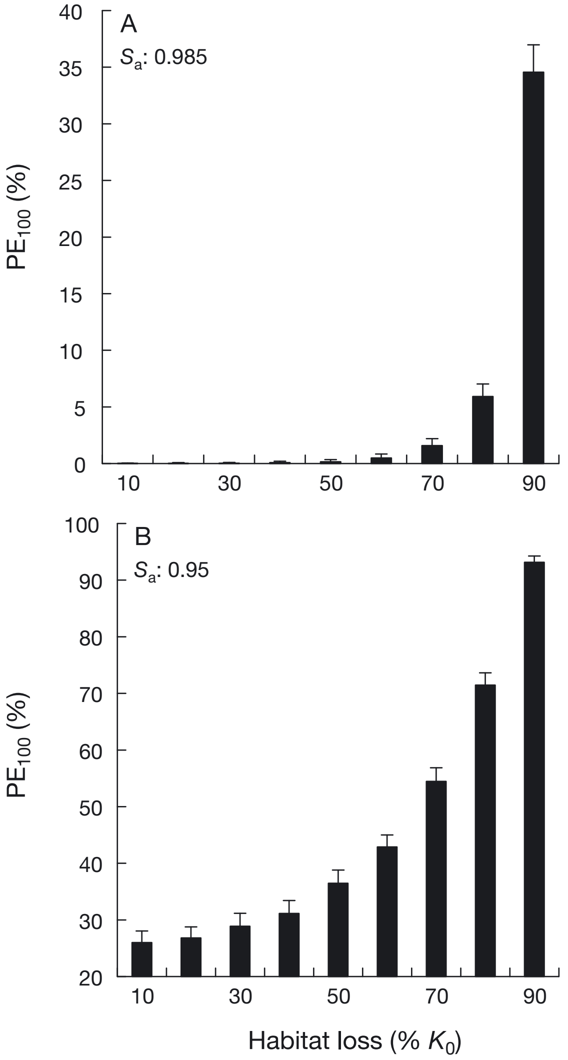

Fig. 6. Sensitivity test of population survival (measured with the probabilities of extinction in 100 yr, PE_{100}) at different extents of habitat-loss impact, presented as % of the initial carrying capacity (K_0); (A) S_a = 0.985 and (B) S_a = 0.95, where S_a is a non-calf survival rate

DISCUSSION

Factors affecting the results of trend projection and status assessment

The trajectory of population trend projections and, consequently, the predictions of extinction risk rely on the accuracy of demographic parameter estimates and the number and magnitude of different impacts included in a population model (Lacy 1993). The accuracy of demographic parameter estimates, in turn, depends on the accuracy of other estimates such as life-history parameters, age-specific survivorship and reproductive rates. Some of these parameters, however, such as the expected lifespan (A_x), age at maturity (A_m) and age-specific survivorship ($l(x)$), are currently not available for TWC humpback dolphins. To calculate these parameters, one would require access to a substantial number of stranded or bycaught specimens, the accumulation of which takes a long time even in substantially larger populations (Jefferson 2000, Jefferson et al. 2012, Mei et al. 2012). Such a representative number of specimens is unlikely to ever be available for the TWC humpback dolphins due to the very small population size.

Wang et al. (2012) claim that the non-calf survival rate ($\overline{S}_a$) of the TWC humpback dolphin approximates 0.985 with a very wide variation, from 0.832 to 0.998, which was the range applied in our study reported here. This $\overline{S}_a$ estimate, however, contradicts some earlier findings and should therefore be treated with caution. The TWC humpback dolphin population has been classified as CR under Criteria C2 and D of the IUCN Red List of Threatened Species (Reeves et al. 2008). This classification stipulates 'a continuing decline, observed, projected, or inferred, in numbers of mature individuals' (IUCN 2001, p. 18). In the case of $\overline{S}_a = 0.985$, however, as suggested by Wang et al. (2012), the TWC humpback dolphin population would actually be increasing with a moderate rate, $\overline{r} = 0.0256$ (SD = 0.006), equivalent to a 2.59% $N(t)$ increase per annum or a 75.44% $N(t)$ increase per generation (~22 yr). If the $\overline{S}_a$ estimate (0.985) indeed truly represents the non-calf survival rate, the TWC humpback dolphins should be viewed as highly resilient to anthropogenic impacts, especially fishery bycatch (Wade 1998). This inference contradicts the currently gathered evidence on the status of TWC humpback dolphins (Wang et al. 2007, Reeves et al. 2008, Ross et al. 2010, Slooten et al. 2013).

Recent demographic analysis for the Pearl River Estuary humpback dolphin population based on age-structure data reports a declining trend ($\overline{r} = -0.0245$; Huang et al. 2012b), indicating an S_a estimate far lower than 0.94 (W. C. Lam, unpubl. data) corresponding to the S_c estimate (0.61; Jefferson et al. 2012), which is comparable to many other cetacean populations under high anthropogenic pressure (Slooten et al. 1992, Stolen & Barlow 2003, Currey et al. 2009a,b). The real non-calf survival rate (or lower bound of the S_a estimate) for the TWC humpback dolphins is likely lower, possibly substantially lower than the 0.985 suggested by Wang et al. (2012).

Considering the extensive environmental degradation of the shallow-water coastal habitats off the TWC in recent decades due to land reclamation and exploitation of adjacent terrestrial environments (Huang et al. 2013), the actual rate of decline, risk of extinction and susceptibility to anthropogenic impacts such as bycatch and habitat loss are likely to be higher than the estimates presented here. As our analyses had to incorporate recently published estimates, the resulting PE estimates are affected by the evident imprecision of the earlier studies (Wang et al. 2012) and the real risk of extinction is likely to be more severe than our current models predict.

The accuracy of the trend projection and risk assessment presented here may be further affected by impacts of inbreeding, genetic drift and loss of genetic diversity in a small population (Souléa & Simberloff 1986, Lacy 1993, Mills & Smouse 1994, Sato & Harada 2008). A minimum population size, at least 250 adults (Shaffer 1981, Nunney & Campbell 1993) but usually up to thousands of adults (Harcourt 2002, Brito & Figueiredo 2003, Reed et al. 2003, Traill et al. 2007), is needed in mammals to resist the minimal level of stochastic genetic diversity loss. The current population size of TWC humpback dolphins (fewer than 100 animals; Wang et al. 2007, 2012, Yu et al. 2010), is substantially lower than the lowest predicted limit of at least 250 adults, and genetic exchange with neighboring populations, e.g. those off Xiamen and in the Pearl River Estuary, is unlikely (Wang et al. 2008). Therefore, applications of models that factor in genetic impacts, such as the VORTEX model (Lacy 1993), although currently not possible due to the lack of genetic data, would very likely generate predictions of higher extinction risks than those presented here.

Most demographic models assume constant environmental conditions where the extent of anthropogenic impacts and environmental stochasticity does not change over time (Lacy 1993, Caswell et al. 1999, Winship & Trites 2006). This, however, can hardly be the case under ever-increasing human pressures, such as off the TWC. Recent analyses indicate that the habitat quality of coastal waters inhabited by the TWC humpback dolphin has been substantially degraded in past decades (Huang et al. 2013), and there are no signs that this process is likely to come to a halt, let alone be reversed in the foreseeable future (Ross et al. 2010). The cumulative impacts of habitat destruction and alteration of coastal environments on dolphin ecology and survival across temporal scales remain little understood (e.g. Currey et al. 2009b, Mei et al. 2012). This is yet another reason for caution when considering the population trend predictions presented in this study, as the current analytical limitations have likely generated an overly optimistic projection.

Status and threats to the persistence of TWC humpback dolphins

Our study indicates that the status of humpback dolphins off the TWC can be classified as CR under 3 of the 5 IUCN criteria, A3b, C1 and D, although the average percentage of decline appears to be lower than the threshold: 80% of the original abundance within 3 generations (IUCN 2001). This classification does not contradict the current status under IUCN classification (Reeves et al. 2008); in fact, it provides a quantitative basis for such a classification and emphasizes the actual risk that the TWC humpback dolphins are currently facing. Under the assumed condition (S_c = 0.62, S_a = 0.832 − 0.998), more than 60% of the current population numbers may be lost in the next 3 generations (approximately 64 yr). This decline might be even higher with a non-calf survival rate lower than recently published S_a estimates. As all current and recent population estimates indicate a very small population size (Wang et al. 2007, 2012, Yu et al. 2010), such a drastic decline in numbers will place the TWC humpback dolphins under an ever-increasing risk of the effects of demographic and genetic stochasticity, with diminished resilience to anthropogenic impacts.

Direct mortality caused by fishery bycatch and vessel collisions can present real threats to the long-term persistence of a dolphin population (Wade 1998, D'agrosa et al. 2000, Dans et al. 2003, Read et al. 2006, Slooten et al. 2006, Cramer et al. 2008, Moore & Read 2008, Ross et al. 2010). Although Wade (1998) proposes the PBR calculation for marine mammals that defines the upper limit of tolerable incidental mortality, the calculation of PBR (2–4% abundance per annum) should not be directly applied to the TWC humpback dolphin population to define the upper tolerable bycatch removal. According to our simulations, there is a high probability that the TWC humpback dolphin population will decline even under the apparently most optimistic scenario and without factoring in the impacts of bycatch. With bycatch mortality included, even as low as 1% per annum, the decline of the population will escalate substantially. If the 2% PBR per annum was directly applied in the management plan of TWC humpback dolphins, not accounting for the ongoing population decline, we can anticipate a far greater drop in population numbers on time scales shorter than the projections presented in this study. Therefore, we postulate that a direct application of the PBR calculation in population management strategies without projecting the trend of the population concerned should be done with caution, even if this calculation appears to be numerically tolerable.

Unlike fishery bycatch or vessel collisions, which cause immediate mortality of impacted animals, the demographic consequences of habitat degradation are usually not obvious but are long-lasting and can be irreversible (Huang et al. 2012a). Impacts of coastal development activities, especially land reclamation (Huang et al. 2013), sand dredging and bottom trawling, have immediate effects by reducing the extent, integrity and quality of suitable habitats, and effectively reducing the habitat carrying capacity. Other indirect impacts, such as overfishing, which causes resource depletion (Bearzi et al. 2006, 2008, 2010, Piroddi et al. 2011), and pollutant accumulation, which functionally alters the plankton fauna and breaks down the energetic function of local ecosystems, may not cause immediate threats but cumulative impacts that may, over time, be irreversible (Huang et al. 2012a).

Although the scale of habitat loss simulated in our study, up to 90% of initial carrying capacity, may seem unreasonably high, it is likely to occur in a narrow strip of shallow-water coastal habitats. Off the TWC, as in various other locations inhabited by humpback dolphins, suitable habitat does not extend far offshore but along the shore and at times for hundreds of kilometers (Corkeron et al. 1997, Karczmarski et al. 1999, 2000, Parra et al. 2004, Ross et al. 2010, Yeh 2011). Alteration of such coastal environments through urban and industrial coastal developments, large-scale land reclamation or sand dredging can disrupt habitat continuity and integrity, fragmenting it to ever-smaller discontinuous patches (Huang et al. 2013). The carrying capacity of such a fragmented mosaic of patches is drastically reduced and can drop below 10% K_0. Consequently, the risk of local extinction in the fragmented habitats is high and increases with further decreases in patch size (e.g. Fig. 6). Severe habitat discontinuity with large-scale habitat loss, as off the Taiwan central west coast, may lead to population fragmentation (Chang 2011), likely escalating further the rate of population decline and increasing the risk of extinction.

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