A Population Viability Analysis for the Chinese White Dolphin (*Sousa chinensis*) in the Pearl River Estuary

Final Report

Prepared by:

Philip S. Miller, PhD
Senior Program Officer
IUCN-SSC Conservation Breeding Specialist Group

In consultation with:

Participants of Chinese White Dolphin PVA Workshop
Hong Kong SAR, China: 30 March – 1 April, 2016

A Component of the
Chinese White Dolphin Conservation Research Framework

29 December, 2016

A contribution of the IUCN/SSC Conservation Breeding Specialist Group, in collaboration with Ocean Park Conservation Foundation Hong Kong and workshop participants.

Workshop support provided by Airport Authority Hong Kong.

Suggested Citation:

Miller, P.S. 2016. *A Population Viability Analysis for the Chinese White Dolphin (*Sousa chinensis*) in the Pearl River Estuary: Final Report.* Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

A Population Viability Analysis
for the Chinese White Dolphin (*Sousa chinensis*)
in the Pearl River Estuary

Final Report

Table of Contents

A Population Viability Analysis
for the Chinese White Dolphin (*Sousa chinensis*)
in the Pearl River Estuary

Introduction

The Indo-Pacific humpback dolphin (*Sousa chinensis*) is known along the mainland coast of China and Taiwan as the Chinese white dolphin (CWD). However, the population that is endemic to the waters off western Taiwan is also often known locally as the Taiwanese white dolphin and was recently described as a distinct subspecies, *S. c. taiwanensis* (Wang et al. 2015). The range of the species extends from central China to eastern India, and throughout much of Southeast Asia (Jefferson and Smith 2016). The preferred habitat is shallow coastal waters, with the highest densities of individuals seen in estuarine habitat. The species was listed on the IUCN Red List in 2008 as Near Threatened (Reeves et al. 2008). Given a taxonomic reclassification of the genus *Sousa*, and in the light of updated information, Jefferson and Smith (2016) proposed that *S. chinensis* should be re-listed as Vulnerable. A new formal Red List assessment of the species is underway but will probably not be finalized and published for several months (R. Reeves, pers. comm.).

The Chinese white dolphins inhabiting southeast China’s Pearl River Estuary (PRE), near the large industrial urban centers of Hong Kong, Shenzhen and Guangzhou, is believed to be the largest putative population of the species. In anticipation of the need to identify geographically specific threats for more refined species conservation planning, the decision was made in this workshop to recognize the PRE as a putative biological population and to subdivide the Estuary into three geographic subunits (Hong Kong SAR, Eastern PRE from Hong Kong SAR to Zhuhai-Macau, and Western PRE from Zhuhai-Macau to Hailing Island). The entire PRE area is under intense pressure from human activities, both offshore and onshore, which results in significant threats to the long-term viability of the PRE CWD population. In order to improve the population’s long-term viability, we must better understand the anthropogenic threats to its reproduction and survival and use this information to predict long-term population dynamics in the presence of these threats. Additionally, it is important to predict the effectiveness of population and/or habitat management alternatives so that an effective and efficient species conservation strategy can be designed and implemented.

Toward this end, the Chinese White Dolphin Conservation Research Framework includes a population viability analysis (PVA) for the PRE population. This PVA was initiated at a workshop held in Hong Kong in March/April 2016. Participants included more than 25 experts in the biology and conservation of cetaceans and, in particular, CWD in the PRE. The report from that workshop (Miller et al. 2016) documents the information discussed among the participants, and the results of the preliminary demographic analyses that define the PVA. This report expands upon that earlier document by presenting the structure and results of additional analyses carried out after the March/April 2016 workshop. Specifically, the broad objectives for this present analysis are to:

- Build upon existing models of CWD population dynamics in the PRE to create a realistic simulation tool for projecting population abundance into the future;
- Develop reliable estimated values of demographic parameters that, when used as simulation model input, generate realistic projections of CWD population dynamics;
- Identify specific demographic parameters – fecundity (offspring production), age-specific mortality, etc. – that are influential drivers of population growth or decline; and

- Identify factors that threaten long-term CWD population persistence and determine how those threatening factors can be evaluated using this demographic modeling tool.

PVA can be a valuable tool for investigating current and future risk of endangered animal or plant population decline under specific scenarios of human activity, locally and globally, which may compromise a population's ability to reproduce successfully or survive (e.g., Beissinger and McCullough 2002; Morris and Doak 2002). The technique can be used as a way of identifying management options to reduce the risk of population decline and enhance opportunities for the population to recover in its natural habitat. PVA methods are not intended to give absolute and accurate "answers" for what the future will bring for a given wildlife species or population. This limitation arises from two fundamental facts about these populations: (i) they are inherently unpredictable in their detailed behavior, and (ii) we will have only a partial understanding of a population's long-term demographic dynamics, i.e., rates of reproduction and survival. Consequently, many researchers have cautioned against the exclusive use of absolute results from a PVA in order to promote specific management actions for threatened populations (e.g., Ludwig 1999; Beissinger and McCullough 2002; Reed et al. 2002; Lotts et al. 2004). Indeed, the true value of this type of analysis lies in the assembly and critical analysis of the available information on the species (or population) and its ecology, in the identification of data gaps, and in the ability to consider and compare quantitative metrics of population dynamics across simulated scenarios. Each simulation represents a specific scenario and its inherent assumptions about the available data and a proposed method of population and/or habitat management. Interpretation of this type of output depends strongly upon our knowledge of the PRE Chinese white dolphins and their habitat, the threatening processes affecting the population, and possible future changes in these processes.

Vortex, a simulation software package developed for PVA (Version 10: Lacy and Pollak 2014), has been used here as a vehicle to conduct the analysis. The *Vortex* package is a simulation of the effects of a number of different natural and human-mediated forces – some, by definition, acting unpredictably from year to year – on the health and integrity of wildlife populations. *Vortex* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by recreating the essential series of events that describe the typical life cycles of sexually reproducing organisms. *Vortex* simulations have been confirmed to produce population trajectories that are consistent with monitored wildlife populations (Brook et al. 2000a) and with other population models (Brook et al. 2000b). The overall structure of the program was published in Lacy (2000), and the compiled program and documentation are distributed freely at www.vortex10.org/Vortex10.aspx. For a more detailed explanation of *Vortex* and its use in population viability analysis, refer to Appendix 1.

A Preliminary Analysis of Threats to Chinese White Dolphins in the Pearl River Estuary

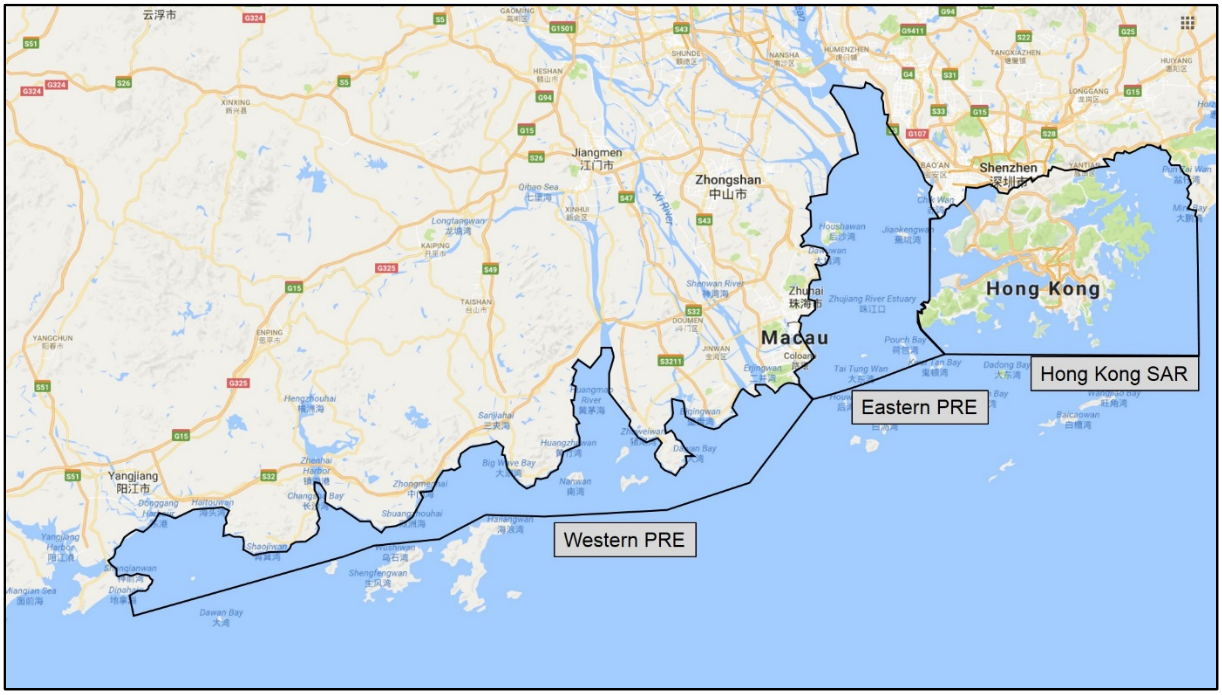
As an initial step in the PVA process, it is important to understand the threats to the species in the habitat of interest, and to prioritize those threats to identify those that are considered to have the greatest impact on the population's long-term viability. PVA workshop participants began this process by developing a simple qualitative analysis of the types of threats acting in different sections of the PRE, and the aspects of the dolphins' life history – reproduction, survival, dispersal, etc. – that would be affected by these threats.

To begin this threats analysis process, participants agreed to consider the putative PRE population as being composed of three regional subunits (Figure 1), defined largely by the extent of threats that exist within the subunit areas and the types of management (often related to political jurisdictions) that are currently being implemented or may be implemented in those areas in the future:

- Hong Kong SAR – the waters within the designated boundaries of the Hong Kong SAR;
- Eastern PRE – the waters extending from the Hong Kong SAR westward to the Zhuhai-Macau area;
- Western PRE – the waters extending from the Zhuhai-Macau area westward to Hailing Island, just south of the city of Yangjiang.

The subdivision of the PRE into three subunits does not necessarily imply a formal metapopulation structure, i.e., with distinct subpopulations operating semi-independently with only limited dispersal of individuals between them. Rather, the value of considering this subdivision will be in the development and evaluation of specific risk assessment scenarios that feature population or habitat management concentrated within a specific area of the PRE.

Figure 1. Geographic subunits of the Pearl River Estuary (PRE) identified for this analysis. Boundaries for the Eastern and Western PRE subunits are approximate.



The specific threats or threatening factors considered in this analysis were:

- Fishing – primarily commercial, but smaller-scale subsistence fishing is included here as well. This threat would be manifested as prey depletion and entanglement in nets, lines or hooks.
- Shipping – primarily considered to be the passage of large commercial freighters, which can lead to significant disturbance and direct mortality through vessel strikes.
- High-speed Ferries – passage of fast ferries across the eastern portion of the PRE, primarily between Hong Kong and the Zhuhai-Macau area. Ferry traffic leads to vessel strike mortality and disturbance.

- Dolphin Watching – disturbance from tourist activities designed specifically to bring vessels to, and remain near, dolphins, often for extended periods of time.
- Construction– a broad suite of onshore and offshore construction activities, including those directed at dredge and fill land creation and bridge construction. These activities lead to disturbance through noise and ship traffic, and changes in water quality through sediment disturbance.
- Dredging – offshore dredging of shallow sea-floor areas as part of construction and other projects altering water quality and prey habitat.
- Dumping – offshore dumping of sediments, contaminants, etc. as part of construction projects.
- Habitat Removal – the culmination of specific land creation projects that lead to elimination of aquatic habitat (including that occupied by dolphins or their prey).
- Sewage – introduction of sewage into the estuary, primarily waste (including pharmaceuticals and pathogens) from major urban centers.
- Agricultural Effluent – introduction of pesticides, herbicides, fertilizers and animal waste and pathogens from rural farming areas through run-off, etc.
- Industrial Effluent – introduction of industrial waste from heavy industrial centers through run-off, etc.

These threats were assessed for their potential impacts on the following aspects of Chinese white dolphin life history:

- Reproductive rate – the number of calves produced per year.
- Calf survival – the proportion of the calves produced per year that survive to age 1.
- Non-calf survival – the survival of sub-adults (>1 year) and adults per year.
- Dispersal – the rate of movement of dolphins into or out of a given PRE subunit. [Note that a given threat may result in decreased or increased movement of dolphins across subunits, depending on the nature of the activity. Also note that this movement is not necessarily permanent, i.e., animals may move among subunits over time.]

This analytical structure is based on the earlier threat identification and analysis presented in Wilson et al. (2008). Severity of threats was assessed on a qualitative basis — because we do not have specific quantitative data on the magnitude of the threat or the severity of its effect on any specific demographic parameter identified above. In this context, we also identified where we have significant levels of uncertainty in our assessment of the intensity of threats across the PRE subunits. Our goal here is to begin assessing the magnitude of threats across each of the three PRE subunits so that we can begin developing meaningful management scenarios that target key threats in specific subunits.

Note that species experts who participated in the March/April 2016 PVA workshop were unable to assign accurate quantitative estimates of the severity of these threats to specific population demographic rates. There are no detailed data on the causal factors that contribute to changes in survival, reproduction, or dispersal. Rather, the information in these tables was used to inform scenarios of overall impact of human activities on survival, reproduction or dispersal of dolphins occupying each of the PRE subunits in order to assess relative risk.

The preliminary results of the threats analysis are shown in Tables 1 – 3 below. A few important patterns emerge from this preliminary analysis:

1. The Eastern PRE is likely exposed to the widest range of threatening activities, including fishing, high-speed ferries, construction, habitat removal, and discharge of agricultural and industrial effluent.
2. Although the Hong Kong subunit may be subjected a less diverse set of threatening activities, many of those activities operating in that subunit are considered to be potentially quite severe.
3. Threats to the Western PRE appear to be less diverse and relatively less severe, although participants recognized the strong impact that fishing activities are likely to have in this area.
4. There is considerable uncertainty around the qualitative estimation of the intensity of a given threat's impact, even among the recognized experts on the species in this portion of its distribution. This qualitative uncertainty makes it very challenging at best to derive quantitative measures of the impact of a given activity on rates of survival or reproduction among PRE dolphins.

Table 1. Preliminary assessment of the nature and severity of impacts arising from human activities in the Hong Kong SAR subunit of the Pearl River Estuary. Impact severity shaded as Low or Absent (green), Medium (yellow), or High (red). "U" denotes threats for which the nature and intensity of impact is considered highly uncertain.

	Non-calf Survival	Calf Survival	Reproduction	Dispersal
Fishing	🟨	🟨	🟩	🟩 U
Shipping	🟨	🟨	🟩	🟨 U
High-Speed Ferries	🟥 U	🟥 U	🟩	🟥
Dolphin Watching	🟩	🟨 U	🟩	🟩
Construction (including reclamation)	🟥 U	🟥 U	🟩	🟥 U
Dredging	🟩	🟩	🟩	🟩
Dumping	🟩	🟩	🟩	🟩
Habitat Removal	🟨 U	🟨 U	🟩 U	🟥
Sewage	🟩	🟩	🟩	🟩
Agricultural Effluent	🟨 U	🟥 U	🟥 U	🟩
Industrial Effluent	🟨 U	🟥 U	🟥 U	🟩

Table 2. Preliminary assessment of the nature and severity of impacts arising from human activities in the Eastern subunit of the Pearl River Estuary. Impact severity shaded as Low or Absent (green), Medium (yellow), or High (red). "U" denotes threats for which the nature and intensity of impact is considered highly uncertain.

	Non-calf Survival	Calf Survival	Reproduction	Dispersal
Fishing	🟥	🟥	🟩	🟩 U
Shipping	🟨	🟨	🟩	🟨
High-Speed Ferries	🟥 U	🟥 U	🟩	🟥
Dolphin Watching	🟩	🟩	🟩	🟩
Construction (including reclamation)	🟥 U	🟥 U	🟩	🟥 U
Dredging[1]	🟨	🟨	🟩	🟨
Dumping	🟩	🟩	🟩	🟩
Habitat Removal[2]	🟥 U	🟥 U	🟩 U	🟥
Sewage	🟨 U	🟨 U	🟨 U	🟩
Agricultural Effluent	🟨 U	🟥 U	🟥 U	🟩
Industrial Effluent	🟨 U	🟥 U	🟥 U	🟩

1 Includes sand mining
2 Proposed wind farm

Table 3. Preliminary assessment of the nature and severity of impacts arising from human activities in the Western subunit of the Pearl River Estuary. Impact severity shaded as Low or Absent (green), Medium (yellow), or High (red). "U" denotes threats for which the nature and intensity of impact is considered highly uncertain.

	Non-calf Survival	Calf Survival	Reproduction	Dispersal
Fishing[1]	🟥	🟥	🟩	🟩 U
Shipping	🟩	🟩	🟩	🟩
High-Speed Ferries	🟨 U	🟨 U	🟩	🟩
Dolphin Watching	🟩	🟩	🟩	🟩
Construction (including reclamation)	🟨 U	🟨 U	🟩	🟨 U
Dredging[2]	🟨	🟨	🟩	🟩
Dumping	🟩	🟩	🟩	🟩
Habitat Removal	🟨 U	🟨 U	🟩 U	🟨
Sewage	🟩	🟩	🟩	🟩
Agricultural Effluent	🟨 U	🟥 U	🟥 U	🟩
Industrial Effluent	🟨 U	🟨 U	🟨 U	🟩

1 Includes coastal gill netting and oyster farming
2 Includes sand mining

PVA Model Structure and Demographic Data Input

Our population viability analysis for this project borrows heavily from previous demographic descriptions of Indo-Pacific humpback dolphin populations in and near the PRE. Specifically, the PVA for the CWD population in the PRE by Huang et al. (2012) is a valuable resource for obtaining reasonable estimates of reproductive and survival rates for the species in this particular part of its distribution. Additionally, the demographic analyses of the Taiwanese humpback dolphin (*S. c. taiwanensis*) by Araújo et al. (2014) and Huang et al. (2014) were consulted where appropriate. Both of these analyses used demographic data from the analysis of species life history information by Jefferson et al. (2012). Note that the analysis described here does not replace the work reported by Huang et al. (2012), but is instead an extension of that work designed to explore in more detail the impact of various threats to CWD population stability and the consequences of our uncertainty in the magnitude of those threats.

Generalized approach to model construction: PRE geographic population structure

Our initial approach to the PVA treats that the dolphins occupying the Pearl River Estuary as a single population with no discernible substructure across the three regions discussed above. This structure is used in our exploration of population trends across the PRE and in the demographic sensitivity analysis.

Further scenarios examine population dynamics under the assumption that the PRE dolphin population exhibits a form of metapopulation spatial structuring in the form of the three subunits discussed previously. Examining this hypothesis may shed some light on the role that movement of individuals among subunits might play in recently observed trends in population abundance, particularly in Hong Kong waters.

Simulation structure and duration

Stochastic projections of population abundance through time were simulated 1000 times for each scenario, with each projection extending to 100 years. Given the relatively long generation time for this species, it is important to extend these projections far enough into the future to be able to see demographic dynamics across multiple generations. By default, *Vortex* conducts a pre-breeding census, meaning that total population abundance is calculated immediately before the year's breeding season. In the case of Indo-Pacific humpback dolphins, this means that the census would be taken in the spring, before the year's crop of calves is produced. (We recognize that calf production in this species does not follow a classic "birth pulse" model but is instead distributed across a number of months.) Demographic information may be obtained at annual intervals throughout the duration of the simulation. All simulations are conducted using *Vortex* version 10.2.2.0 (October 2016).

Breeding age

The best evidence from detailed examination of physical characteristics of stranded individuals suggests that females give birth for the first time at approximately ten years of age, on average. Researchers assume that males require a longer period of time to reach sexual maturity, so we set male breeding age (meaning capable of insemination) at 13 years. Previous demographic analyses indicate that Indo-Pacific humpback dolphins typically do not survive for more than 35 or 40 years, so we set the mean maximum age at 38 years.

Calf production

Indo-Pacific humpback dolphins have a low rate of reproduction throughout their adult lifespan. Females give birth to just one calf at a time, with a typical inter-birth interval of 3 – 4 years based in part on the duration of observations of mothers with calves. Specifically, we assume for our baseline model that the probability of an adult female producing a calf in any given year is 29%. Over the duration of a given simulation, across multiple iterations, this probability will correspond to the desired interval between birthing events. This calving rate is an average value across years, with some variability around that mean reflecting annual environment-driven stochastic fluctuations. In addition, we assume that the maximum age of female reproduction is 36 years, based on the observation (Jefferson et al. 2012) that calves are typically associated with their mothers for approximately two years. We assign a standard deviation of 8.0% to the mean annual calving rate. This level of environmental variability is reasonable for a species with this type of life history.

Mortality

Vortex defines mortality as the annual rate of age-specific death from year x to $x + 1$; in the language of life-table analysis, this is equivalent to $q(x)$. The age-specific mortality schedule for our baseline model is taken from the statistical analysis of survival conducted by Huang et al. (2012) using stranding data from direct field records and from Jefferson et al. (2012). Note that stranding data may result in mortality estimates biased upwards for certain age classes, particularly calves and adults (Araújo et al. 2014). Other methods for collecting individual-animal data in the field, such as mark-recapture techniques applied to photo-identification data as described in Araújo et al. (2014), may yield additional information that can be used to refine future analyses.

Huang et al. (2012) used Siler's competing risk model of survivorship to estimate age-specific $l(x)$ values, or the probability of an individual surviving from birth to age x. From these estimates, one can use standard life-table analytical methods to calculate the probability of an individual surviving from age (x) to age (x+1) and, therefore, the complementary probability of dying within that same annual age interval, or $q(x)$. Data for adult mortality were expressed in *Vortex* as a simple exponential regression as a function of increasing adult age. Figure 2 gives the functional form of $q(x)$ for adults from Huang et al. (2012), expressed as the exponential function (rate = ae^{bx}), and Table 4 gives the mean annual mortality values for each of the age classes included in our *Vortex* model.

In order to explore the impact of the potential upward bias in mortality estimates from the use of stranding data, we developed alternative expressions for adult mortality in which the value of the exponential coefficient in the fitted regression (b = 0.0876) was reduced by 10% to 50% of its original value.

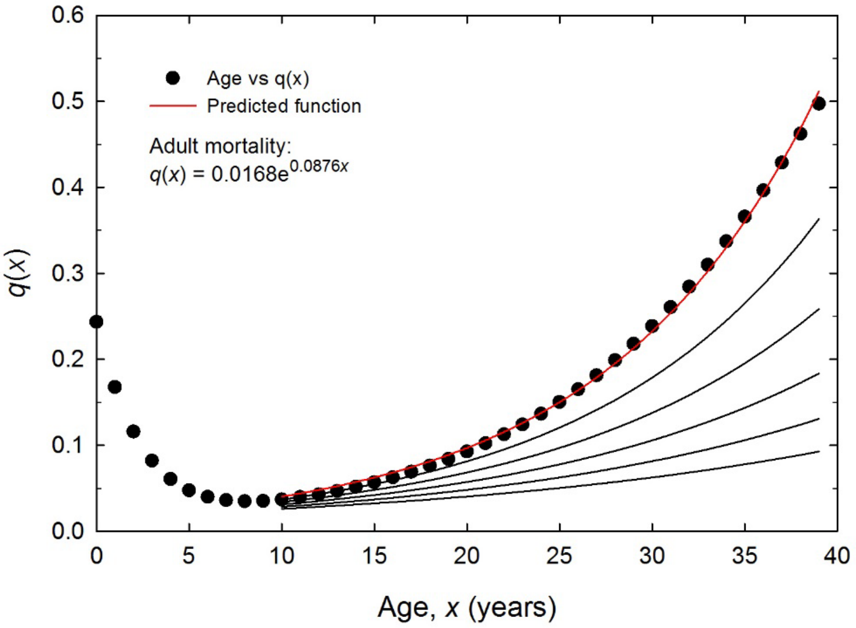


Figure 2. Functional form of age-specific mortality in Chinese white dolphin PVA. Analysis based on data and methodology in Huang et al. (2012). Red line gives the expression for adult mortality according to the equation in the plot legend, while black lines plot the same expression but with the value of the exponential coefficient (0.0876) reduced by 10% (upper black line) to 50% (lower black line) of its original value. See accompanying text for additional information.

Table 4. Mean annual mortality rates of each age class of Indo-Pacific humpback dolphins derived from literature for this demographic analysis. The specified rates describe the average proportion of individuals of age *x* that die before reaching age (*x*+1). Numbers in parentheses indicate the annual environmental variability, expressed as a binomial standard deviation.

Age (*x*)	Mean mortality,% (SD) Female	Mean mortality,% (SD) Male
0	24.3 (10.0)	24.3 (10.0)
1	16.8 (3.0)	16.8 (3.0)
2	11.6 (3.0)	11.6 (3.0)
3	8.2 (3.0)	8.2 (3.0)
4	6.1 (3.0)	6.1 (3.0)
5	4.7 (3.0)	4.7 (3.0)
6	4.0 (3.0)	4.0 (3.0)
7	3.6 (3.0)	3.6 (3.0)
8	3.5 (3.0)	3.5 (3.0)
9	3.5 (3.0)	3.5 (3.0)
10	= 100*(0.017*EXP(0.0876*Age)) (3.0)	3.7 (3.0)
11		4.0 (3.0)
12		4.7 (3.0)
13		= 100*(0.017*EXP(0.0876*Age)) (3.0)

Environmental variability (EV) for each age-specific mortality estimate was set at 3.0% with the exception of calf mortality which was given a value of 10%. Furthermore, we assumed in all our models that measures of environmental variability (EV) for fecundity and survival will be correlated within a year. Note that this variability is designed to simulate environmentally-induced fluctuations in mortality from year to year, and is therefore not equivalent to the measurement uncertainty reported in studies such as Huang et al (2012). Sensitivity analysis (see below) is used to evaluate the impact of our measurement uncertainty across a range of demographic parameters, thereby providing support for directed research and management programs to improve our understanding of population dynamics.

Initial population size and carrying capacity

We must initialize our prospective PVA model with a CWD population abundance that is informed by recent data. Based on analyses reported by Chen et al. (2010) and Hung (2015), the total abundance of Indo-Pacific humpback dolphins in the PRE was estimated to be approximately 2600 individuals in the early part of this decade. Therefore, we use this value to initialize our model, but with the understanding that population abundance at the time of this analysis is likely to be different. It is also important to note that there is considerable uncertainty associated with the Chen et al. (2010) estimate.

The long-term equilibrium abundance of a given population in a specific habitat is represented by defining that habitat's carrying capacity (*K*). The carrying capacity defines an upper limit for the population size, above which additional mortality is imposed randomly across all age classes in order to return the population at the end of a specific timestep to the value set for *K*. There is currently no credible estimate of Indo-Pacific humpback dolphin carrying capacity in the PRE, although we are confident that the current population abundance is below this value, and likely well below the abundance prior to the large-scale anthropogenic impacts that have been occurring over many decades. For our exploratory simulations, we set the carrying capacity across the PRE at 4000 individuals. This value for *K* is chosen with the underlying assumption that mortality factors are currently operating to limit population growth to an abundance that is below the carrying capacity. This assumption is largely speculative but is employed here as a testable hypothesis.

We also assume that habitat loss throughout the Estuary is gradually reducing carrying capacity. For these exploratory simulations, we assume that a total of approximately 30.5% of the currently available habitat (and, by extension, 30.5% of the current carrying capacity) will be lost over the next 25 years, after which time management activities will be successful in maintaining that carrying capacity into the future. This translates into a 1.22% annual reduction in *K* for simulation years 1 to 25. This value of *K* reduction across the full extent of the PRE aligns with subunit-specific estimates of carrying capacity featured in metapopulation scenarios to be discussed later in this report.

Table 5 below summarizes the baseline input dataset upon which subsequent models are based.

Table 5. Basic demographic input parameters for the baseline single-population Chinese white dolphin simulation model. See accompanying text for more information.

Model Input Parameter	Baseline Value
Breeding System	Polygynous (promiscuous)
Age of first calving (♀ / ♂)	10 / 13
Maximum age of reproduction	36
Longevity	38
Annual % adult females reproducing (SD)	29.0 (10.0)
Density-dependent reproduction?	No
Overall offspring sex ratio	0.5
Adult males in breeding pool	100%
% annual mortality, ♀ / ♂ (SD)	
Age 0 – 1 (calf)	24.3 (10.0)
1 – 2	16.8 (3.0)
2 – 3	11.6 (3.0)
3 – 4	8.2 (3.0)
4 – 5	6.1 (3.0)
5 – 6	4.7 (3.0)
6 – 7	4.0 (3.0)
7 – 8	3.6 (3.0)
8 – 9	3.5 (3.0)
9 – 10	3.5 (3.0)
10 – 11 (♂)	3.7 (3.0)
11 – 12 (♂)	4.0 (3.0)
12 – 13 (♂)	4.7 (3.0)
Adult Female (10+)	100*(0.017*EXP(0.088*Age)) (3.0)
Adult Male (13+)	100*(0.017*EXP(0.088*Age)) (3.0)
Initial population size / carrying capacity	2585 / 4000
Decline in carrying capacity	Linear, 1.22% per year for 25 years

A “metapopulation” approach to analyzing viability of Chinese white dolphins in the PRE

In addition to our standard approach of treating the entire CWD population in the PRE as a single population, we considered an alternative model structure in which the three subunits described earlier in this report – Hong Kong, Eastern PRE and Western PRE – are considered semi-distinct components of a metapopulation. In this alternative structure, we are able to specify different demographic rates for each subunit in accordance with our underlying assumptions about the nature and intensity of anthropogenic threats experienced by dolphins within those subunits. In this way, we can construct models that test hypotheses about dolphin population dynamics across the PRE and how dolphins occupying discrete subunits of the PRE respond to specific threats. This analytical goal motivated our work on identifying subunit-specific threats that is summarized in Tables 1 – 3.

Classic models of wildlife metapopulation dynamics feature at least semi-isolated subpopulations occupying discrete patches of suitable habitat, with those patches typically separated in space by lower-quality “matrix” habitat. Subpopulations may be demographically linked through movement (dispersal) of individuals across space and time, leading to complex demographic and genetic patterns across the full metapopulation configuration. The PRE population of Chinese white dolphins would not typically be described as a metapopulation in the classic sense, as the dolphin population subunits defined here are not separated spatially by a matrix of poor-quality habitat. Nevertheless, analysis of this alternative structural description is intended to explore the impacts of differential threats across PRE dolphin population subunits and their subunit-specific demographic impacts. These analyses could inform future data collection/analysis and population management activities across the region. The characteristics of these metapopulation models are largely speculative, as the information required to develop accurate demographic input data is not yet available. Consequently, these models should be seen as exploratory and not accurately predictive of dolphin population dynamics within selected PRE subunits.

Our metapopulation models feature a number of modifications to the demographic input that defines are baseline single-population model described earlier in this report. These modifications are discussed in more detail below.

> Mortality: We assume relatively broad differences in the mortality rates across different population subunits. These differences are meant to portray differential levels of impact of anthropogenic threats among PRE subunits, such as high-speed ferry collisions, cumulative impacts of water pollutants, net entanglements, etc. Specifically, we assume that the Hong Kong and Eastern PRE subunits experience relatively greater impact from anthropogenic threats than the Western PRE subunit. This is expressed in our models as a 5% proportional increase in the baseline mortality rates across all age classes; in other words, all mean annual mortality rates in the HK and Eastern PRE subunits, defined as they were in the single-population model scenario as above, are multiplied by 1.05. As an example of this transformation, calf mortality in the HK and Eastern PRE subunits becomes (24.3%)*(1.05) = 25.52%. We also assume that dolphins occupying the Western PRE subunit experience relatively lesser impacts from anthropogenic threats. This is expressed in our models as a 10% proportional decrease in age-specific mortality. As an example of this transformation, calf mortality in the Western PRE subunit becomes (24.3%)*(0.9) = 21.87%. This reduction in mortality in the Western PRE subunit does not mean that dolphins occupying this subunit are not impacted by anthropogenic activities, but are instead impacted to a slightly lesser extent than dolphins occupying subunits to the east.
>
> Fecundity: Similar to our specification of differential mortality across subunits, we assume that the HK and Eastern PRE subunits are characterized by lower rates of annual calf production. Specifically, we assume the Western PRE subunit retains the baseline 29% annual probability of adult females producing a calf, while mean breeding rates for the Hong Kong and Eastern PRE subunits are set at 25% and 26%, respectively. Again, these specific values are not supported by field observations in

each subunit, but are meant to portray the relatively greater impact of anthropogenic disturbance in these subunits.

Initial population abundance: Our total population abundance across the three subunits is identical to that in the single-population model, or 2585 individuals. In our metapopulation configuration, both the Eastern and Western PRE subunits are initialized with 1250 individuals, and the Hong Kong subunit begins with 85 individuals. The HK abundance was set to simulate the abundance reported for the year 2010 by Hung (2016), with abundance estimates for Eastern and Western PRE set to generate a total abundance across the region of 2585 individuals.

Carrying capacity: In the same manner as the specification of subunit initial abundance, we set the total carrying capacity for the three subunits to that for the single-population simulation (4000 individuals). We assume that *K* for the Eastern and Western PRE subunits is 1875, which is 50% higher than the initial abundance. In this manner, we assume that anthropogenic threats limiting survival and calf production are keeping the population below carrying capacity for each subunit. The estimate for *K* in the Hong Kong subunit was set to 250, which is approximately three times the specified initial abundance of 85 individuals reported by Hung (2016) in 2010. This value is informed in part by recent unpublished research by Chan and Karczmarski (cited in Karczmarski et al. (2016)) which suggests that as many as 400 dolphins use Hong Kong waters for part of their home range. While this information is not strictly descriptive of carrying capacity, it does suggest the presence of dolphin habitat that can support a larger number of dolphins than are likely to exist today in this subunit. Additionally, Hung (2016) has observed the increased use of habitat in the southwestern portion of the Hong Kong SAR by dolphins that are likely moving away from heavy anthropogenic activity around the Hong Kong International Airport on the northern side of Lantau Island.

We also assume that each subunit loses carrying capacity over time as a result of habitat loss/modification. The total loss of *K* is the same as that for the single-population model discussed above, and habitat is lost over the same 25-year time horizon, but now each subunit loses carrying capacity at a different rate that is meant to reflect at least in part the different levels of anthropogenic activity occurring in each subunit. Over the first 25 years of the simulation, the Hong Kong subunit loses 50% of its carrying capacity (2% annually), the Eastern PRE loses 33% (1.32% annually), and the Western PRE loses 25% (1% annually). Therefore, at simulation year 25, carrying capacity becomes 125 for Hong Kong, 1250 for Eastern PRE, and 1406 for Western PRE. Again, the magnitude of these changes are speculative but intended to be reflective of the subunit-specific threat analysis initiated in the earlier phases of this analysis project.

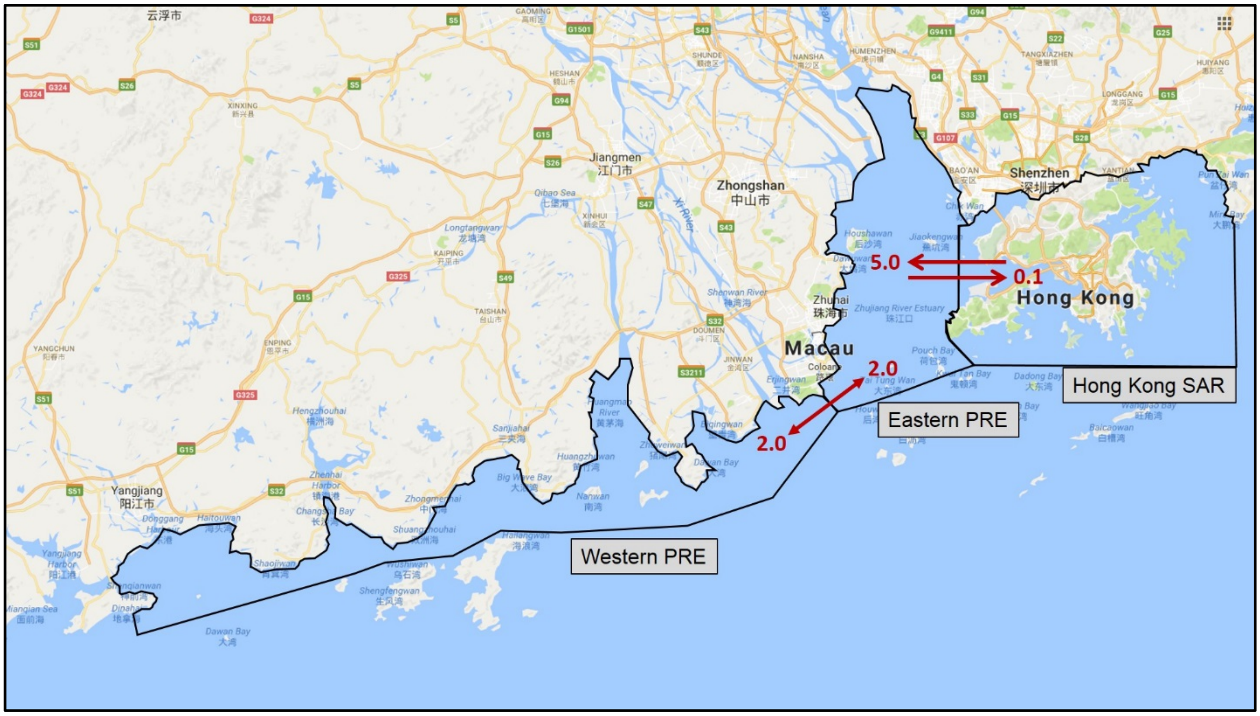
Movement between subunits: Our metapopulation model structure must also specify the annual rate of movement of individuals across subunit boundaries, which describes the extent of demographic connectivity across the metapopulation as a whole. Again, data to estimate these rates are very sparse. Chen et al. (2010) reported the movement of individuals between Eastern to Western PRE subunits, as well as "…frequent cross-boundary movements of many individuals" between Lingding Bay (Eastern PRE) and Hong Kong waters. While the authors provide absolute numbers of dolphins observed moving across subunit boundaries, the proportion of the total abundance engaging in this movement cannot be reliably estimated from the data. Similarly, Karczmarski et al. (2016) suggest "…fluid cross-boundary (Hong Kong – mainland China) movement" of dolphins, and the observation of relatively high dolphin densities along the southwest border of the Hong Kong subunit by Hung (2016) suggests the possibility of annual movement to and from the Eastern PRE.

In the absence of more specific data, our process for estimating annual dolphin movement rates across subunit boundaries of our metapopulation demographic model is guided by the following general principles:

1. Movement rates across the Eastern – Western PRE boundary are likely to be approximately equal.
2. Significant levels of anthropogenic activity in the Hong Kong subunit lead to relatively high rates of emigration out of the subunit to the Eastern PRE.
3. While the intensity of anthropogenic threats affecting dolphins in the Eastern PRE is also high, the restricted spatial extent of the Hong Kong subunit and the associated high "density" of impact tends to deter immigration into the Hong Kong subunit from the Eastern PRE.

Based on the available information and these guiding principles, a movement rate matrix for the PRE metapopulation model was constructed as displayed in Figure 3. The numerical values for movement rates are expressed as percent probabilities of individual movement; for example, a 5% movement rate from Hong Kong to Eastern PRE means that each candidate individual has a 5% chance of moving from the Hong Kong subunit to the Eastern PRE subunit each year. Note that movement of dolphins is restricted to neighboring subunits, so that the Western PRE and Hong Kong subunits do not directly exchange individuals within a simulated year.

Figure 3. Estimates of dolphin movement rates across boundaries of the geographic subunits comprising the Pearl River Estuary (PRE) used in this analysis. Movement rates are expressed as percent annual probability of individual movement from one subunit to the neighboring subunit. Boundaries for the Eastern and Western PRE subunits are approximate. See accompanying text for more information on metapopulation model structure and input.



Both males and females are assumed to move across subunit boundaries, with all but the oldest individuals (>35 years of age) capable of movement during a simulated year. Although dolphin calves are known to associate with their mothers for approximately two years (Jefferson et al. 2012), this explicit linkage is not built in to the demographic model dispersal function. This may lead to slight deviations from the expected outcome of annual dispersal mechanics, but these deviations are unlikely to significantly affect model results.

Other factors not included in initial simulation model

The following factors or processes are not currently included in our initial baseline simulation of CWD population dynamics in the PRE.

- Inbreeding depression – Inbreeding depression (such as reduced viability of inbred offspring) and the gradual loss of genetic variability (heterozygosity) resulting from a small effective population size through time are often considered important factors to include in population viability analyses of endangered species (e.g., Reed et al. 2002). In particular, if the adult female component of the population shows highly skewed levels of reproductive success, this could lead to a significant reduction in the effective population size, higher rates of inbreeding, and more rapid loss of population genetic diversity. The extent of inbreeding depression observed in wildlife populations can vary widely. For example, while the northern elephant seal (*Mirounga angustirostris*) appears to be unaffected by inbreeding despite a severe population bottleneck in the 19th century (Weber et al. 2004), the North Atlantic right whale (*Eubalaena glacialis*) appears to be suffering from reduced fertility and juvenile survival following a similar reduction in population abundance with associated inbreeding (Schaeff et al. 1997; Fraser et al. 2007). While acknowledging these potential impacts, we do not have sufficient data to quantify these processes to any defensible extent; consequently, we have chosen to exclude genetic impacts from our current PVA while recognizing their potential influence on outcomes and events.
- Density dependence in reproductive rates – The process of detecting and parameterizing density dependence in PVA models is complicated and challenging (e.g., Lande et al. 2002, 2006; Freckleton et al. 2006). We simply do not have the types and amounts of appropriate data on recruitment and population density needed to reliably estimate the mode and intensity of density dependence on this species. If abundance estimates (or proxies thereof) are measured with error, this can lead to biased estimates of key density-dependence parameters such as $R_{\max}$ in a Beverton-Holt mechanism of density dependence. Exploration of these processes outside of the *Vortex* modeling environment on other species (results not reported here) indicates that long-term population growth rates and extinction risks are indeed strongly influenced by the strength of density dependence, even under very modest levels of $R_{\max}$ (e.g., 0.05 – 0.10). In light of the high levels of uncertainty around this highly sensitive model parameter, the models discussed here included a simpler ceiling model of density dependence which is specified through the carrying capacity parameter, *K*.
- "Catastrophic" events in the Pearl River Estuary –Singular or discrete environmental events that are outside the bounds of normal environmental variation affecting reproduction or survival are typically referred to by conservation biologists as catastrophes. These events can originate naturally, as in the case of typhoons, harmful algal blooms, disease epidemics, or similar events. Additionally, we can identify anthropogenic events that may act in a similar way, for example oil or chemical spills. These events are modeled in *Vortex* by assigning an annual probability of occurrence for each specified type of event and, once it is deemed to occur in a given year, by ascribing the type of impact the event would have in that year on one or more demographic parameters specified in the model. The workshop participants were unable to identify and quantitatively describe specific catastrophic events that should be included in the baseline model of PRE CWD population dynamics, and we have therefore chosen to exclude this feature from our current analysis. We could in the future explore options around including one or more events if considered appropriate.

PVA Model Results

Single-population model: Baseline model performance

Given the demographic data used as simulation model input as described in the previous section, our baseline model resulted in an instantaneous growth rate of $r = -0.024$, equivalent to an annual growth rate $\lambda = e^r = 0.976$ (Figure 4). This means that the CWD dolphin population inhabiting the Pearl River Estuary is predicted to decline, under the assumptions built into our demographic simulation model, at an annual rate of approximately 2.4% over the next 100 years.

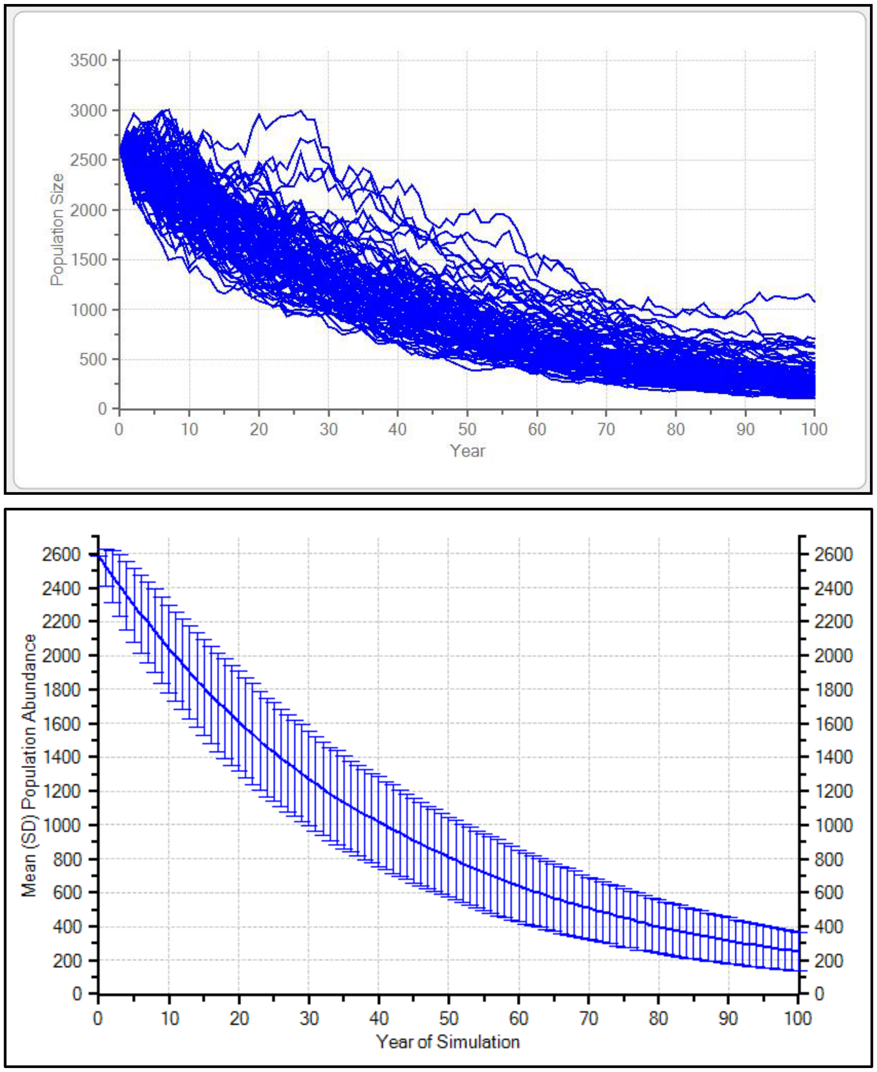


Figure 4. Selection of 100 iterations from a full simulation totaling 1000 iterations (top panel) and mean±SD across 1000 iterations (bottom panel) showing a 100-year abundance trajectory for a simulated population of the Chinese white dolphin in the Pearl River Estuary. See text for more information on baseline model input and model structure.

Specifically, the important assumptions underlying this projection of CWD population abundance in the PRE include:

- The stranding data analyzed by Huang et al. (2012) are a reliable source of information from which to estimate realistic rates of age-specific mortality.
- The mortality rates generated by the use of stranding data collected from a portion of the full geographic extent of the PRE can be reasonably extrapolated to the entire region.

- The factors contributing to dolphin mortality across the PRE will continue into the future, and at the same levels of intensity at which they operate in the present day.

The projection reported here is very similar to the findings discussed in Huang et al. (2012), where their PVA demonstrated an annual growth rate $\lambda = 0.975$. The slight difference between the two estimated growth rates is likely due to small differences in the estimation of calf production. Despite this relatively minor difference in model performance, an analysis of the available demographic data strongly suggest that the CWD population in the PRE is declining steadily at a relatively high rate. The simulated population declines to 50% of its original abundance (i.e., in approximately the year 2000) – from 2585 to about 1300 individuals – in about 32 years after the initiation of the simulation , and the final population after 100 years is 250 (just less than 10% of the initial population abundance).

Single-population model: Demographic sensitivity analysis

During development of the baseline model input dataset, it quickly became apparent that a number of demographic parameter values were being estimated with varying levels of uncertainty. This type of measurement uncertainty, which is distinctly different from the annual variability in demographic rates due to extrinsic environmental stochasticity and other factors, makes it more difficult to generate accurate predictions of population dynamics with any degree of confidence. Nevertheless, an analysis of the sensitivity of our models to this measurement uncertainty can aid in identifying priorities for detailed research and/or management projects targeting specific elements of the population's biology and ecology.

A preliminary sensitivity analysis conducted as part of the March/April 2016 CWD PVA workshop (Miller et al. 2016) demonstrated the importance of adult survival in driving the growth of Chinese white dolphin populations. To extend this analysis, a series of model scenarios was constructed in which the coefficient for the exponential function relating annual mortality rate $q(x)$ to age x was reduced in value by 10% to 50% of its baseline value (see Figure 2 for more information on this transformation). The outcome of this analysis is shown in Figure 5.

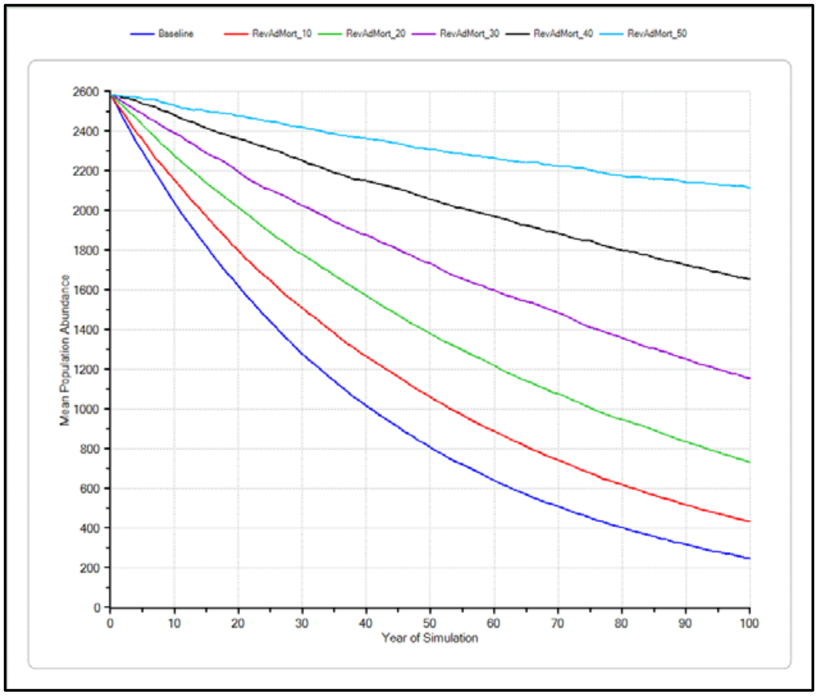


Figure 5. Projections of population abundance for a simulated Chinese white dolphin population in the Pearl River Estuary, under alternative models of age-specific adult mortality. Dark blue line (bottom) features the baseline mortality function, while additional lines give trajectories assuming a 10% (red line, second from bottom) to 50% (light blue line, top) reduction in the exponential mortality coefficient. See text for more information on model input and structure.

As is evident from the figure above, modifications to the relationship describing age-specific adult mortality led to significant changes in the simulated population trajectory. When the exponential mortality coefficient was reduced by 30%, the simulated population growth rate was *r* = -0.0086. When the coefficient was reduced by 50%, the growth rate became *r* = -0.0012.

The interaction between mortality rates and calf production was evident in the trajectories plotted in Figure 6. In these scenarios, the mean annual percentage of adult females breeding was reduced by 25%, from the baseline value of 29% to 21.75% with the spectrum of adult mortality rates expressed in the same way as presented in the analyses summarized in Figure 5.

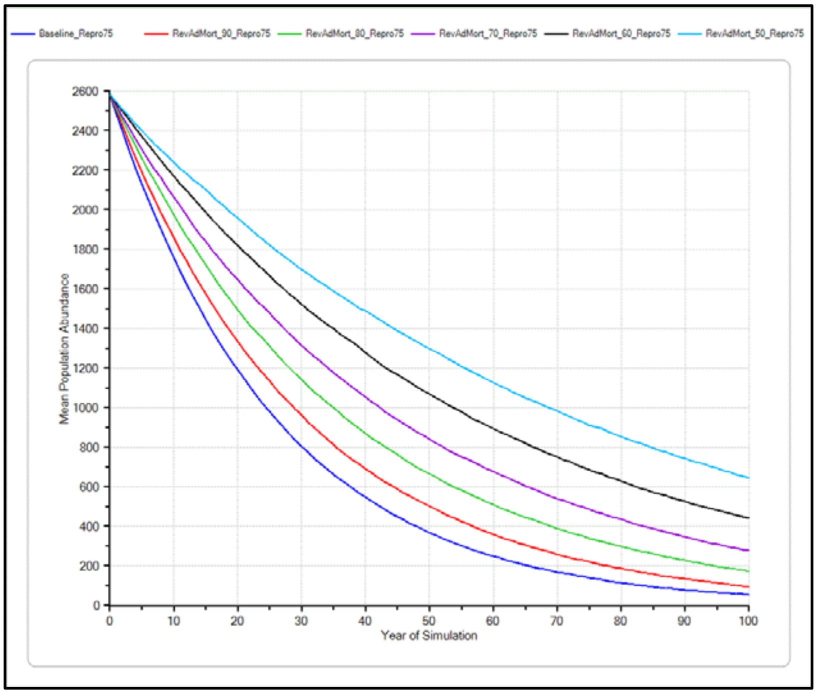


Figure 6. Projections of population abundance for a simulated Chinese white dolphin population in the Pearl River Estuary, under alternative models of age-specific adult mortality and with a 25% reduction in the mean annual rate of calf production among adult females. Refer to Figure 5 for information on scenario structure, and see accompanying text for more information on model input and structure.

A 25% reduction in the mean annual rate of calf production led to substantial decreases in annual population growth rates under alternative models of adult mortality. Under baseline conditions of adult mortality, the mean growth rate with depressed calf production was *r* = -0.0403 – a 66% decrease compared to the growth rate of the model featuring the baseline level of calf production (*r* = -0.0243). When the exponential coefficient describing adult mortality was reduced by 50%, the simulated population growth rate became *r* = -0.0146 under depressed calf production rates, which is again a major reduction in growth rate compared to the same scenario that includes the baseline rate of calf production (*r* = -0.0012: Figure 5). The results of this combined sensitivity analysis are summarized in Figure 7.

The results of our demographic sensitivity analysis are consistent with what we would expect from a more formal analysis of the sensitivity and elasticity (proportional sensitivity) of our baseline demographic model. As described at length in the population ecology literature (e.g., Heppell et al. 2000), species such as marine mammals with “slow” life histories – characterized by late sexual maturation, low reproductive rates and high adult survival rates – will be highly sensitive on a consistent unit-change basis to changes in adult survival, moderately sensitive to changes in juvenile survival, and less sensitive to changes in fecundity.

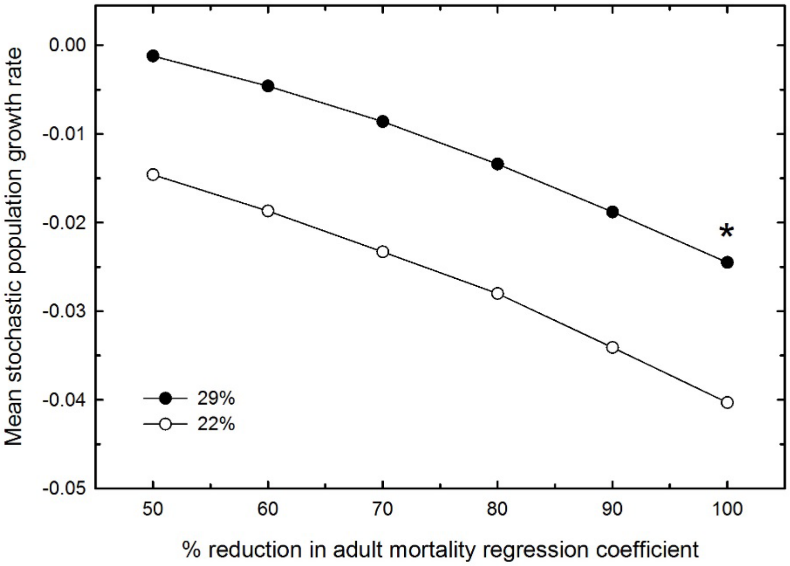


Figure 7. Summary plot of the sensitivity of the baseline model of Chinese white dolphin demographics to changes in adult mortality (expressed as the reduction in the exponential coefficient describing adult mortality as a function of age) and fecundity (calf production). Numbers in the figure legend refer to the mean annual percentage of adult females producing a calf. Data point with the asterisk identifies the baseline population model. See accompanying text for more information on model input and structure.

Metapopulation model: Baseline model performance

Under an assumed metapopulation configuration featuring three subunits, and when using slightly modified demographic rates used in the single-population baseline model, the PRE population of Chinese white dolphins showed marked rates of decline in population abundance when projected into the future, with growth rates differing among subunits. Moreover, the risk of extinction of the Hong Kong subunit became apparent approximately 20 years into the simulation, and grew steadily over time (Figure 8). The Western PRE subunit had a mean growth rate of r = -0.0211, the Eastern PRE subunit had a growth rate of r = -0.0256, and the Hong Kong subunit had a growth rate of r = -0.0464.

The differences in growth rate across the subunits is a reflection of the assumed conditions defined in the specific input parameters. The Western PRE subunit, considered to be under relatively lower levels of anthropogenic threat, showed the lowest rate of decline in abundance. The Eastern PRE and Hong Kong subunits showed higher rates of decline that arise from increased mortality and lower rates of calf production. The greatest rate of abundance decline in the Hong Kong subunit results from the additional impact of a net out-flow of individuals from the subunit over the first 20 years of the simulation, as the rate of emigration to the neighboring Eastern PRE subunit is greater than the rate of immigration into Hong Kong (Figure 9). This figure also shows the net positive movement into the Eastern PRE as dolphins move in from both Western PRE (which is demographically more robust) and from Hong Kong. Similarly, Figure 9 shows the net negative movement out of the Western PRE as the subunit exchanges dolphins with the Eastern PRE that is declining at a faster rate. As all three subunits decline to small abundances later in the simulation, overall movement across subunit boundaries becomes rarer and, therefore, the net movement approaches zero.

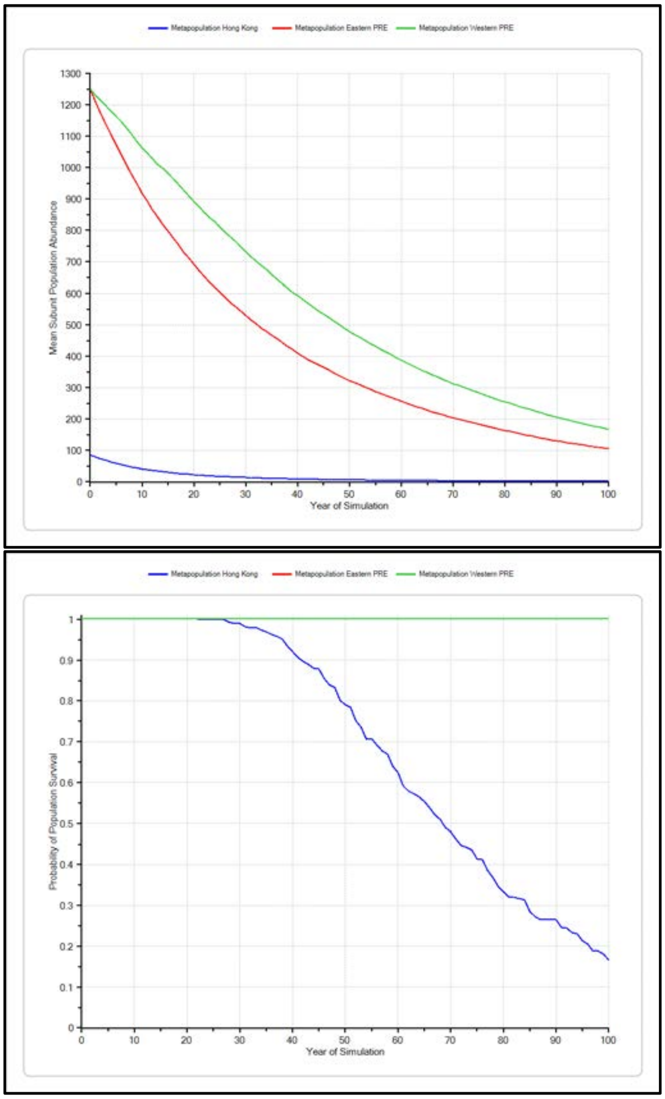
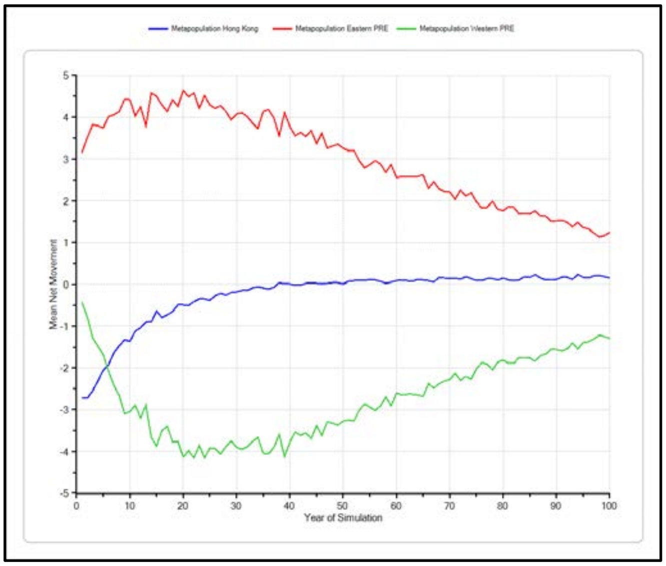


Figure 8. Trajectories of mean population abundance (top panel) and probability of population survival (bottom panel) for each of the three subunits making up the PRE Chinese white dolphin metapopulation demographic model. See accompanying text for more information on model input and structure.

Figure 9. Net annual movement of individuals ([# immigrants] – [# emigrants]) for each of the three subunits making up the PRE Chinese white dolphin metapopulation demographic model. Positive values indicate net addition of individuals to the subunit. See accompanying text for more information on model input and structure.



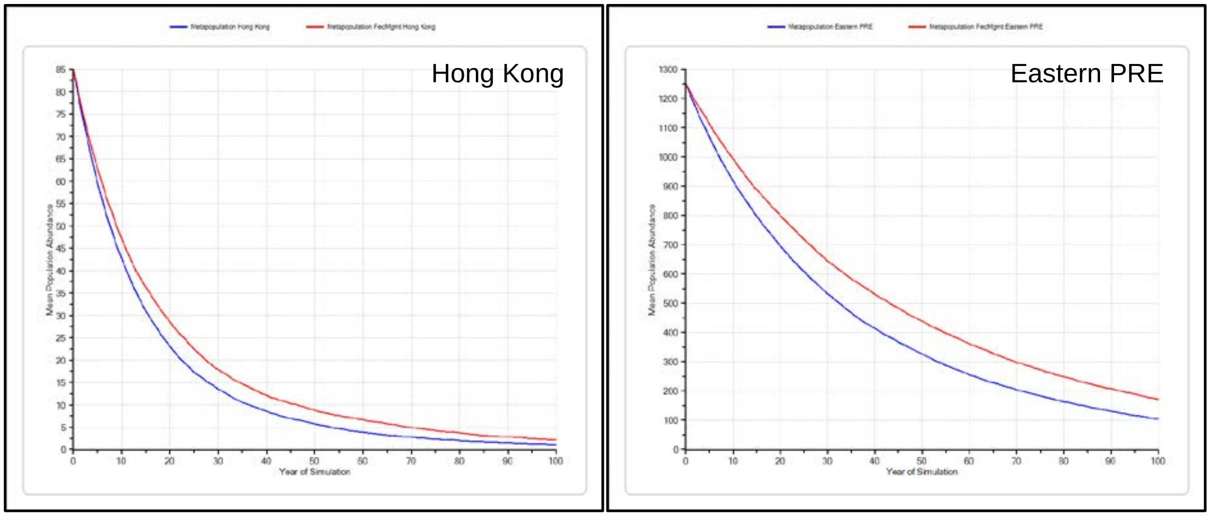
There are no specific estimates of changes in dolphin abundance in the Eastern and Western subunits of the PRE. However, Hung (2016) reports estimates of annual change in observed dolphin abundance in the Hong Kong subunit from data obtained through line-transect vessel surveys. Over the period 2010 – 2015, the dolphin abundance in Hong Kong waters declined from 85 to 65 individuals. [Note, however, that the decline in abundance over this period was not a steady annual decline but instead featured periods of population increase as well as decrease.] Our simulated Hong Kong subunit population declined to 60 individuals in the same period of time. While the data reported by Hung in the HKCRP annual monitoring reports may not be a measure of true population abundance, it is reasonable to propose that documented declines in abundance result from a combination of high rates of mortality among dolphins in HK waters and from a net out-flow of individuals that may be escaping areas of intense human activity such as the waters north and northwest of Lantau Island. Our demographic model attempts to account for both of these processes, and therefore may be a reasonably realistic simulation of the varied demographic impacts of anthropogenic disturbance on Chinese white dolphin population dynamics.

Metapopulation model: Demographic management scenario results

If we accept the current analysis of stranding data that suggest a declining abundance of Chinese white dolphins in the PRE (Huang et al. 2012), and as confirmed by the results obtained in that same study and from the demographic simulations described in this report, we should then use our demographic model to begin exploring the demographic conditions under which we might expect to see positive growth of this population. Each of the scenarios described in this section were based on the metapopulation model defined by the three subunits described in the previous section. Note that the scenarios presented here do not describe the details of specific management activities that would be carried out at a given level of effort in specific locations within the waters of the Pearl River Estuary; instead, we only describe changes in specific vital rates that would perhaps result from one or more unspecified management actions. This limitation of the current simulation-based approach to conservation planning will be discussed in more detail in a later section.

First, we may explore the degree to which population growth could be increased through improvements to calf production alone. We simulate this by increasing the mean percentage of adult females that produce a calf each year. The shortest interbirth interval for Chinese white dolphins in the PRE is approximately three years (Jefferson et al. 2012), which means that the mean annual percentage of adult females producing a calf is not likely to exceed about 30%. Therefore, a model scenario was constructed in which the % adult females producing a calf was increased to 30% for each metapopulation subunit. Given that the baseline values for this parameter ranged from a minimum of 25% in the Hong Kong subunit to 29% for the Western PRE subunit, this manipulation represents a rather modest absolute change in demographic performance for each subunit.

The results of this analysis are shown for each subunit in Figure 10. The trajectories clearly showed that the relatively small absolute improvement in calf production defining this scenario is not sufficient to make a significant improvement in growth rate in any of the subunits. Population growth in the Hong Kong subunit increased from $r = -0.046$ to $r = -0.038$, in the Eastern PRE subunit from $r = -0.026$ to $r = -0.021$, and in the Western PRE from $r = -0.021$ to $r = -0.017$. This is not a surprising result, given that we are making only modest improvements to a relatively insensitive demographic parameter. Unfortunately, since we do not have good data on the actual rate of calf production across the three PRE subunits, we don't know the extent to which this parameter can be manipulated. Nevertheless, it is likely that focusing on managing threats to calf production alone will not produce significant improvements to dolphin population growth.



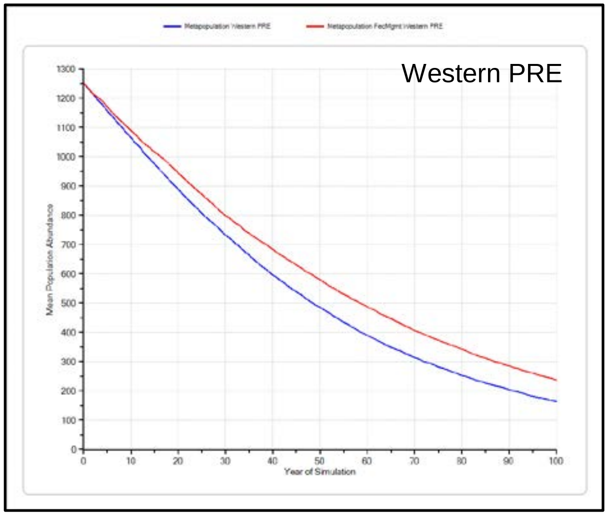


Figure 10. Abundance trajectories for the three subunits comprising the PRE metapopulation of Chinese white dolphins, under conditions of improved annual calf production (red line). The baseline model trajectory is shown by the lower blue line. See accompanying text for more information on model input and structure.

Second, we can assess how our simulated dolphin population will respond to improvements made to age-specific survival alone, leaving fecundity (calf production) at its baseline value. We simulated this by assuming that all age-specific mortality rates for each of the three subunits are reduced proportionally by 20% relative to the baseline values used for the single-population model presented earlier. In this way, the numerical factor used to modify mortality in the Hong Kong and Eastern PRE subunits was reduced from 1.05 to 0.8, and the factor used in the Western PRE subunit was reduced from 0.9 to 0.8. This scenario therefore implies a more aggressive approach to manipulating vital rates in the Hong Kong and Eastern PRE subunits, which may or may not be realistic given the realities of dolphin population management options. Despite this uncertainty, the modeling approach described here can be useful for assessing the value of a given improvement in population demographic performance.

The results of this analysis for each subunit are shown in Figure 11. The impacts of this manipulation on population growth rate were greater than those observed when calf production alone was improved, especially for the Eastern and Western PRE subunits. Population growth in the Hong Kong subunit increased from r = -0.046 to r = -0.020 in the Eastern PRE subunit from r = -0.026 to r = -0.005, and in the Western PRE subunit from r = -0.021 to r = -0.004. Overall, it is clear that the improvement in mortality simulated here could have a major influence on future dolphin population growth among the mainland China subunits of the PRE population of the Chinese white dolphin. Again, this should not be surprising given the relative magnitude of demographic improvement being simulated here, and with that level of improvement being imposed on a sensitive demographic parameter responsible for driving population growth. However, it remains uncertain how realistic this level of mortality improvement may be in the field and how this improvement could actually be achieved.

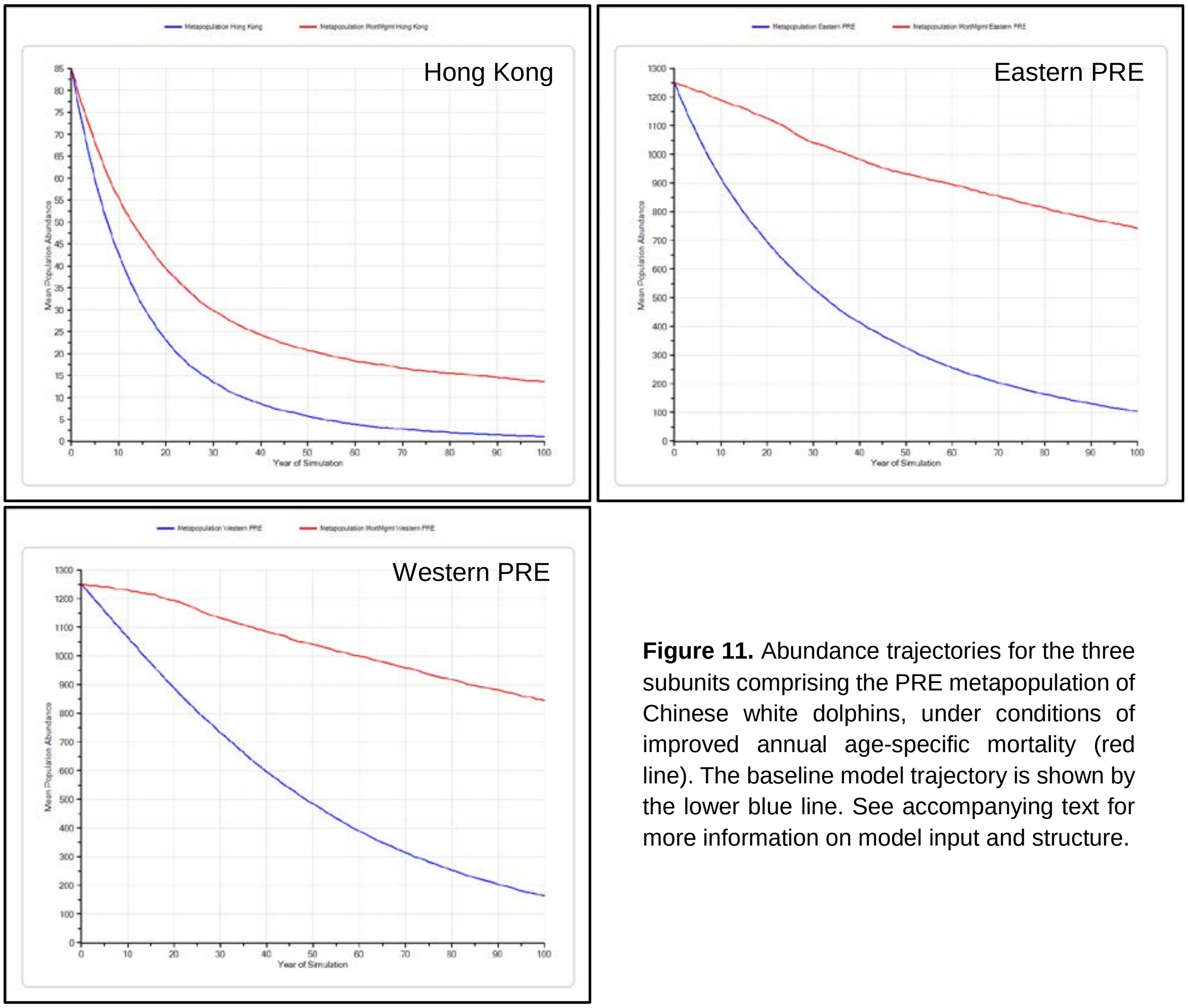


Figure 11. Abundance trajectories for the three subunits comprising the PRE metapopulation of Chinese white dolphins, under conditions of improved annual age-specific mortality (red line). The baseline model trajectory is shown by the lower blue line. See accompanying text for more information on model input and structure.

When both calf production and age-specific mortality were targeted for improvement through management, the Eastern PRE and Western PRE subunits showed positive population growth for the first 10-15 years of the simulation (Figure 12). This growth, however, was then attenuated and the population began to decline as the lower carrying capacity of the subunits restricted growth. Interestingly, the trajectory for the Hong Kong subunit continued to show a steady decline in dolphin abundance, even under the relatively favorable scenario of improved fecundity (calf production) and age-specific mortality. This result suggests that the continued emigration of individuals out of this subunit, which we assume to be in response to anthropogenic disturbance, is greater than the intrinsic capacity of that subunit to grow in abundance.

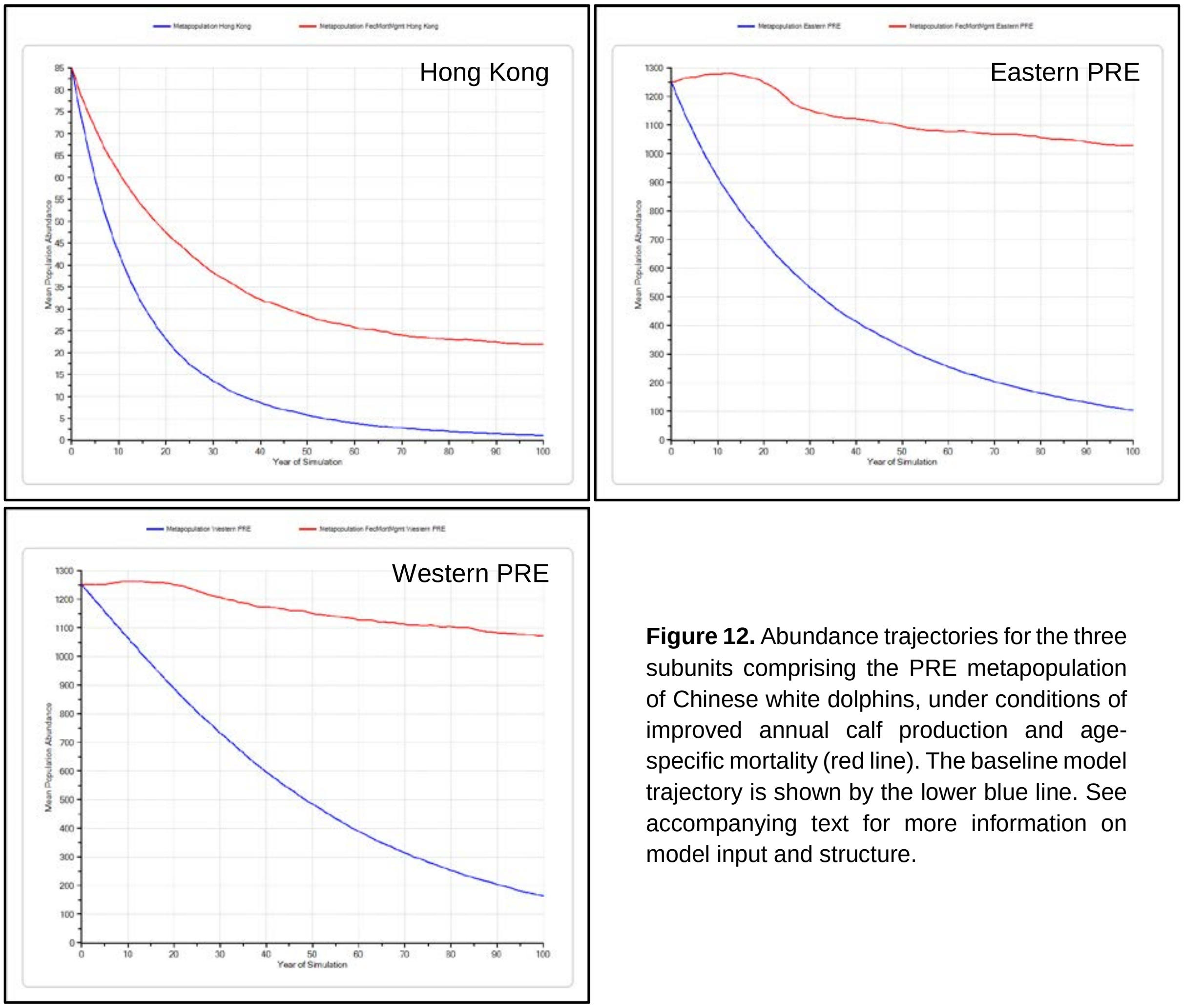


Figure 12. Abundance trajectories for the three subunits comprising the PRE metapopulation of Chinese white dolphins, under conditions of improved annual calf production and age-specific mortality (red line). The baseline model trajectory is shown by the lower blue line. See accompanying text for more information on model input and structure.

To explore this dispersal mechanic a bit further, the above scenario featuring combined management of calf production and age-specific mortality was modified so that the annual emigration rate of dolphins out of the Hong Kong subunit was cut in half from 5% to 2.5%, and the immigration rate into that subunit from the Eastern PRE was doubled from 0.1% to 0.2%. As shown in Figure 13, the result of this seemingly modest change to demographic connectivity was a dramatic increase in population abundance and stability in the Hong Kong subunit. The population was able to grow for the first 20 years at a rate of approximately 0.5% per year, after which time the loss of carrying capacity began to limit growth. The figure also shows that this growth was aided by the retention of dolphins within the Hong Kong subunit. The net movement of individuals in this subunit was very slightly positive over the first 25 years of the simulation, instead of the strongly negative net movement observed when emigration of dolphins out of Hong Kong was assumed to be high. The improved stability of the Hong Kong subunit was certainly also aided by increased connectivity with the neighboring Eastern PRE subunit. Taken together, this improvement in metapopulation dynamics resulted in an additional 3-4 dolphins counted in the Hong Kong subunit in early stages of the simulation.

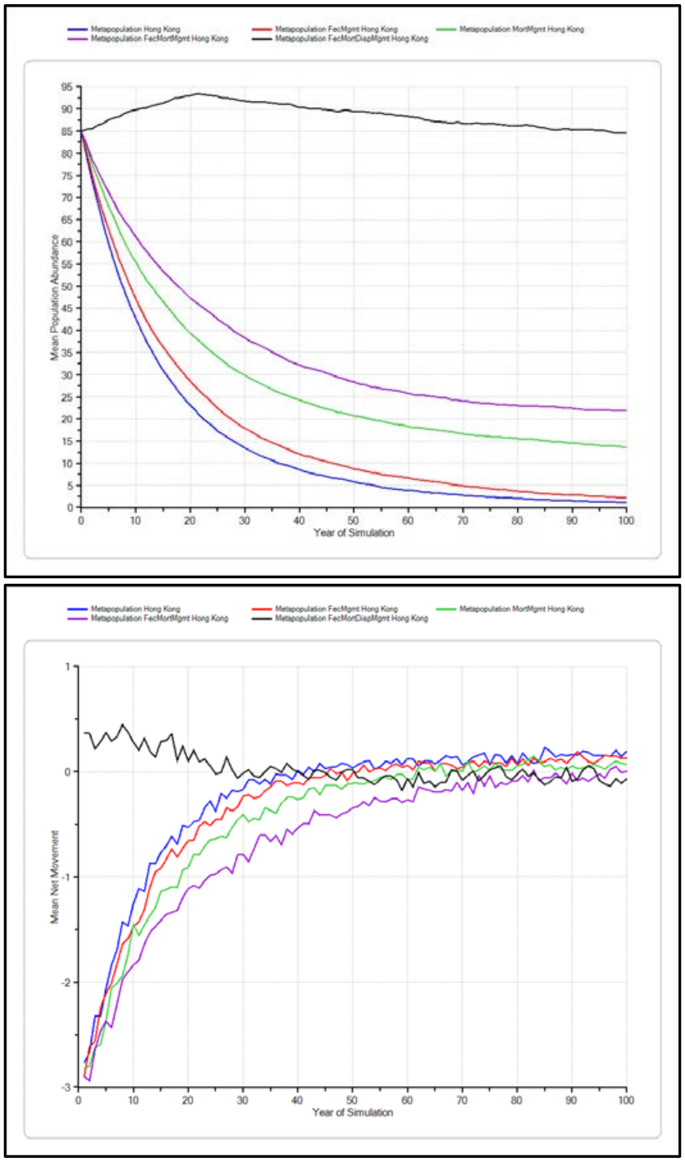


Figure 13. Abundance trajectories (top panel) and mean annual net movement of individuals (bottom panel) for the Hong Kong subunit of Chinese white dolphins in the Pearl River Estuary, under alternative demographic management scenarios. The blue line in each panel is the current baseline scenario. Red line, management for increased calf production; green line, management of age-specific mortality; purple line, management of both calf production and age-specific mortality; black line, inclusion of reduced emigration rate from Hong Kong to the Eastern PRE subunit. See accompanying text for more information on model input and structure.

If the gradual loss of carrying capacity through elimination of dolphin habitat was removed from the simulation, each of the three subunit population showed very slight increases in abundance over the duration of the simulation with growth rates in the range of $r = 0.0001$ to $r = 0.001$. In this scenario, given what we believe to be rather generous estimates of calf production, achieving increased rates of growth would require continued reductions in impacts of anthropogenic threats to mortality, particularly of older age classes.

Conclusions

The population of Indo-Pacific humpback dolphin (*Sousa chinensis*) occupying the Pearl River Estuary (PRE), known locally as the Chinese white dolphin (CWD), is under intense pressure from human activities around Hong Kong and in the coastal waters to the west. The demographic analysis described in this report was designed to evaluate the current demographic status of the population, to identify those vital rates that are critical for sustained population growth, and to develop preliminary assessments of the demographic and ecological conditions necessary for long-term population growth and stability. Two alternative simulation modeling approaches were used to evaluate current demographic status of the population. First, we treated the dolphins occupying the PRE as a single population without spatial structure, and used published demographic analyses to derive reproduction and survival rates for use as model input. Our second approach featured a metapopulation structure with three population subunits (Hong Kong, Eastern PRE, and Western PRE), thereby allowing us to develop demographic rates for each subunit that, at least qualitatively, reflected our hypotheses regarding the nature and intensity of threats to dolphins resulting from human activities in the area.

Our population viability models, using both approaches and based on the best available data on CWD reproduction and survival in the PRE, predicted that the dolphin population is likely to be declining at a rate of more than 2% per year and will continue to decline if the situation in the waters of the PRE does not change. However, there is a considerable amount of uncertainty around this prediction as we have incomplete information on the rates of reproduction and survival for the species in this habitat. There is even greater uncertainty when we think about demographics in a metapopulation context where vital rates will likely differ among population subunits. Sensitivity analysis using our baseline demographic model demonstrated that even modest changes to survival rates – particularly of adults – can lead to significant changes in our prediction of future dynamics of the PRE dolphin population. It is therefore imperative that the long-term research projects currently ongoing in the eastern portion of the PRE be continued and expanded to produce more reliable estimates of dolphin demography. Moreover, this research needs to be expanded westward in order to improve our understanding of CWD demographic dynamics in the western portion of the PRE population distribution. The extensive photo-identification databases of dolphins across the eastern portions of the PRE could be a critically important resource for documenting the demographics of individuals through time. A protocol for integrating these databases was discussed at the March/April 2016 PVA workshop (Miller et al. 2016); achieving this functional integration is seen as a high priority for improved conservation research and management of the species in the PRE.

Related to these needs, and even more importantly from the perspective of wildlife conservation management, is the critical need to better understand and characterize the impacts of anthropogenic activities on CWD behavior and resulting demographics in the PRE. Improved demographic analysis across PRE subunits will require in-depth analysis of the quantitative impacts of specific anthropogenic activities (disturbance) on dolphin behavior and physiology, which will ultimately impact vital rates. Efforts to specify this information to date have been largely descriptive (i.e., qualitative threats analysis as presented in Wilson et al. (2008) and Miller et al. (2016)), but the research on quantifying impacts of disturbance on CWD behavior is expanding (see Piwetz at al. (2016) and Würsig et al. (2016) for reviews).

The specification of impacts of multiple anthropogenic threats on wildlife populations is often referred to as cumulative effects (impact) analysis. In order to use such an analysis in concert with a population viability analysis, ideally one must specify the unit change in a given demographic parameter that results from a unit change in a specific activity. For example, consider the impact of vessel traffic on dolphin calf mortality, where the unit of activity is the number of vessels observed to move through a defined area per unit time. If we measure dolphin calf mortality in the absence of vessel activity to be $q(0)$, we would then specify that mortality in the presence of vessel traffic as $q(0) + \alpha$, where α is additional mortality imposed on calves per unit of vessel activity in the area of measurement. If we also propose that calf mortality is affected by another factor such as the concentration of persistent organic pollutants (POPs) in animal tissue, we would then need to identify the impact of this threat as $q(0) + \beta$, where β is the additional mortality imposed on calves per unit concentration of specific POPs in the animal's tissue. [Note that various contaminants such as POPs are currently considered to be an important threat to Chinese white dolphins (e.g., Jia et al. 2015).] The cumulative impact of these activities on dolphin calf mortality may therefore be equal to $q(0) + \alpha + \beta$, or perhaps some other more complex expression that features interactions between the two measures of impacts.

However these activities are defined and quantitatively characterized, this type of analytical process is fundamental to the proper integration of a cumulative effects analysis into a PVA. The process has been formalized as the PCoD (population consequences of disturbance) framework for marine mammals (NRC 2005) (Figure 14) and was applied by New et al. (2014) to an assessment of disturbance on southern elephant seals (*Mirounga leonine*) in Australia. An extension of applying this framework to wildlife conservation decision-making was conducted by King et al. (2015) in assessing the impacts of disturbance in the form of wind farm construction on a population of harbor porpoise (*Phocoena phocoena*) in the North Sea. In this application, formal expert elicitation methods (Martin et al. 2012) were used to estimate the quantitative impacts of anthropogenic disturbance of population vital rates, which were then incorporated into a population dynamics model for viability analysis. This study demonstrates the value of combining field research with sophisticated information analysis methods to derive consensus estimates of how disturbance affects wildlife populations.

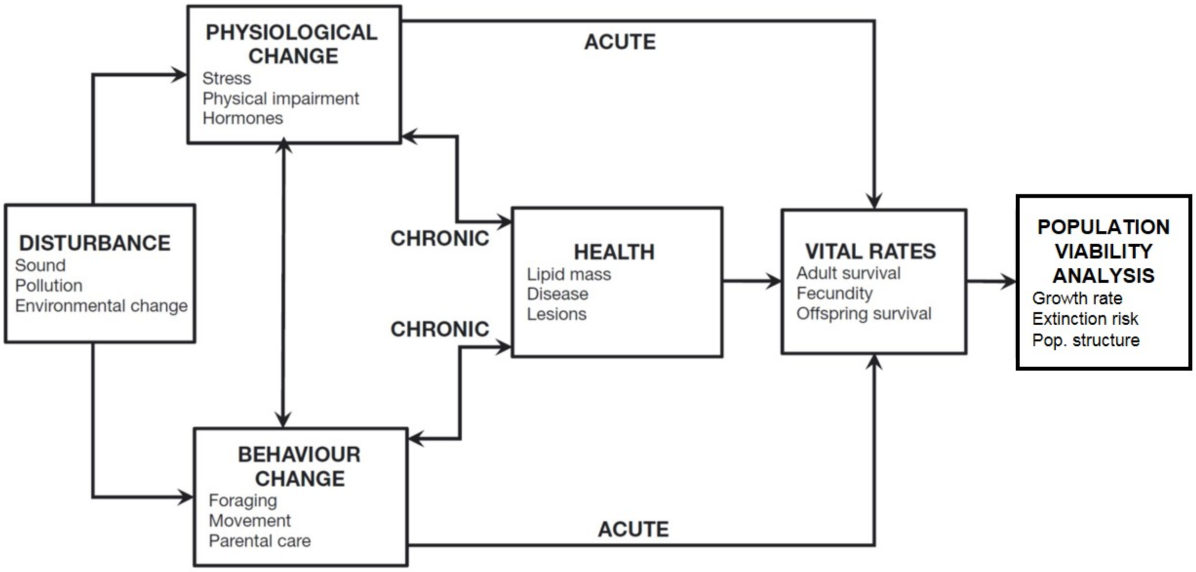


Figure 14. Graphical representation of the population consequences of disturbance (PCoD) framework for evaluating impacts of anthropogenic threats on wildlife populations. Figure adapted from New et al. (2014).

Unfortunately, the analysis described in this report did not include the type of cumulative effects analysis described in New et al. (2014) or King et al. (2015). Our inability to conduct such an analysis results from insufficient detailed information on (1) the true rate of abundance change for dolphins inhabiting different geographic subunits of the PRE, (2) age-specific estimates of CWD reproduction and survival rates in the absence of anthropogenic disturbance in the PRE, and (3) the quantitative impacts of specific anthropogenic threats across those subunits. It may be possible to generate these data from a combination of focused field research, more detailed analysis of existing animal data such as that making up the photo-ID databases, and careful implementation of expert elicitation methods to generate information where data are lacking. In the absence of these data, the analysis presented here must be considered largely exploratory and illustrative of the kinds of assessments that can be constructed using a predictive demographic modeling tool like *Vortex*.

References

Araújo, C.C., J.Y. Wang, S.K. Hung, B.N. White, and D. Brito. 2014. Viability of the Critically Endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphin *Sousa chinensis*. *End. Species Res.* **24**:263-271.

Beissinger, S. and D. McCullough (eds.). 2002. *Population Viability Analysis*. University of Chicago Press, Chicago, IL.

Brook, B.W., J.J. O'Grady, A.P. Chapman, M.A. Burgman, H.R. Akcakaya, and R. Frankham. 2000a. Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**:385-387.

Brook, B.W., Burgman, M.A., and R. Frankham. 2000b. Differences and congruencies between PVA packages: The importance of sex ratio for predictions of extinction risk. *Conservation Ecology* **4.1**. Online: http://www.consecol.org/vol4/iss1/art6/index.html

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

Freckleton, R.P., A.R. Watkinson, R.E. Green, and W.J. Sutherland. 2006. Census error and the detection of density dependence. *J. Anim. Ecol.* **75**:837-851.

Heppell, S.S., H. Caswell, and L.B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* **81**:654-665.

Huang, S.-L., L. Karczmarski, J. Chen, R. Zhou, W. Lin, H. Zhang, H. Li, and Y. Wu. 2012. Demography and population trends of the largest population of Indo-Pacific humpback dolphins. *Biol. Cons.* **147**:234-242.

Huang, S.-L., W.-L. Chang, and L. Karczmarski. 2014. Population trend and vulnerability of humpback dolphins *Sousa chinensis* off the west coast of Taiwan. *End. Species Res*. **26**:147-159.

Hung S.K. 2015. Monitoring of marine mammals in Hong Kong waters – final report (2014 - 15). Agriculture, Fisheries and Conservation Department of the Hong Kong Special Administrative Region Government, Hong Kong.

Hung, S.K. 2016. Monitoring of marine mammals in Hong Kong waters – final report (2015 - 16). Agriculture, Fisheries and Conservation Department, Hong Kong Special Administrative Region Government, Hong Kong.

Jefferson, T.A., S.K. Hung, K.M. Robertson, and F.I. Archer. 2012. Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. *Mar. Mamm. Sci.* **28**:84-104.

Jefferson, T.A., and B.D. Smith. 2016. Re-assessment of the conservation status of the Indo-Pacific humpback dolphin (Sousa chinensis) using the IUCN Red List criteria. *Adv. Mar. Biol.* **73**:1-26.

Jia, K., L. Ding, L. Zhang, M. Zhang, M. Yi, and Y. Wu. 2015. In vitro assessment of environmental stress of persistent organic pollutants on the Indo-Pacific humpback dolphin. *Toxic. in Vitro* **30**:529-535.

Karczmarski, L., S.-L. Huang, C.K.M. Or, D. Gui, S.C.Y. Chan, *et al*. 2016. Humpback dolphins in Hong Kong and the Pearl River Delta: Status, threats and conservation challenges. *Adv. Mar. Biol*. **73**:27-64.

King, S.L., R.S Schick, C. Donovan, C.G. Booth, M. Burgman, L. Thomas, and J. Harwood. 2015. An interim framework for assessing the population consequences of disturbance. *Meth. Ecol. Evol.* **6**:1150-1158.

Lacy, R.C. 2000. Structure of the *VORTEX* simulation model for population viability analysis. *Ecol. Bull.* 48:191-203.

Lacy, R.C., and J.P. Pollak. 2014. *VORTEX: A Stochastic Simulation of the Extinction Process. Version 10.0*. Chicago Zoological Society, Brookfield, IL.

Lande, R., S. Engen, B.-E. Sæther, F. Filli, E. Matthysen, and H. Weimerskirsch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. *Am. Nat.* **159**:321-337.

Lande, R., S. Engen, B.-E. Sæther, and T. Coulson. 2006. Estimating density dependence from time series of population age structure. *Amer. Nat.* **168**:76-87.

Lotts, K.C., T.A. Waite, and J.A. Vucetich. 2004. Reliability of absolute and relative predictions of population persistence based on time series. *Cons. Biol.* **18**:1224-1232.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* **80:**298–310.

Martin, T., M. Burgman, F. Fidler, P. Kuhnert, S. Low-Choy, M. McBride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. *Cons. Biol.* **26**:29-38.

Miller, P.S., R.L. Brownell, R.J.C. Currey, W. Ding, S. Gendron, F.M.D. Gulland, L. Karczmarski, R.R. Reeves, R.S. Wells, J.Y. Wang and B. Würsig (Eds.). 2016. *Population Viability Analysis for the Chinese White Dolphin in the Pearl River Estuary: Progress Report.* Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Morris, W.F., and D.F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA.

New, L.F., J.S. Clark, D.P. Costa, E. Fleishman, M.A. Hindell, T. Klanjšček, et al. 2014. Using short-term measures of behavior to estimate long-term fitness of southern elephant seals. *Mar. Ecol. Prog. Ser.* **496**:99-108.

NRC. 2005. *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*. Washington, DC: The National Academy Press.

Piwetz, S., D. Lundquist, and B. Würsig. 2016. Humpback dolphin (Genus *Sousa*) behavioral responses to human activities. *Adv. Mar. Biol.* **72**:17-45.

Reed, J.M., L.S. Mills, J.B. Dunning Jr., E.S. Menges, K.S. McKelvey, R. Frye, S.R. Beissinger, M.-C. Anstett, and P.S. Miller. 2002. Emerging issues in population viability analysis. *Cons. Biol.* **16**:7-19.

Reeves, R.R., M.L. Dalebout, T.A. Jefferson, L. Karczmarski,, K. Laidre, G. O'Corry-Crowe, L. Rojas-Bracho, E.R. Secchi, E. Slooten, B.D. Smith, J.Y. Wang, and K. Zhou. 2008. *Sousa chinensis*. In: *The IUCN Red List of Threatened Species*. Version 2014.3. www.iucnredlist.org.

Schaeff, C.M., S.D. Kraus, M.W. Brown, J. Perkins, R. Payne and B.N. White. 1997. Comparison of genetic variability of north and south Atlantic right whales (*Eubalaena*) using DNA fingerprinting. *Can. J. Zool.* **75**:1073-1080.

Wang, J.Y., S.C. Yang, and S.K. Hung. 2015. Diagnosability and description of a new subspecies of Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), from the Taiwan Strait. *Zool. Stud.* **54**:36.

Weber, D.S., B.S. Stewart, J. Schienmann, and N. Lehman. 1997. Major histocompatibility complex variation at three class II loci in the northern elephant seal. *Mol. Ecol.* **13**:711-718.

Wilson, B., L. Porter, J. Gordon, J. Hammond, N. Hodgins, L. Wei, J. Lin, D. Lusseau, A. Tsang, K. van Waerebeek, and Y.P. Wu. 2008. *A Decade of Management Plans, Conservation Initiatives and Protective Legislation for Chinese White Dolphin (*Sousa chinensis*): An Assessment of Progress and Recommendations for Future Management Strategies in the Pearl River Estuary, China.* Workshop Report, 7-11 April, 2008. Hong Kong: WWF Hong Kong. 65pp.

Würsig, B., E.C.M. Parsons, S. Piwetz, and L. Porter. 2016. The behavioral ecology of Indo-Pacific humpback dolphins in Hong Kong. *Adv. Mar. Biol.* **73**:65-90.

Appendix I:
Population Viability Analysis and Simulation Modeling

Philip S. Miller, Ph.D.
Conservation Breeding Specialist Group (IUCN/SSC)

Robert C. Lacy, Ph.D.
Chicago Zoological Society

Introduction

Thousands of species and populations of animals and plants around the world are threatened with extinction within the coming decades. For the vast majority of these groups of organisms, this threat is the direct result of human activity. The particular types of activity, and the ways in which they impact wildlife populations, are often complex in both cause and consequence; as a result, the techniques we must use to analyze their effects often seem to be complex as well. But scientists in the field of conservation biology have developed extremely useful tools for this purpose that have dramatically improved our ability to conserve the planet's biodiversity.

Conservation biologists involved in recovery planning for a given threatened species usually try to develop a detailed understanding of the processes that put the species at risk, and will then identify the most effective methods to reduce that risk through active management of the species itself and/or the habitat in which it lives. In order to design such a program, we must engage in some sort of predictive process: we must gather information on the detailed characteristics of proposed alternative management strategies and somehow predict how the threatened species will respond in the future. A strategy that is predicted to reduce the risk by the greatest amount – and typically does so with the least amount of financial and/or sociological burden – is chosen as a central feature of the recovery plan.

But how does one predict the future? Is it realistically possible to perform such a feat in our fast-paced world of incredibly rapid and often unpredictable technological, cultural, and biological growth? How are such predictions best used in wildlife conservation? The answers to these questions emerge from an understanding of what has been called "the flagship industry" of conservation biology: population viability analysis, or PVA. And most methods for conducting PVA are merely extensions of tools we all use in our everyday lives.

The Basics of PVA

To appreciate the science and application of PVA to wildlife conservation, we first must learn a little bit about population biology. Biologists will usually describe the performance of a population by describing its demography, or simply the numerical depiction of the rates of birth and death in a group of animals or plants from one year to the next. Simply speaking, if the birth rate exceeds the death rate, a population is expected to increase in size over time. If the reverse is true, our population will decline. The overall rate of population growth is therefore a rather good descriptor of its relative security: positive population growth suggests some level of demographic health, while negative growth indicates that some external process is interfering with the normal population function and pushing it into an unstable state.

This relatively simple picture is, however, made a lot more complicated by an inescapable fact: wildlife population demographic rates fluctuate unpredictably over time. So if we observe that 50% of our total population of adult females produces offspring in a given year, it is almost certain that more or less than

50% of our adult females will reproduce in the following year. And the same can be said for most all other demographic rates: survival of offspring and adults, the numbers of offspring born, and the offspring sex ratio will almost always change from one year to the next in a way that usually defies precise prediction. These variable rates then conspire to make a population's growth rate also change unpredictably from year to year. When wildlife populations are very large – if we consider seemingly endless herds of wildebeest on the savannahs of Africa, for example – this random annual fluctuation in population growth is of little to no consequence for the future health and stability of the population. However, theoretical and practical study of population biology has taught us that populations that are already small in size, often defined in terms of tens to a few hundred individuals, are affected by these fluctuations to a much greater extent – and the long-term impact of these fluctuations is always negative. Therefore, a wildlife population that has been reduced in numbers will become even smaller through this fundamental principle of wildlife biology. Furthermore, our understanding of this process provides an important backdrop to considerations of the impact of human activities that may, on the surface, appear relatively benign to larger and more stable wildlife populations. This self-reinforcing feedback loop, first coined the "extinction vortex" in the mid-1980's, is the cornerstone principle underlying our understanding of the dynamics of wildlife population extinction.

Once wildlife biologists have gone out into the field and collected data on a population's demography and used these data to calculate its current rate of growth (and how this rate may change over time), we now have at our disposal an extremely valuable source of information that can be used to predict the *future* rates of population growth or decline under conditions that may not be so favorable to the wildlife population of interest. For example, consider a population of primates living in a section of largely undisturbed Amazon rain forest that is now opened up to development by logging interests. If this development is to go ahead as planned, what will be the impact of this activity on the animals themselves, and the trees on which they depend for food and shelter? And what kinds of alternative development strategies might reduce the risk of primate population decline and extinction? To try to answer this question, we need two additional sets of information: 1) a comprehensive description of the proposed forest development plan (how will it occur, where will it be most intense, for what period of time, etc.) and 2) a detailed understanding of how the proposed activity will impact the primate population's demography (which animals will be most affected, how strongly will they be affected, will animals die outright more frequently or simply fail to reproduce as often, etc.). With this information in hand, we have a vital component in place to begin our PVA.

Next, we need a predictive tool – a sort of crystal ball, if you will, that helps us look into the future. After intensive study over nearly three decades, conservation biologists have settled on the use of computer simulation models as their preferred PVA tool. In general, models are simply any simplified representation of a real system. We use models in all aspects of our lives; for example, road maps are in fact relatively simple (and hopefully very accurate!) 2-dimensional representations of complex 3-dimensional landscapes we use almost every day to get us where we need to go. In addition to making predictions about the future, models are very helpful for us to: (1) extract important trends from complex processes, (2) allow comparisons among different types of systems, and (3) facilitate analysis of processes acting on a system.

Recent advances in computer technology have allowed us to create very complex models of the demographic processes that define wildlife population growth. But at their core, these models attempt to replicate simple biological functions shared by most all wildlife species: individuals are born, some grow to adulthood, most of those that survive mate with individuals of the opposite sex and then give birth to one or more offspring, and they die from any of a wide variety of causes. Each species may have its own special set of circumstances – sea turtles may live to be 150 years old and lay 600 eggs in a single event, while a chimpanzee may give birth to just a single offspring every 4-5 years until the age of 45 – but the fundamental biology is the same. These essential elements of a species' biology can be incorporated into a computer program, and when combined with the basic rules for living and the general characteristics of the population's surrounding habitat, a model is created that can project the demographic behavior of our real observed population for a specified period of time into the future. What's more, these models can explicitly incorporate random fluctuations in rates of birth and death discussed earlier. As a result, the models can be much more realistic in their treatment of the forces that influence population dynamics, and in particular how human activities can interact with these intrinsic forces to put otherwise relatively stable wildlife populations at risk.

Many different software packages exist for the purposes of conducting a PVA. Perhaps the most widely-used of these packages is *Vortex*, developed by the Chicago Zoological Society for use in both applied and educational environments. *Vortex* has been used by CBSG and other conservation biologists for more than 20 years and has proven itself to be a very useful tool for helping make more informed decisions in the field of wildlife population management.

The *Vortex* Population Viability Analysis Model

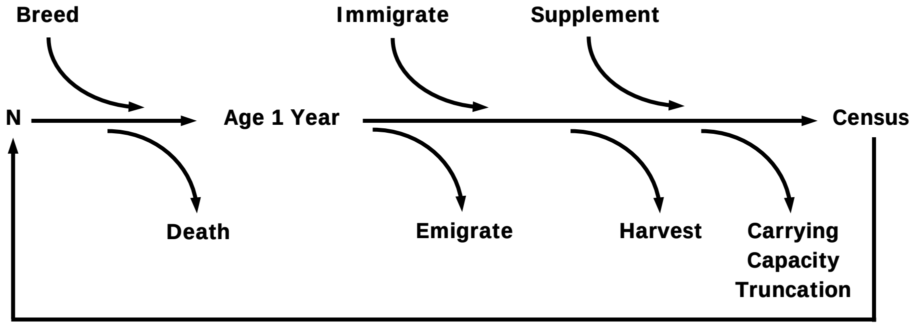
Vortex models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. *Vortex* also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations.

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

Vortex models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, *Vortex* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *Vortex* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Vortex is an *individual-based* model. That is, *Vortex* creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *Vortex* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX Simulation Model Timeline



Events listed above the timeline increase N, while events listed below the timeline decrease N.

Vortex requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *Vortex* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on *Vortex* is available in Lacy (2000) and Lacy et al. (2015).

Results reported for each scenario include:

> Deterministic r -- The deterministic population growth rate, a projection of the mean rate of growth of the population expected from the average birth and death rates. Impacts of harvest, inbreeding, and density dependence are not considered in the calculation. When r = 0, a population with no growth is expected; r < 0 indicates population decline; r > 0 indicates long-term population growth. The value of r is approximately the rate of growth or decline per year.
>
> The deterministic growth rate is the average population growth expected if the population is so large as to be unaffected by stochastic, random processes. The deterministic growth rate will correctly predict future population growth if: the population is presently at a stable age distribution; birth and death rates remain constant over time and space (i.e., not only do the probabilities remain constant, but the actual number of births and deaths each year match the expected values); there is no inbreeding depression; there is never a limitation of mates preventing some females from breeding; and there is no density dependence in birth or death rates, such as a Allee effects or a habitat "carrying capacity" limiting population growth. Because some or all of these assumptions are usually violated, the average population growth of real populations (and stochastically simulated ones) will usually be less than the deterministic growth rate.
>
> Stochastic r -- The mean rate of stochastic population growth or decline demonstrated by the simulated populations, averaged across years and iterations, for all those simulated populations that are not extinct. This population growth rate is calculated each year of the simulation, prior to any truncation of the population size due to the population exceeding the carrying capacity. Usually, this

stochastic r will be less than the deterministic r predicted from birth and death rates. The stochastic r from the simulations will be close to the deterministic r if the population growth is steady and robust. The stochastic r will be notably less than the deterministic r if the population is subjected to large fluctuations due to environmental variation, catastrophes, or the genetic and demographic instabilities inherent in small populations.

P(E) -- the probability of population extinction, determined by the proportion of, for example, 500 iterations within that given scenario that have gone extinct in the simulations. “Extinction” is defined in the *Vortex* model as the lack of either sex.

N -- mean population size, averaged across those simulated populations which are not extinct.

SD(N) -- variation across simulated populations (expressed as the standard deviation) in the size of the population at each time interval. SDs greater than about half the size of mean N often indicate highly unstable population sizes, with some simulated populations very near extinction. When SD(N) is large relative to N, and especially when SD(N) increases over the years of the simulation, then the population is vulnerable to large random fluctuations and may go extinct even if the mean population growth rate is positive. SD(N) will be small and often declining relative to N when the population is either growing steadily toward the carrying capacity or declining rapidly (and deterministically) toward extinction. SD(N) will also decline considerably when the population size approaches and is limited by the carrying capacity.

H -- the gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity (Lacy 1993), with a 10% decline in gene diversity typically causing about 15% decline in survival of captive mammals (Ralls et al. 1988). Impacts of inbreeding on wild populations are less well known, but may be more severe than those observed in captive populations (Jiménez et al. 1994). Adaptive response to natural selection is also expected to be proportional to gene diversity. Long-term conservation programs often set a goal of retaining 90% of initial gene diversity (Soulé et al. 1986). Reduction to 75% of gene diversity would be equivalent to one generation of full-sibling or parent-offspring inbreeding.

Strengths and Limitations of the PVA Approach

When considering the applicability of PVA to a specific issue, it is vitally important to understand those tasks to which PVA is well-suited as well as to understand what the technique is not well-designed to deliver. With this enhanced understanding will also come a more informed public that is better prepared to critically evaluate the results of a PVA and how they are applied to the practical conservation measures proposed for a given species or population.

The dynamics of population extinction are often quite complicated, with numerous processes impact the dynamics in complex and interacting ways. Moreover, we have already come to appreciate the ways in which demographic rates fluctuate unpredictably in wildlife populations, and the data needed to provide estimates of these rates and their annual variability are themselves often uncertain, i.e., subject to observational bias or simple lack of detailed study over relatively longer periods of time. As a result, the elegant mental models or the detailed mathematical equations of even the most gifted conservation biologist are inadequate for capturing the detailed nuances of interacting factors that determine the fate of a wildlife population threatened by human activity. In contrast, simulation models can include as many factors that influence population dynamics as the modeler and the end-user of the model wish to assess. Detailed interactions between processes can also be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes.

PVA models have also been shown to stimulate meaningful discussion among field biologists in the subjects of species biology, methods of data collection and analysis, and the assumptions that underlie the analysis of these data in preparation for their use in model construction. By making the models and their underlying data, algorithms and assumptions explicit to all who learn from them, these discussions become a critical component in the social process of achieving a shared understanding of a threatened species' current status and the biological justification for identifying a particular management strategy as the most effective for species conservation. This additional benefit is most easily recognized when PVA is used in an interactive workshop-type setting, such as the Population and Habitat Viability Assessment (PHVA) workshop designed and implemented by CBSG.

Perhaps the greatest strength of the PVA approach to conservation decision-making is related to what many of its detractors see as its greatest weakness. Because of the inherent uncertainty now known to exist in the long-term demography of wildlife populations (particularly those that are small in size), and because of the difficulties in obtaining precise estimates of demographic rates through extended periods of time collecting data in the field, accurate predictions of the future performance of a threatened wildlife population are effectively impossible to make. Even the most respected PVA practitioner must honestly admit that an accurate prediction of the number of mountain gorillas that will roam the forests on the slopes of the eastern Africa's Virunga Volcanoes in the year 2075, or the number of polar bears that will swim the warming waters above the Arctic Circle when our great-grandchildren grow old, is beyond their reach. But this type of difficulty, recognized across diverse fields of study from climatology to gambling, is nothing new: in fact, the Nobel Prize-winning physicist Niels Bohr once said "Prediction is very difficult, especially when it's about the future." Instead of lamenting this inevitable quirk of the physical world as a fatal flaw in the practice of PVA, we must embrace it and instead use our very cloudy crystal ball for another purpose: to make **relative**, rather than **absolute**, predictions of wildlife population viability in the face of human pressure.

The process of generating relative predictions using the PVA approach is often referred to as <u>sensitivity analysis</u>. In this manner, we can make much more robust predictions about the relative response of a simulated wildlife population to alternate perturbations to its demography. For example, a PVA practitioner may not be able to make accurate predictions about how many individuals of a given species may persist in 50 years in the presence of intense human hunting pressure, but that practitioner can speak with considerably greater confidence about the relative merits of a male-biased hunting strategy compared to the much more severe demographic impact typically imposed by a hunting strategy that prefers females. This type of comparative approach was used very effectively in a PVA for highly threatened populations of tree kangaroos (*Dendrolagus* sp.) living in Papua New Guinea, where adult females are hunted preferentially over their male counterparts. Comparative models showing the strong impacts of such a hunting strategy were part of an important process of conservation planning that led, within a few short weeks after a participatory workshop including a number of local hunters (Bonaccorso et al., 1998), to the signing of a long-term hunting moratorium for the most critically endangered species in the country, the tenkile or Scott's tree kangaroo (*Dendrolagus scottae*).

PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models often underestimate the threats facing the population, or the total risk these threats collectively impose on the population of interest. To address this limitation, conservation biologists must try to engage a diverse body of experts with knowledge spanning many different fields in an attempt to broaden our understanding of the consequences of interaction between humans and wildlife.

Additionally, models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed (see Lacy and Miller (2002), Nyhus et al. (2002) and Westley and Miller (2003) for more details).

Finally, it is also important to understand that a PVA model by itself does not define the goals of conservation planning of a given species. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used.

Sequence of *Vortex* Program Flow

(1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{max} = (K + 3s)(1 + L)$$

in which *K* is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), *s* is the annual environmental variation in the carrying capacity expressed as a standard deviation, and *L* is the specified maximum litter size.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.

(5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (e.g., Caswell 2001). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7 through 26 below.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *Vortex* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum \left(p_i^2 \right)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *Vortex* is the mean inbreeding coefficient of the population.

(9) For each of the10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.

(10) Years are iterated via steps 11 through 25 below.

(11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal *A*, and another existing animal, *B*, is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals *i* and *j*, *M* is the mother of *A*, and *P* is the father of *A*. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_{A} = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1-\Pr[Lethals])F}$$

in which *b* is the number of lethal equivalents per haploid genome, and Pr[*Lethals*] is the proportion of this inbreeding effect due to lethal alleles.

(18) The age of each animal is incremented by 1.

(19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *Vortex* continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (*N*) exceeds the carrying capacity (*K*) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to (*N* - *K*)/*N*, so that the expected population size after the additional mortality is *K*.

(25) Summary statistics on population size and genetic variation are tallied and reported.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.

References

Ballou, J.D. 1983. Calculating inbreeding coefficients from pedigrees. In: Pages 509-520 in: Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde, and W.L. Thomas (eds.) *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Menlo Park, CA, USA: Benjamin/Cummings.

Beissinger, S. and D. McCullough (eds.). 2002. *Population Viability Analysis*. Chicago, IL, USA: University of Chicago Press.

Bonaccorso, F., P. Clark, P.S. Miller and O. Byers (eds.). 1999. *Conservation Assessment and Management Plan for the Tree Kangaroos of Papua New Guinea and Population and Habitat Viability Assessment for Matschie's Tree Kangaroo* (Dendrolagus matschei): *Final Report*. Apple Valley, MN, USA: IUCN/SSC Conservation Breeding Specialist Group.

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Second edition. Sunderland, MA, USA: Sinauer Associates.

Crow, J.F., and M. Kimura. 1970. *An Introduction to Population Genetics Theory*. New York, NY, USA: Harper & Row.

Fraser, T.R., B.A. Mcleod, R.M. Gillett, M.W. Brown, and B.N. White. 2007. Right whales past and present as revealed by their genes. In: Kraus, S.D. and R.M. Rolland (Eds.). *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Boston, MA, USA: Harvard University Press.

Gilpin, M.E., and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19 – 34 in: Soulé, M.E. (ed.). *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA, USA: Sinauer Associates.

Jiménez, J.A., K.A. Hughes, G. Alaks, L. Graham, and R.C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271-273.

Lacy, R.C. 1993. Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology and Medicine* 36:480-496.

Lacy, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.

Lacy, R.C., and P.S. Miller. 2002. Incorporating human activities and economics into PVA. Pages 490 – 510 in: Beissinger, S. and D. McCullough (eds.), *Population Viability Analysis*. Chicago, IL, USA: University of Chicago Press.

Lacy, R.C., P.S. Miller, and K. Traylor-Holzer. 2015. *Vortex 10 User's Manual*. Apple Valley, Minnesota, USA and Chicago, IL, USA: IUCN SSC Conservation Breeding Specialist Group and Chicago Zoological Society.

Morris, W.F., and D.F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA, USA: Sinauer Associates.

Nyhus, P.J., F.R. Westley, R.C. Lacy, and P.S. Miller. 2002. A role for natural resource social science in biodiversity risk assessment. *Society and Natural Resources* 15:923-932.

Ralls, K., J.D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185-193.

Reed, J.M., L.S. Mills, J.B. Dunning Jr., E.S. Menges, K.S. McKelvey, R. Frye, S.R. Beissinger, M.-C. Anstett, and P.S. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16:7-19.

Soulé, M., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101-113.

Westley, F.W., and P.S. Miller (eds.). 2003. *Experiments in Consilience: Integrating Social and Scientific Responses to Save Endangered Species*. Washington, DC, USA: Island Press.