APPLIED ISSUE

Common pattern of population decline for freshwater cetacean species in deteriorating habitats

SHIANG-LIN HUANG*,†, YUJIANG HAO*, ZHIGANG MEI*,‡, SAMUEL T. TURVEY§ AND DING WANG*

*Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China
†Department of Environmental Biology and Fishery Science, National Taiwan Ocean University, Keelung, Taiwan
‡Graduate School of Chinese Academy of Sciences, Beijing, China
§Institute of Zoology, Zoological Society of London, Regent's Park, London, U.K

SUMMARY

1. Freshwater cetacean species, including the baiji (*Lipotes vexillifer*), Amazon River dolphin (*Inia geoffrensis*), Ganges/Indus River dolphins (*Platanista* spp.) and Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*), apex predators in megariver ecosystems, face serious challenges owing to the deterioration of habitat quality.
2. We simulated population change of four freshwater cetacean species under increasing habitat deterioration. Carrying capacity (*K*) was used to represent the habitat quality, and a logistic model was used to describe the rate of habitat deterioration (*dK*).
3. An individual-based Leslie matrix model showed that population declines and extinctions in freshwater cetaceans under increasing habitat deterioration exhibit a consistent pattern irrespective of the initial level of *K* or population size. When *dK* is low, population abundance fluctuates stochastically around initial *K*, but a rapid increase in *dK* is accompanied by a sharp population decline, with a residual population ultimately declining continuously to extinction.
4. Simulations show that traditional census survey techniques used in cetacean species are unlikely to detect early signs of population decline before a critical level is reached.
5. Empirical data of the likely extinction of baiji strongly agree with our simulation exercise, implying that extinction of other freshwater cetacean species may occur sooner than previously considered. Hence, precautionary approaches for habitat restoration and landscape management should be implemented before freshwater cetacean population declines are detected, and ideally, before habitat quality begins to deteriorate.

Keywords: carrying capacity, extinction debt, habitat conservation, population viability analysis, power analysis, precautionary approach

Introduction

Freshwater cetacean species, including the Yangtze River dolphin or baiji (*Lipotes vexillifer* Miller, 1918), Amazon River dolphin (*Inia geoffrensis* Blainville, 1817), Ganges/Indus River dolphins (*Platanista* spp. Lebeck, 1801) and Yangtze finless porpoise [*Neophocaena asiaeorientalis asiaeorientalis* (Pilleri and Gihr, 1972)], apex predators in their freshwater ecosystems (Behera, 1995; Smith & Smith, 1998; Chaudhary, 2007), face serious challenges to their

long-term survival (Kreb *et al.*, 2010). Indeed, freshwater cetaceans are among the most threatened groups of vertebrates (Reeves, Smith & Kasuya, 2000), and most of these taxa are now classified as Endangered (EN) (Ganges/Indus River dolphins, Yangtze finless porpoise) or Critically Endangered (CR) (baiji) by IUCN (2011). Suitable river habitat for freshwater cetaceans, comprising megariver systems such as the Yangtze River (baiji, Yangtze finless porpoise), the Amazon River (Amazon River dolphin) and the Ganges–Brahmaputra and Indus

drainages (Ganges/Indus River dolphins), also provide food, water security and other ecosystem services for billions of people (Dudgeon, 2000; Lundberg *et al.*, 2000; Dudgeon *et al.*, 2006; Kreb *et al.*, 2010), and are experiencing escalating economic growth, urbanisation and human population growth. As freshwater cetaceans are high-profile taxa, their threatened status indicates the severe and increasing levels of habitat deterioration occurring in megarivers (Caro & O'Doherty, 1999; Carignan & Villard, 2002; Dudgeon *et al.*, 2006; Kreb *et al.*, 2010; Wang, Wei & Zou, 2011).

Freshwater cetaceans are threatened by proximal factors that drive unsustainable levels of direct mortality, such as fisheries by-catch and vessel collisions, and by distal factors that reduce the availability or quality of their freshwater habitat (Reeves *et al.*, 2000). Although the specific threats may vary geographically, common threats associated with deteriorating habitat quality include resource depletion, accumulation of pollutants, habitat degradation and flow modification (Reeves, Chaudhry & Khalid, 1991; Senthilkumar *et al.*, 1999; Braulik, 2006; Dudgeon *et al.*, 2006; Kreb *et al.*, 2010). The magnitude and long-term effects of habitat modification on freshwater cetacean populations are difficult to quantify, unlike direct mortalities associated with fisheries by-catch and vessel collisions (Wade, 1998; Kreb *et al.*, 2010; Raby *et al.*, 2011). Characteristics of cetacean life histories, notably their low intrinsic rate of increase and long lifespan (Taylor *et al.*, 2007a; Huang, Ni & Chou, 2008), suggest that populations may not respond instantly to environmental changes (Abrams, 2002). As a result, although it is clear that habitat deterioration is probably driving many populations to extinction, it has been difficult to define and quantify the causative relationships between habitat degradation and population declines of freshwater cetaceans (Hallam & Clark, 1981; Doak, 1995; Drake & Griffen, 2010). This difficulty has led to biases in conservation measures that are proposed for threatened freshwater cetaceans, with actions to mitigate direct mortality (e.g. from by-catch) often receiving considerably more attention than actions to reduce habitat deterioration or restore degraded cetacean habitats (Reeves *et al.*, 2003).

Implementing precautionary conservation in lieu of empirical evidence of population declines has become a fundamental standard for sound conservation management (Richards & Maguire, 1998; Thompson *et al.*, 2000). Indeed, delaying implementation of conservation action plans until population declines become evident is likely to lead to substantial loss of the original populations (Taylor & Gerrodette, 1993; Thompson *et al.*, 2000). However, there is little comparable understanding of the relationship between delaying habitat conservation and loss of habitat quality. In practice, scientific demonstration of the existence of habitat deterioration is still regularly requested by policy makers, stakeholders and many scientists, which imposes substantial delays for minimising or reversing habitat loss. Such delays may have catastrophic consequences where habitat disturbance continues to increase, such as in areas with rapid population growth and urbanisation, a situation typical of the megariver systems containing threatened freshwater cetaceans (Kreb *et al.*, 2010).

The fluctuation of habitat carrying capacity (K), which defines the upper bound of fluctuation in a given population (Lacy, 1993; Lande, 1993), often corresponds to habitat quality (Gibson, 1994; Luo *et al.*, 2001; Thomas *et al.*, 2001; Griffen & Drake, 2008) and has an immediate effect on population sustainability (Lacy, 1993; Hilderbrand, 2003; Griffen & Drake, 2008). In regions of increasing anthropogenic disturbance, deterioration of habitat quality usually accompanies the accelerating decline of K (Clausen & York, 2008; Wang *et al.*, 2011; Xiao & Duan, 2011). Analysing the process of population decline under a scenario of an accelerating decline of K will provide an essential baseline, providing a quantitative basis for precautionary habitat conservation. However, this method has not yet been explored for threatened freshwater cetaceans. Our study simulates population fluctuation in freshwater cetacean populations under different scenarios of accelerating decline of K to elucidate the effects of deteriorating habitat quality on population declines.

Methods

Power analysis: the lower threshold of detectable population decline

Power analysis shows that the power of census surveys to detect a declining trend depends upon the rate of population change (r), the length/span of the available time-series of census data and the coefficient of variation (CV) in the population abundance estimate (Gerrodette, 1987; Taylor & Gerrodette, 1993; Thompson *et al.*, 2000; Taylor *et al.*, 2007b; Huang *et al.*, 2012). For populations that are being surveyed on an annual basis, the lowest time period (T_d) necessary to detect a population decline will be

$$r^2 T_d^3 \geq 156\,CV^2 \text{ (Thompson et al., 2000)}$$

or

$$T_d \geq 5.38\,CV^{\frac{2}{3}}\,r^{-\frac{2}{3}}. \qquad (1)$$

Under Criterion A2-4 of the IUCN Red List Categories and Criteria Version 3.1, populations are assigned to one of the three threatened categories [Vulnerable (VU), EN, CR] if the rate of decline exceeds 30% (VU), 50% (EN) or 80% (CR) of original population abundance within three generations (IUCN, 2001). For freshwater cetaceans, three generations represent an interval of *c.* 30 years (Taylor *et al.*, 2007a). We therefore selected values of *r* that will result in a 30, 50 and 80% decline of abundance within 30 years ($r = -0.012$, -0.023 and -0.054, respectively). We then calculated T_d values under a range of different values of CV from 10 to 100% using the number $r = -0.012$, -0.023 and -0.054 represent the rate of decline reaches 30%, 50% and 80% within three generations of freshwater cetaceans, corresponding to VU (vulnerable), EN (endangered) and CR (critically endangered) status under Criterion A2-4 (IUCN, 2001). In other words, for $0 < r < -0.012$ (% decline within three generations = 0–30%), the status is NT (near threatened), for $-0.012 \leq r < -0.023$, (% decline = 30–50%) the status is VU, for $-0.023 \leq r < -0.054$, (% decline = 50–80%), the status is EN, and for $r \leq -0.054$, (% decline $\geq$ 80%), the status is CR, under Criterion A2-4.

Accordingly, the three number of *r*, $r = -0.012$, -0.023 and -0.054, represent the cut-off lines that distinguish the four different status (NT, VU, EN and CR).

The detectable population decline (*D*) was defined by an exponential model as

$$D = 1 - \exp(r \times T_d). \tag{2}$$

Our values of *D* were calculated using different combinations of our chosen values of *r* and CV. Finally, we used the median of *D* between $r = -0.012$ and -0.054 at CV = 10% as the lowest threshold of detectable population decline (D_{min}).

Demographic parameters and population trend modelling

We collected life-history parameters for four freshwater cetacean taxa (Amazon River dolphin, baiji, Ganges/Indus River dolphins and Yangtze finless porpoise), including age at female maturation (Am in years), reproductive (interbirth) interval (RI in years) and longevity or oldest age of reproducing females (Ax in years), from the published literature (Table 1). Direct values of RI for baiji and Ganges/Indus River dolphins are not known; we assumed a value of 2 years with a variance of 25%, following available reproductive data (12-month gestation period and subsequent 6- to 18-month lactation period) for other phylogenetically and/or ecologically similar cetacean species (Amazon River dolphin, franciscana *Pontoporia blainvillei*, Irrawaddy dolphin *Orcaella brevirostris*, and tucuxi *Sotalia fluviatilis*; Brownell, 1984; Liu, 1988; Rosas & Monteiro-Filho, 2002; Taylor *et al.*, 2007a; Huang *et al.*, 2008). We incorporated uncertainty for all life-history parameters used in this study by randomly resampling relevant parameters (LHP(*i*), where *i* = the *i*th iteration) between their upper (LHP$_u$) and lower (LHP$_l$) limits:

$$LHP(i) = LHP_l + (LHP_u - LHP_l) \times \sigma \tag{3}$$

where σ was a random number ranging between 0 and 1 that was generated using the MATLAB function (rand) in MATLAB 7.0 (Mathworks, 2005). We also incorporated uncertainty about survival rates, including survival both in first-year calves (S_c) and in animals older than 1 year (S_a), by randomly adjusting S_c from 0.60 to 0.85 and solving S_a with a given value of the instantaneous rate of population growth (*r*).

We used an individual-based Leslie matrix model that further incorporates demographic stochasticity into

Table 1 Life-history parameters for four freshwater cetacean species, including age at maturation (Am in years), reproductive interval (RI in years) and longevity or oldest age of reproducing females (Ax in years). As direct measures of RI for baiji and Ganges/Indus River dolphin are not known, we assumed a value of 2 years with a variance of 25%, following available reproductive data (12-month gestation period and subsequent 6- to 18-month lactation period) for other phylogenetically and/or ecologically similar cetacean species

Species	Am	RI	Ax	Source
Baiji (*Lipotes vexillifer*)	6	2 (±25% CV)	24.5–33	Taylor *et al.* (2007a); Huang *et al.* (2008)
Amazon River dolphin (*Inia geoffrensis*)	5–6	1.25–3	18–28	Brownell (1984); Best & da Silva (1989); Taylor *et al.* (2007a)
Ganges/Indus River dolphin (*Platanista* spp.)	9	2 (±25% CV)	28–29.5	Brownell (1984); Taylor *et al.* (2007a); Huang *et al.* (2008)
Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*)	4.5–5.5	1.41–1.43	18–21	Zhang (1992); Gao & Zhou (1993); Zhang & Wang (1999); Hao *et al.* (2007); Huang *et al.* (2008)

CV, coefficient of variation.

abundance fluctuation (Slooten, Fletcher & Taylor, 2000; Currey, Dawson & Slooten, 2009a; Huang *et al.*, 2012) to examine population trends under deteriorating habitat over 100 years. The initial population structure was defined at $\bar{r} \approx 0.04$, based on studies of undisturbed cetacean populations (Wade, 1998; Stolen & Barlow, 2003; Moore & Read, 2008). We set the initial population abundance, N_0, to equal the initial carrying capacity, K_0, that ranged randomly between 100 and 5000 animals. A density-dependent effect was introduced to r using $r(t) = rN(1 - N/K)$, to further determine the survival rates for a given year. To avoid having values of $r(t)$ decline to an unreasonably low level, we defined the lower boundary of $r(t)$ at -0.20. We ran the individual-based modelling according to the following process (Slooten *et al.*, 2000; Currey *et al.*, 2009a; Huang *et al.*, 2012):

1. An individual survived from age x at year t to age $x + 1$ at year $t + 1$ whenever the random number σ that ranges between 0 and 1 exceeded the mortality rate (1- survival rate, either S_c or S_a depending on the stage). To factor in environmental stochasticity, we added 10% CV of survival rate, either positively or negatively, in defining mortality rate (Lacy, 1993; Thompson *et al.*, 2000; Currey *et al.*, 2009a,b). When $\sigma \leq$ mortality rate, the individual was interpreted as having died; otherwise, it survived.

2. A female that survived to the next year was determined to give birth when $\sigma \leq 1/RI_i$.

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.

We ran 500 simulation replications for each freshwater cetacean species. Each replication used different starting values of K_0, randomly selected between 100 and 5000 animals, and ran 5000 iterations. To make the results comparable between replications with different values of K_0 and between different species, we calculated values for the relative abundance and carrying capacity as $N(t)/K_0$ (relative abundance) and $K(t)/K_0$ (relative carrying capacity), where $N(t)$ and $K(t)$ were the abundance and habitat carrying capacity of freshwater cetaceans at year t. We defined the first point when $N(t)/K_0 \leq 0.95$ as representing the starting point of the population decline; $N(t)/K_0 \leq (1 - D_{\min})$ as representing the point when the population decline became detectable; and $K(t)/K_0 \leq 0.05$ as representing the end-point of habitat deterioration.

Deterioration of habitat quality

We described habitat deterioration according to the change in habitat carrying capacity (K) by the model:
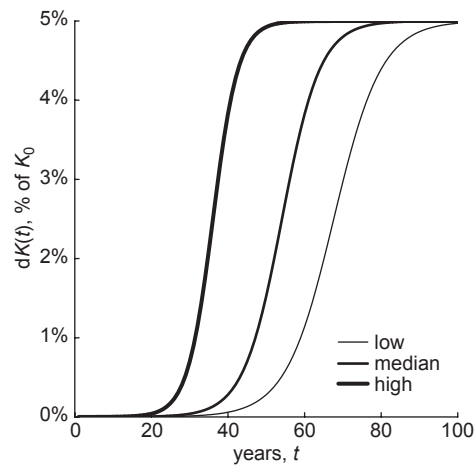

Fig. 1 Rates of habitat deterioration, represented by the rate of decline in carrying capacity, $dK(t)$, using the logistic function. Low rate: $dK(t)$ reaches ceiling value within 100 years; medium rate: $dK(t)$ reaches ceiling value within 80 years; high rate: $dK(t)$ reaches ceiling value within 50 years.

$$K(t + 1) = K(t) - dK(t) \times K_0, \qquad (4)$$

where $dK(t)$ is the rate of decline in K per year. A logistic function was used to describe $dK(t)$,

$$dK(t) = \frac{0.05 \times d_0 \times \exp(\delta \times t)}{0.05 + d_0 \times (\exp(\delta \times t) - 1)}, \qquad (5)$$

where d_0 was defined as 1×10^{-6} to allow $dK(t)$ to start from close to zero. As t increases, $dK(t)$ approaches the asymptotic value (or ceiling) of 5% of K_0 per year. We varied the values of δ to allow $dK(t)$ to reach this ceiling value within 100 years, 80 years and 50 years, corresponding to low, medium and high levels of habitat deterioration, respectively (Fig. 1). Means ($\pm$SD) of $dK(t)$ were calculated under low, medium and high levels of habitat deterioration for the four freshwater cetacean species for the following three situations: the point at which each population starts to decline ($N(t)/K_0 \leq 0.95$); the point at which population decline becomes detectable in the field ($N(t)/K_0 \leq (1 - D_{\min})$); and the end-point of habitat deterioration ($K(t)/K_0 \leq 0.05$.)

Results

Detectable population decline

Under a low CV of abundance estimates (CV = 10%), at least 8–9 years of time-series abundance data are needed for detecting the population decline that meets the
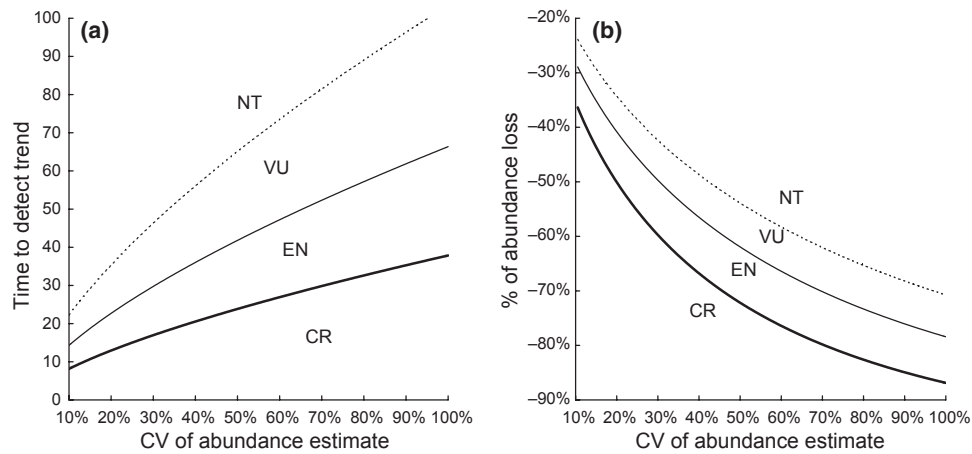
Fig. 2 (a) Time needed to detect population decline by periodic census investigation; (b) % of abundance loss when abundance declines becomes detectable at different levels of abundance estimate CV. Cut-off lines represent the boundary conditions (r = −0.012, −0.023 and −0.054, top-down respectively) meeting the classifications of Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) status under IUCN Criterion A2-4, where population decline is higher than 30% (VU), 50% (EN) or 80% (CR) of initial abundance within three generations for freshwater cetaceans (IUCN, 2001).

classification of CR status ($r \leq -0.054$, Fig. 2a). A higher abundance estimate CV or lower rate of population decline requires longer time-series of census data, up to 56 years at CV = 40%, to detect population decline meeting the classification of VU ($r \leq -0.012$, Fig. 2a). By the time that population decline is first detected, the initial population will already have declined by between 23.9% (at rate of decline meeting VU status) and 36.4% (at rate of decline meeting CR status) at 10% of abundance estimate CV, and between 48.7% (at rate of decline meeting VU status) and 66.8% (at rate of decline meeting CR status) at 40% of abundance estimate CV (Fig. 2b). We therefore defined the D_{min} = 30%, the median of D between VU and CR status at 10% of abundance estimate CV, as the lowest threshold of detectable population decline.

Characteristics of population decline

Patterns of population change under low, medium and high levels of habitat deterioration show a consistent pattern across the four cetacean species (Fig. 3). When $dK(t)$ is low, population abundance fluctuates stochastically near K_0 until the tipping point when population starts to decline ($N(t)/K_0 \leq 0.95$). Population abundance decline becomes obvious when $dK(t)$ increases to 0.77% (SD 0.02%), 0.97% (SD 0.04%) and 1.42% (SD 0.08%) of K_0 under low, medium and high levels of habitat deterioration, respectively (Fig. 3). By the time that population decline becomes detectable in the field ($N(t)/K_0 \leq (1 - D_{min}) = 0.70$ or less), $dK(t)$ has increased to 3.15% (SD 0.40%), 3.43% (SD 0.47%) and 4.29% (SD 0.73%) under low, medium and high levels of habitat deteriora-

tion, representing four to seven decades (depending on the level of habitat deterioration) since habitat quality first started to deteriorate (Fig. 3). Even after the end-point of habitat deterioration is reached ($K(t)/K_0 \leq 0.05$), a residual population of cetaceans remains under all scenarios and for all cetacean species, with a residual abundance of 11.5% (SD 1.74%) K_0, but which declines continuously towards extinction within another 20 years (Fig. 3).

Discussion

Integrating trends in population abundance change with long-term environmental data, especially data on anthropogenic activities, provides an empirical base to quantify the relationships between habitat deterioration and population persistence (as in Currey *et al.*, 2009b), whilst allowing for the calibration of theoretical models to fit real-world situations. However, the current techniques of census investigation used for cetacean populations, either mark–recapture analysis by individual photo-ID histories (Reisinger & Karczmarski, 2010; Mansur, Strindberg & Smith, 2011) or systematic transect-line investigation (Vidal *et al.*, 1997; Dawson *et al.*, 2008; Zhao *et al.*, 2008; Chen *et al.*, 2010), lack statistical power to reveal population trends within relatively short time-frames (Taylor & Gerrodette, 1993; Taylor *et al.*, 2007b; Huang *et al.*, 2012). Furthermore, systematic census surveys are seldom implemented across the entire geographical range of a population until declines become apparent, and are often associated with an increase in conservation awareness, as demonstrated in the recent history of baiji conservation research (Wang *et al.*, 2006). Moreover, standard
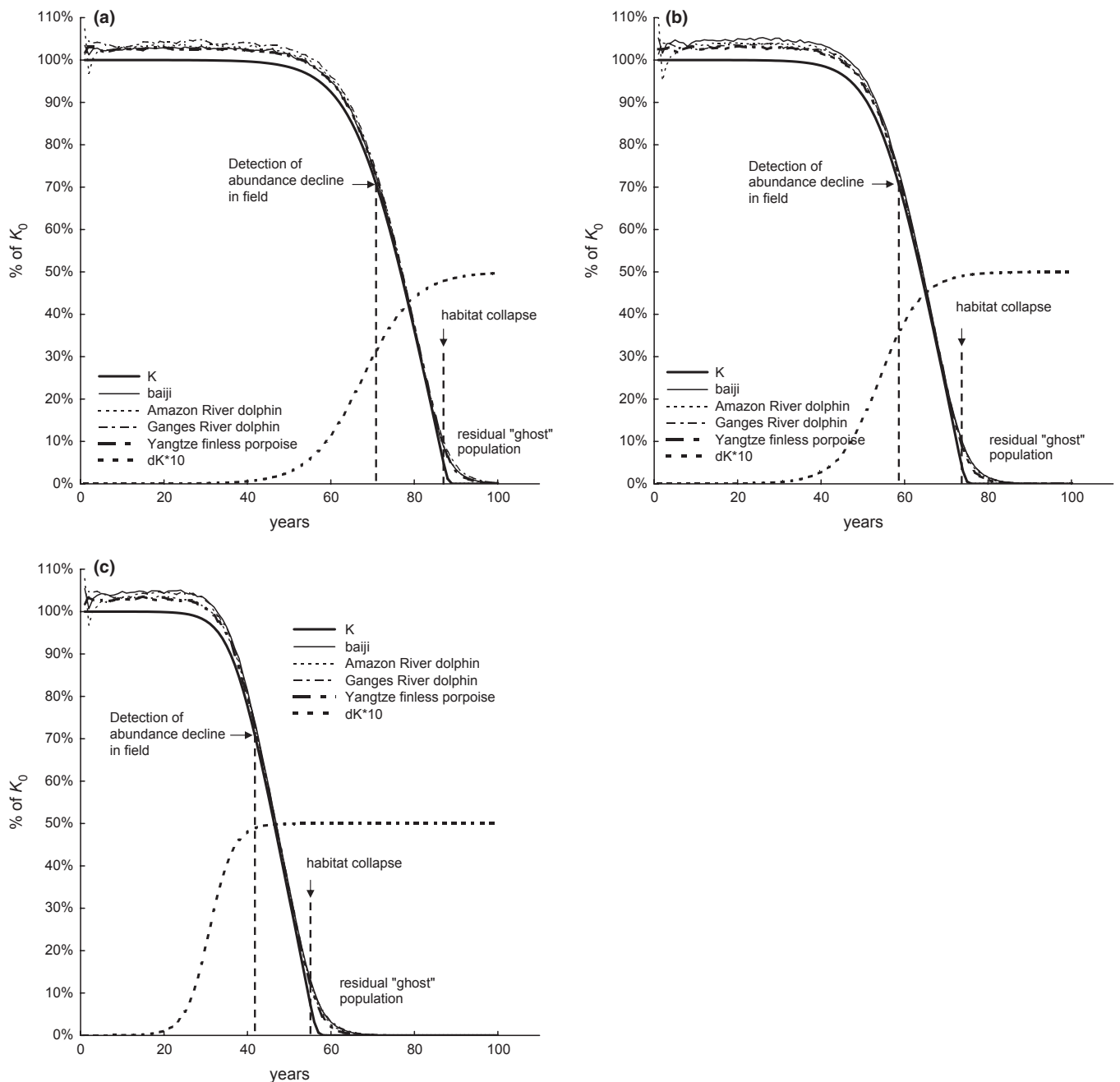
Fig. 3 Relative abundance of four freshwater cetacean species (—— baiji, ---- Amazon River dolphin, -·-· Ganges/Indus River dolphins, – ·– Yangtze finless porpoise), relative environmental carrying capacity (*K*) and rate of habitat deterioration (*dK*), represented in % of K_0 at year *t* (note that *dK* is multiplied by 10), under (a) low, (b) medium and (c) high scenarios of habitat deterioration. The dates when population declines become detectable ($N(t)/K_0 \leq 70\%$) and when habitat quality collapses ($K(t)/K_0 \leq 0.05$) are indicated.

monitoring of environmental data corresponding to anthropogenic activities in megariver systems containing freshwater cetaceans is rarely implemented before conservation concerns are raised. Consequently, analysis of correlations between long-term data sets of population trends and human-driven environmental change is not feasible for understanding freshwater cetacean declines.

Our theoretical modelling exercise provides therefore a precautionary warning before the empirical relationship between population decline and habitat deterioration is fully understood.

Our analyses support the conjecture that habitat deterioration is one of the major concerns for the long-term persistence of many freshwater cetacean populations,

especially for populations impacted by intense anthropogenic activities. It is possible that the real pattern of $dK(t)$ may not follow a logistic model, and the ceiling value of 5% K_0 for $dK(t)$ used in our models may be too high. However, using alternative (linear, exponential, logarithmic or allometric) model forms for $dK(t)$ only affects the point when the population starts to fluctuate downward, but does not alter the trajectory or patterns towards extinction once the decline phase begins. Conversely, a lower ceiling value of $dK(t)$ does not change the extinction trajectory, but only delays the point when the population begins to decline towards extinction. As long as $dK(t)$ keeps increasing, population extinction is inevitable.

Population decline may not be as drastic as our simulations suggest if $dK(t)$ remains low and constant rather than increasing. However, this alternative scenario does not reflect the ecological reality of a rapidly developing world. The decline of K in river systems does not result from a single factor, but is the combined and cumulative result of multiple anthropogenic factors, such as pollutant accumulation, resource depletion and habitat loss (Dudgeon, 2000; Dudgeon *et al.*, 2006; Zhao *et al.*, 2008; Kreb *et al.*, 2010). Although some components of habitat deterioration may be reversible in the short-to-medium term (e.g. environmentally degradable pollutants; Chevé, 2000), other components can only be addressed over the long term or may be irreversible (e.g. habitat loss from land reclamation and bioaccumulative pollutants). Moreover, many of these factors are closely correlated with exponentially increasing economic and human population growth (Chevé, 2000; Bearzi, Holcer & di Sciara, 2004; Bearzi *et al.*, 2010; Piroddi *et al.*, 2011; Wang *et al.*, 2011). The pattern of $dK(t)$ is highly likely to increase with time, and our model of rapid decline and extinction of freshwater cetacean populations is likely to be a characteristic of regions experiencing similar rapid economic growth and urbanisation, but without corresponding levels of compensatory environmental protection. Indeed, under conditions where cetacean populations are threatened by both habitat deterioration and direct mortality from proximal threats (e.g. incidental fisheries by-catch, vessel collisions), we anticipate more rapid population declines.

Our simulations of population decline under deteriorating habitat quality may provide further precautionary insights for conservation management of freshwater cetaceans. When accumulated levels of habitat deterioration are still low ($\sum dK(t) \leq 0.05$), the effect of increasing demographic stochasticity on population fluctuation is much more significant than on habitat deterioration. Population status during this phase may appear stable, but is actually experiencing a slow decline (Fig. 3). In our simulation, the status transition from apparently stable to sharp decline can happen within a decade under a scenario of increasing habitat deterioration. Standard census surveys in cetacean populations, however, can only detect a rate of population decline higher than 5% abundance per annum within a decade of investigation efforts (Taylor & Gerrodette, 1993), corresponding to the classification of EN status under Criterion A2-4 (IUCN, 2001; Wilson, Kendall & Possingham, 2011). Standard periodic census surveys are therefore unlikely to detect early signs of population declines in freshwater cetacean species related to habitat deterioration. Furthermore, by the time population declines become detectable, habitat quality has likely become substantially degraded and the rate of habitat deterioration has reached a harmful level. Therefore, delaying conservation action plans may result in difficulties to restore habitat quality and reverse a decline.

In our simulations, final population extinction occurs substantially later than the collapse of habitat quality. A residual population representing *c.* 10–12% of K_0 still persists even after habitat K has declined to 5% K_0 (Fig. 3), forming the temporary persistence of a residual 'ghost population', which eventually becomes extinct. Similar patterns of residual population persistence have been demonstrated in other long-lived taxa, representing examples of extinction debt and the future ecological cost of current habitat destruction (e.g. Tilman *et al.*, 1994; Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009). A delayed response of population decline to habitat deterioration can occur even earlier, when $dK(t)$ declines to below *c.* 20% of K_0 (Fig. 3), irrespective of freshwater cetacean species or level (δ) of habitat deterioration. A 20% value of K_0 can still represent a relatively large number of individuals if the original value of K_0 is large (e.g. more than 2500 animals, such as the 1980–1990s population estimate for the Yangtze finless porpoise; Zhang *et al.*, 1993), and above the population size threshold for EN or CR status under Criterion *D* (i.e. <250 (EN) or 50 (CR) adults in the population; IUCN, 2001). Census surveys during this period may underestimate threat status and future extinction date, which may delay the implementation of necessary conservation measures. Moreover, populations may become increasingly fragmented during this phase and may persist in so-called population hotspots identified by standard survey techniques (e.g. Zhang *et al.*, 2003; Braulik *et al.*, 2005; Zhao *et al.*, 2008). However, these 'hotspots' may not represent optimal natural habitat conditions, but may simply be areas that are less affected by anthropogenic activity. Although successful conservation interventions may still be carried

out (Kuussaari *et al.*, 2009), conservation efforts on the residual 'ghost' populations can be challenging if only traditional census survey data are adopted and conservation efforts focus only on supposed hotspots.

The recent rapid decline and probable extinction of the baiji (Turvey *et al.*, 2007, 2010a,b) demonstrates the speed with which widely distributed freshwater cetacean populations can become extinct. Although the majority of known baiji deaths were associated with incidental by-catch in fishing gear (Zhang *et al.*, 2003; Turvey *et al.*, 2007), the Yangtze River drainage has also experienced a progressive decline in habitat quality and availability during recent decades, associated with pollution, overfishing, flow regulation, resource extraction, sedimentation, escalating overpopulation and industrialisation (Wang *et al.*, 2006, 2011; Dudgeon, 2010). It is certain that habitat deterioration as well as direct mortality contributed to the decline of both the baiji and other components of the river's vertebrate megafauna (Turvey *et al.*, 2010a). Indeed, recent analysis of baiji last-sighting records provides evidence for a final remnant 'ghost' population of baiji that persisted across the species' range until shortly before final disappearance of the species, consistent with the predictions of our simulations (Turvey *et al.*, 2010b). Although the extinction of the baiji and decline of the Yangtze finless porpoise have been relatively well documented, and other freshwater cetacean species may experience similar threats from rapidly deteriorating environmental quality (Reeves *et al.*, 1991; Best & da Silva, 1993; Reeves & Chaudhry, 1998; Smith & Smith, 1998; Dudgeon, 2000; Smith *et al.*, 2001; Martin, da Silva & Salmon, 2004; Braulik, 2006; Dudgeon *et al.*, 2006; Kreb *et al.*, 2010), robust demographic or associated environmental data are generally lacking, making interpretations of population change difficult. Our results provide a strong warning that there may be little time left to protect these highly threatened cetacean species and that the development of appropriate habitat restoration and landscape management action plans should not wait for robust data. Effective conservation measures are urgently needed for these species, not only at the population level but also at the ecosystem level. We also emphasise that the precautionary approach to habitat conservation should be adopted before signs of population and habitat loss are apparent in order to develop effective conservation programmes for freshwater cetaceans and other species.

Acknowledgments

References

Abrams P.A. (2002) Will small population sizes warn us of impending extinctions? *American Naturalist*, **160**, 293–305.

Bearzi G., Agazzi S., Gonzalvo J., Bonizzoni S., Costa M. & Petroselli A. (2010) Biomass removal by dolphins and fisheries in a Mediterranean Sea coastal area: do dolphins have an ecological impact on fisheries? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 549–559.

Bearzi G., Holcer D. & di Sciara G.N. (2004) The role of historical dolphin takes and habitat degradation in shaping the present status of northern Adriatic cetaceans. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14**, 363–379.

Behera S.K. (1995) *Studies on Population Dynamics, Habitat Utilization and Conservation Aspects of Gangetic Dolphin (Platanista gangetica) in a Stretch of Ganga River from Rishekesh to Kanpur*. PhD Thesis, School of Studies in Zoology, Jiwaji University, Gwalior.

Best P.B. & da Silva V.M.F. (1989) Amazon river dolphin, Boto, *Inia geoffrensis* (de Blainville, 1817). In: *Handbook of Marine Mammals* (Eds S.M. Ridgway & R.J. Harrison), pp. 1–23. Academic Press Limited, UK.

Best R.C. & da Silva V.M.F. (1993) *Inia geoffrensis*. *Mammalian Species*, **426**, 1–8.

Braulik G.T. (2006) Status assessment of the Indus River dolphin, *Platanista gangetica minor*, March–April 2001. *Biological Conservation*, **129**, 579–590.

Braulik G.T., Reeves R.R., Wang D., Ellis S., Wells R.S. & Dudgeon D. (2005) *Report of the workshop on conservation of the baiji and Yangtze finless porpoise*. World Conservation Union, Gland, Switzerland.

Brownell R.L. Jr (1984) Review of reproduction in platanistid dolphins. *Report of the International Whaling Commission*, (Special Issue), **6**, 149–158.

Carignan V. & Villard M.-A. (2002) Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment*, **78**, 45–61.

Caro T.M. & O'Doherty G. (1999) On the use of surrogate species in conservation biology. *Conservation Biology*, **13**, 805–814.

Chaudhary S. (2007) *Status of, and Threats to, the Ganges River Dolphin (Platanista gangetica) in the Koshi River, Nepal*. Unpublished MSc Thesis, University of Klagenfurt, Austria.

Chen T., Hung S.K., Qiu Y., Jia X. & Jefferson T.A. (2010) Distribution, abundance, and individual movements of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, China. *Mammalia*, **74**, 117–125.

Chevé M. (2000) Irreversibility of pollution accumulation. *Environmental and Resource Economics*, **16**, 93–104.

Clausen R. & York R. (2008) Economic growth and marine biodiversity: influence of human social structure on decline of marine trophic levels. *Conservation Biology*, **22**, 458–466.

Currey R.J.C., Dawson S.M. & Slooten E. (2009a) An approach for regional threat assessment under IUCN Red List criteria that is robust to uncertainty: the Fiordland bottlenose dolphins are critically endangered. *Biological Conservation*, **142**, 1570–1579.

Currey R.J.C., Dawson S.M., Slooten E., Schneider K., Lusseau D., Boisseau O.J. *et al.* (2009b) Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: an information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 658–670.

Dawson S., Wade P., Slooten E. & Barlow J. (2008) Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. *Mammal Review*, **38**, 19–49.

Doak D.F. (1995) Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology*, **9**, 1370–1379.

Drake J.M. & Griffen B.D. (2010) Early warning signals of extinction in deteriorating environments. *Nature*, **467**, 456–459.

Dudgeon D. (2000) Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience*, **50**, 793–806.

Dudgeon D. (2010) Requiem for a river: extinctions, climate change and the last of the Yangtze. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 127–131.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.-I., Knowler D.J., Lévêque C. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Gao A. & Zhou K. (1993) Growth and reproduction of three populations of finless porpoise, *Neophocaena phocaenoides*, in Chinese waters. *Aquatic Mammals*, **19**, 3–12.

Gerrodette T. (1987) A power analysis for detecting trends. *Ecology*, **68**, 1364–1372.

Gibson R.N. (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research*, **32**, 191–206.

Griffen B.D. & Drake J.M. (2008) Effects of habitat quality and size on extinction in experimental populations. *Proceedings of the Royal Society, Series B: Biological Science*, **275**, 2251–2256.

Hallam T.G. & Clark C.E. (1981) Non-autonomous logistic equations as models of populations in a deteriorating environment. *Journal of Theoretical Biology*, **93**, 303–311.

Hanski I. & Ovaskainen O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666–673.

Hao Y., Chen D., Zhao Q. & Wang D. (2007) Serum concentrations of gonadotropins and steroid hormones of *Neophocaena phocaenoides asiaeorientalis* in middle and lower regions of the Yangtze River. *Theriogenology*, **67**, 673–680.

Hilderbrand R.H. (2003) The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation*, **110**, 257–266.

Huang S.-L., Karczmarski L., Chen J., Zhou R., Lin W., Zhang H. *et al.* (2012) Demography and population trends of the largest population of Indo-Pacific humpback dolphins. *Biological Conservation*, **147**, 234–242.

Huang S.-L., Ni I.-H. & Chou L.-S. (2008) Correlations in cetacean life history traits. *The Raffles Bulletin of Zoology*, (Supplement), **19**, 285–292.

IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1.* IUCN Species Survival Commission, IUCN, Gland, Switzerland and Cambridge, UK. ii + 30 p.

IUCN (2011) *IUCN Red List of Threatened Species. Version 2011.1.* Available at: http://www.iucnredlist.org [Accessed October 7, 2011].

Kreb D., Reeves R.R., Thomas P.O., Braulik G.T. & Smith B.D. (Eds). (2010) *Establishing protected areas for Asian freshwater cetaceans: freshwater cetaceans as flagship species for integrated river conservation management*, *Samarinda, 19–24 October 2009*. Final Workshop Report. Yayasan Konservasi RASI, Samarinda, Indonesia, 166 pp. ISBN: 978-602-97677-0-4.

Kuussaari M., Bommarco R., Heikkinen R.K., Helm A., Krauss J., Lindborg R. *et al.* (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, **24**, 564–571.

Lacy R.C. (1993) VORTEX: a computer simulation model for population viability analysis. *Wildlife Research*, **20**, 45–65.

Lande R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911–927.

Liu R. (1988) Study on the regularity of reproduction in *Lipotes*. *Aquatic Mammals*, **14**, 63–68.

Lundberg G., Kottelat M., Smith G.R., Stiassny M.L.J. & Gill A.C. (2000) So many fishes, so little time: an overview of recent ichthyological discovery in continental waters. *Annals of the Missouri Botanical Gardens*, **87**, 26–62.

Luo J., Hartman K.J., Brandt S.B., Cerco C.F. & Rippetoe T.H. (2001) A spatially-explicit approach for estimating carrying capacity: an application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *Estuaries and Coasts*, **24**, 545–556.

Mansur R.M., Strindberg S. & Smith B.D. (2011) Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. *Marine Mammal Science*, doi: 10.1111/j.1748-7692.2011.00520.x.

Martin A.R., da Silva V.M.F. & Salmon D.L. (2004) Riverine habitat preferences of botos (*Inia geofferensis*) and tucuxis (*Stolia fluviatilis*) in the central Amazon. *Marine Mammal Science*, **20**, 189–200.

Mathworks (2005) *MATLAB. The Language of Technical Computing*. MathWorks Inc., Massachusetts, USA.

Moore J.E. & Read A.J. (2008) A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecological Applications*, **18**, 1914–1931.

Piroddi C., Bearzi G., Gonzalvo J. & Christensen V. (2011) From common to rare: the case of the Mediterranean common dolphin. *Biological Conservation*, **144**, 2490–2498.

Raby G.D., Colotelo A.H., Blouin-Demers G. & Cooke S.J. (2011) Freshwater commercial bycatch: an understated conservation problem. *BioScience*, **61**, 271–280.

Reeves R.R. & Chaudhry A.A. (1998) Status of the Indus river dolphin, *Platanista minor*. *Oryx*, **32**, 35–44.

Reeves R.R., Chaudhry A.A. & Khalid U. (1991) Competing for water on the Indus plain: is there a future for Pakistan's river dolphins? *Environmental Conservation*, **18**, 341–350.

Reeves R.R., Smith B.D., Crespo E.A. & Notarbartolo Di Sciara G. (2003) *Dolphins, Whales and Porpoises: 2002–2010 Conservation Action Plan for the World's Cetaceans*. IUCN/SSC Cetacean Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. ix + 139 p.

Reeves R.R., Smith B.D. & Kasuya T. (Eds) (2000) *Biology and conservation of freshwater cetaceans in Asia*. IUCN SSC Occasional Paper 23. IUCN, Gland and Cambridge.

Reisinger R.R. & Karczmarski L. (2010) Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. *Marine Mammal Science*, **26**, 86–97.

Richards L.J. & Maguire J.-J. (1998) Recent international agreements and the precautionary approach: new directions for fisheries management science. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1545–1552.

Rosas F.C.W. & Monteiro-Filho E.L.A. (2002) Reproductive parameters of *Pontoporia blainvillei* (Cetacea, Pontoporiidae), on the coast of Sao Paulo and Parana States, Brazil. *Mammalia*, **66**, 231–245.

Senthilkumar K., Kannan K., Sinha R.K., Tanabe S. & Giesy J.P. (1999) Bioaccumulation profiles of polychlorinated biphenyl congeners and organochlorine pesticides in Ganges river dolphins. *Environmental Toxicology and Chemistry*, **18**, 1511–1520.

Slooten E., Fletcher D. & Taylor B.L. (2000) Accounting for uncertainty in risk assessment: case study of Hector's dolphin mortality due to gillnet entanglement. *Conservation Biology*, **14**, 1264–1270.

Smith A.M. & Smith B.D. (1998) Review of status and threats to river cetaceans and recommendations for their conservation. *Environmental Reviews*, **6**, 189–206.

Smith B.D., Ahmed B., Ali M.E. & Braulik G. (2001) Status of the Ganges river dolphin or shushuk *Platanista gangetica* in Kaptai Lake and the southern rivers of Bangladesh. *Oryx*, **35**, 61–72.

Stolen M.K. & Barlow J. (2003) A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science*, **19**, 630–649.

Taylor B.L., Chivers S.J., Larese J. & Perrin W.F. (2007a) *Generation length and percent mature estimates for IUCN assessments of cetaceans*. S.F.S.C. Administrative Report Lj-07-01, 8604 La Jolla Shores Blvd., La Jolla, CA 92038, USA. 24 p.

Taylor B.L. & Gerrodette T. (1993) The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conservation Biology*, **7**, 489–500.

Taylor B.L., Martinez M., Gerrodette T., Barlow J. & Hrovat Y.N. (2007b) Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science*, **23**, 157–175.

Thomas J.A., Bourn N.A.D., Clarke R.T., Stewart K.E., Simcox D.J., Pearman G.S. *et al.* (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society, Series B: Biological Science*, **268**, 1791–1796.

Thompson P.M., Wilson B., Grellier K. & Hammond P.S. (2000) Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Conservation Biology*, **14**, 1253–1263.

Tilman D., May R.M., Lehman C.L. & Nowak M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Turvey S.T., Barrett L.A., Hao Y., Zhang L., Zhang X., Wang X. *et al.* (2010a) Rapidly shifting baselines in Yangtze fishing communities and local memory of extinct species. *Conservation Biology*, **24**, 778–787.

Turvey S.T., Barrett L.A., Hart T., Collen B., Hao Y., Zhang L. *et al.* (2010b) Spatial and temporal extinction dynamics in a freshwater cetacean. *Proceedings of the Royal Society, Series B: Biological Science*, **277**, 3139–3147.

Turvey S.T., Pitman R.L., Taylor B.L., Barlow J., Akamatsu T., Barrett L.A. *et al.* (2007) First human-caused extinction of a cetacean species? *Biology Letters*, **3**, 537–540.

Vidal O., Barlow J., Hurtado L.A., Torre J., Cendón P. & Ojeda Z. (1997) Distribution and abundance of the Amazon river dolphin (*Inia geoffrensis*) and the tucuxi (*Sotalia fluviatilis*) in the upper Amazon river. *Marine Mammal Science*, **13**, 427–445.

Wade P.R. (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, **14**, 1–37.

Wang J.H., Wei Q.W. & Zou Y.C. (2011) Conservation strategies for the Chinese sturgeon, *Acipenser sinensis*: an overview on 30 years of practices and future needs. *Journal of Applied Ichthyology*, **27**, 176–180.

Wang K., Wang D., Zhang X., Pfluger A. & Barrett L. (2006) Range-wide Yangtze freshwater dolphin expedition: the last chance to see baiji? *Environmental Science and Pollution Research*, **13**, 418–424.

Wilson H.B., Kendall B.E. & Possingham H.P. (2011) Variability in population abundance and the classification of extinction risk. *Conservation Biology*, **25**, 747–757.

Xiao H. & Duan Z.-H. (2011) Hydrological and water chemical factors in the Yichang reach of the Yangtze River pre- and post-impoundment of the Three Gorges Reser-

voir: consequences for the Chinese sturgeon *Acipenser sinensis* spawning population (a perspective). *Journal of Applied Ichthyology*, **27**, 387–393.

Zhang X. (1992) Studies on the age determination, growth and reproduction of finless porpoise *Neophocaena phocaenoides*. *Acta Theriologica Sinica*, **16**, 289–298.

Zhang X., Liu R., Zhao Q., Zhang G., Wei Z., Wang X. *et al.* (1993) Populations of the finless porpoise in the middle and lower reaches of the Yangtze River, China. *Acta Theriologica Sinica*, **13**, 260–270.

Zhang X., Wang D., Liu R., Wei Z., Hua Y., Wang Y. *et al.* (2003) The Yangtze River dolphin or baiji (*Lipotes vexillifer*): population status and conservation issues in the Yangtze River, China. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, 51–64.

Zhang X. & Wang K. (1999) Population viability analysis for the Yangtze finless porpoise. *Acta Ecologica Sinica*, **19**, 529–533.

Zhao X., Barlow J., Taylor B.L., Pitman R.L., Wang K., Wei Z. *et al.* (2008) Abundance and conservation status of the Yangtze finless porpoise in the Yangtze River, China. *Biological Conservation*, **141**, 3006–3018.