

Potential effects of human pressure and habitat fragmentation on population viability of the Antillean manatee *Trichechus manatus manatus*: a predictive model

Delma Nataly Castelblanco-Martínez^{1,*}, Coralie Nourisson², Ester Quintana-Rizzo³, Janneth Padilla-Saldivar¹, Juan J. Schmitter-Soto¹

¹El Colegio de la Frontera Sur, Av. Centenario km 5.5, Chetumal, Quintana Roo, Mexico

²GEOMARE, Av. Miguel Alemán 616-4B, Col. Lázaro Cárdenas, Mazatlán, 82040 Sinaloa, Mexico

³University of South Florida, 140 7th Avenue South, St. Petersburg, Florida 33701, USA

ABSTRACT: We present a population viability analysis for the metapopulation of the Antillean manatee *Trichechus manatus manatus* with the aim of predicting its tendencies under various hypothetical scenarios of conservation. Multiple individual Monte Carlo simulations of deterministic and stochastic factors were run on VORTEX 9.73 software. Populations were defined using genetic structure, geographic barriers, and typical ranging behavior. Demographic characteristics and life history parameters were inferred from the most recent compilation of information on the subspecies or were extrapolated from the Florida manatee *T. m. latirostris*. The baseline model describes a metapopulation with a positive growth. This model was sensitive to changes in mortality, but did not show any significant response to variations in assumed carrying capacity, age at first reproduction, maximum reproductive age, or initial population size. We simulated different scenarios by modifying human pressure, habitat fragmentation, and catastrophic events (i.e. hurricanes). Additional combined models were developed to simulate the best- and worst-case scenarios for human pressure level and fragmentation. The model suggested that the metapopulation would not be able to withstand an annual anthropogenically induced mortality rate >5%. A decrease in the survival of transient individuals could also lead to a decline of the population. Variations of the hurricane parameters did not yield important changes in the population curves, but other effects of climatic change are discussed. The extensive geographical area used by manatees requires international collaboration to ensure the protection of the metapopulation through effective conservation strategies across countries.

KEY WORDS: Population ecology · *Trichechus manatus manatus* · Human-related mortality · Connectivity · Tropical ecosystems · VORTEX

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INTRODUCTION

Knowledge of the viability of populations is crucial in order to elucidate the requirements for species persistence (Shaffer 1990). Population viability analysis (PVA) is the use of quantitative methods to predict the likely future status of a population of conserva-

tion concern (Morris et al. 2002). PVA has 2 defining characteristics: an explicit model of the extinction process and the quantification of threats to survival. Generally, the extinction model considers 2 categories of factors: deterministic and stochastic. Singly or combined, these forces have reduced many wildlife populations to low numbers, and some, to extinc-

*Email: castelblanco.nataly@gmail.com

tion (Miller & Lacy 2005). The analysis involves the prediction of the extinction (or quasi-extinction) probability using analytic (Ludwig 1996) or computer simulation techniques (Lindenmayer et al. 1995).

Manatees (Sirenia: Trichechidae) are classified as 3 species of the genus *Trichechus*: *T. manatus*, *T. inunguis*, and *T. senegalensis*. The Antillean manatee subspecies *T. manatus manatus* occurs from northern Mexico to the northeastern coast of Brazil in a patchy distribution. It is the most adaptable member of the family, occupying marine, estuarine, and freshwater areas (Lefebvre et al. 2001). The status of the Antillean manatee varies among countries from vulnerable to endangered to locally extinct. Estimates by country range from 10 to 1000 animals, with the largest populations reported from Mexico to Belize (Quintana-Rizzo & Reynolds 2010). Manatee populations and their available habitat have declined (Deutsch et al. 2008). In recent decades, the populations of the Antillean manatee have been affected by natural catastrophes (hurricanes) and anthropogenic actions such as hunting, habitat loss, entanglement in fishing gear, boat collisions, and pollution (Quintana-Rizzo & Reynolds 2010). For Florida manatees, the recovery from their depleted state has been slow (Langtimm et al. 1998) due to the low fecundity and reproductive rate of the species (Rathbun et al. 1995). It is expected that Antillean manatees face the same situation. The cumulative actions of natural catastrophes, anthropogenic disturbances, and low recovery rates can cause a progressive decrease in the population throughout the distribution range. For all of these reasons, *T. m. manatus* is considered Endangered on the IUCN Red List of Threatened Species (Self-Sullivan & Mignucci-Giannoni 2008).

The first PVA for a sirenian population was developed for the Florida manatee *Trichechus manatus latirostris* (Marmontel et al. 1997). Other PVAs include the Antillean manatee populations of Costa Rica (Jiménez-Pérez 1998) and Mexico (Guichard et al. 2001). Additionally, PVAs have also been used to investigate the viability of 2 metapopulations of dugong, another member of the order Sirenia, under varying regimes of indigenous hunting (Heinsohn et al. 2004). However, no attempt has yet been made to model the viability of the entire Antillean manatee metapopulation. A metapopulation consists of a system of spatially separated populations of the same species which interact at some level, connected by dispersing individuals (Hanski & Gilpin 1991). The distribution of the Antillean manatee is discontinuous, mostly due to coastal border fragmentation and marine currents, making it suitable for treatment as a metapopulation.

Our objective was to develop a PVA for the entire Antillean manatee metapopulation, in order to identify the way in which fragmentation, environmental uncertainty, demographic stochasticity, and reproductive factors are interrelated and contribute to the extinction process. We developed projections of the extinction trends of the metapopulation under various hypothetical scenarios to understand how the subspecies could be affected. The results of the model were used to provide recommendations to policy and decision makers that could help develop appropriate management plans for the subspecies.

METHODS

Overview

The Antillean manatee model was built using the software VORTEX 9.73 (Miller & Lacy 2005), which is an individual-based simulation model for PVA. VORTEX is a popular tool to model the extinction probability of small populations and analyzes the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on the dynamics of wildlife populations (Lacy 2000b). A minimum viable population is one of sufficient size to endure the effects of perturbations within its particular biogeographic context (Shaffer 1981). Input information required by VORTEX includes metapopulation structure, demographic characteristics, migratory dynamics, life history parameters, environmental effects, and anthropogenic causes of mortality. On the basis of these parameters, the software predicts the extinction risk within a specific time interval, the probability of persistence, and the mean size of the final population (Lindenmayer et al. 1993, Miller & Lacy 2005). A baseline model was created with biological parameters taken from previous research on other manatee species or subspecies, mainly the Florida manatee *Trichechus manatus latirostris*. However, some important variations were made for the Antillean manatee model, as explained in the following section.

Baseline model parameters

Metapopulation structure

We divided the metapopulation into subpopulations based on genetic, geographic, and ecological

criteria. The mtDNA phylogeny for *Trichechus manatus* indicates that there are 3 lineages: (1) Florida and the West Indies, (2) the Gulf of Mexico and Antillean rivers of South America, and (3) the northeastern coast of South America (García-Rodríguez et al. 1998). The Florida population was not included in this study because it has been classified as a separate subspecies, *T. m. latirostris*, based on morphological characteristics (Domning & Hayek 1986). Using this genetic division, the isolation level between subpopulations was estimated from obvious geographic characteristics, local genetic structure, ranging behavior, and habitat use, to determine the most likely subpopulations. Specific arguments to determine the separation between subpopulations are described in the following.

Data from the Bahamas were not included in the analysis because all local sightings correspond to *Trichechus manatus latirostris* (Lefebvre et al. 2001). Two likely genetic barriers exist (Vianna et al. 2006); the first isolates the Greater Antilles from the continental populations, and the other separates the coast of South America from Guyana to Brazil (Fig. 1). We took into account the ranging movements of the species, which mainly occur along coastlines, as manatees rarely venture across open oceans. This latter behavior appears to be related to water depth, lack of vegetation for food, increased predation in offshore

waters, and lack of fresh water (Reynolds & Ferguson 1984). Therefore, we assumed that the transit of individuals between the Greater Antilles and the continent, and vice versa, is unlikely.

Two distinct genetic populations appear to exist in Mexico: one along the Caribbean coast and one in the riverine systems connected to the Gulf of Mexico (Nourisson et al. 2011). For this reason, the manatee population inhabiting the Gulf of Mexico was separated from the Caribbean population.

The Colombian population was separated from Mesoamerica because strong currents and submarine canyons could prevent the transit between these 2 subpopulations. Manatees have been reported in the southern part of the Gulf of Uraba (northern Colombia), but no sightings have been recorded near the Panama border (Caicedo-Herrera et al. 2005).

Thus, the metapopulation was divided into 6 subpopulations (Fig. 1): Subpopulation 1: Greater Antilles (Puerto Rico, Jamaica, Dominican Republic, Haiti, and Cuba); Subpopulation 2: Gulf of Mexico (Gulf coast of Mexico); Subpopulation 3: Mesoamerica (Caribbean coast of Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panamá); Subpopulation 4: Coasts of Colombia; Subpopulation 5: Orinoquia, Venezuelan coasts, and Lesser Antilles; and Subpopulation 6: Guyana, Suriname, French Guiana, and coastal Brazil.

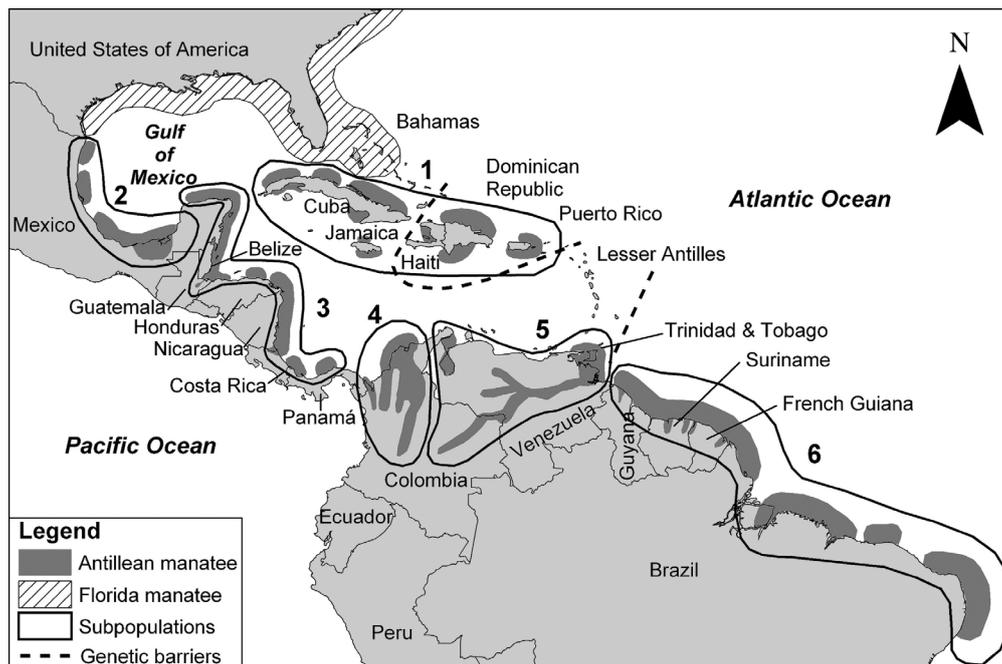


Fig. 1. Antillean manatee *Trichechus manatus manatus* subpopulations (Polygons 1–6) used for the analysis. Dark grey area shows the distribution of Antillean manatees; hatched area shows that of Florida manatees *T. m. latirostris*. Dashed lines are likely genetic barriers (Vianna et al. 2006)

Demographic characteristics and migratory dynamics

The information on population size was based on the most recent compilation of information available for the species in the Regional Management Plan for the West Indian Manatee of the United Nations Environment Programme (Quintana-Rizzo & Reynolds 2010). Some data were updated by personal communications with local experts (Table 1).

Recent studies have not detected high levels of inbreeding in various manatee populations (Hunter et al. 2010, Nourisson et al. 2011), because the occasional long-distance movements between subpopu-

lations could maintain the heterozygosity observed within those studied populations. Furthermore, movements between subpopulations are more likely to occur along the coasts due to the behavioral characteristics and habitat requirements. Therefore, we did not assume inbreeding depression.

We assumed low migration rates, based on the fact that currents and other geographic factors can affect the movement of individuals between subpopulations (Jiménez-Pérez 1998). We arbitrarily set a migration rate of 2% between neighboring subpopulations, e.g. between the Gulf of Mexico and Mesoamerica (subpopulations 2 and 3, Fig. 1), and 1% between non-neighboring subpopulations, e.g. be-

Table 1. *Trichechus manatus manatus*. Population size estimates and subpopulations of Antillean manatees used as input for the model. Adapted from Quintana-Rizzo & Reynolds (2010). S: stable, D: declining, U: unknown

Subpopulation	Possible trend	Minimum population size	Estimated population size	Source
1. Greater Antilles				
Puerto Rico (US)	S	300	450	J. Collazos (pers. comm.)
Jamaica	U/D	50	50	Quintana-Rizzo & Reynolds (2010)
Dominican Republic	D	30–45	200	H. Domínguez (pers. comm.)
Haiti	U	8	100	Quintana-Rizzo & Reynolds (2010)
Cuba	U/D	U	500	A. Álvarez-Alemán (pers. comm.)
Total			1300	
2. Gulf of Mexico				
Gulf of Mexico	U	1000–2000	1250	Quintana-Rizzo & Reynolds (2010)
Total			1250	Quintana-Rizzo & Reynolds (2010)
3. Mesoamerica				
Caribbean Mexico	U	220	250	Quintana-Rizzo & Reynolds (2010)
Belize	U/D	400–700	1000	N. Auil (pers. comm.)
Guatemala	U	53 ± 44 (SD)	150	E. Quintana-Rizzo (pers. obs.)
Honduras	S	11	100	Quintana-Rizzo & Reynolds (2010)
Nicaragua	D	71	500	Quintana-Rizzo & Reynolds (2010)
Costa Rica	D	31–66	200	C. Espinoza-Marín (pers. comm.)
Panama	U	10–100	150	K. Ruiz (pers. comm.)
Total			2350	
4. Colombia				
Colombia (Pacific and Caribbean region)	U/D	100–1000	400	Quintana-Rizzo & Reynolds (2010)
Total			400	
5. Venezuela				
Trinidad and Tobago	D	25–30	100	Quintana-Rizzo & Reynolds (2010)
Colombia (Orinoco Region)	D	U	100	D. N. Castelblanco-Martínez (pers. obs.)
Venezuela (Caribbean and Orinoco regions)	D	U	200	A. Manzanilla (pers. comm.)
Total			400	
6. Brazil				
French Guiana	S	U	100	Quintana-Rizzo & Reynolds (2010)
Guyana	D	U	100	Quintana-Rizzo & Reynolds (2010)
Suriname	D	U	100	Quintana-Rizzo & Reynolds (2010)
Brazil	U/D	155–1447	700	J. Borges (pers. comm.)
Total			1000	
Total for all populations			6700	

tween Subpopulations 1 and 6 (Fig. 1). It is accepted that manatees acquire their migratory patterns and seasonal ranges from their mothers during the 1.5 to 2 yr dependency period (Deutsch et al. 2003). The dispersal was assumed without distinction of sex or age class, because calves can travel along with their mother. Manatees have a remarkably efficient and responsive immune system (Bossart et al. 2003) and appear to be highly resistant to natural disease processes and lethal effects of traumatic injury (Buergelt et al. 1984). Thus, a 95% survival probability was arbitrarily assigned to transients during migration.

Finally, all growing populations are constrained by one or more limiting resources that slow or prevent continued growth when populations become large. This density-dependent growth leads to the general observation that large populations tend to grow more slowly, or even shrink, relative to small populations, as is the case with the Florida manatee population (Haubold et al. 2006). A primary limiting factor for the population growth of Florida manatees is believed to be the availability of warm water refugia during periods of prolonged cold weather in winter (Haubold et al. 2006). However, this is not a factor that could limit the growth of the Antillean manatee population through intraspecific competition. High-density effects on reproduction have not yet been observed or inferred for the Antillean manatee. The conventional density-dependence model for population growth is

based on the premises that populations have the potential to increase exponentially and that there is a density-dependent feedback that progressively reduces the actual rate of increase (Hassell 1975). In the case of Antillean manatees, this is probably not an issue, given the low densities of the subspecies. Additionally, an Allee effect, or inverse density dependence at low density (Courchamp et al. 1999), would probably not affect manatees. Manatees are semi-social mammals (Reynolds 1979) that do not need a group effect to successfully mate, do not need others for their survival, and travel long distances to find a mate. Thus, similar to other PVAs of sirenian populations (Marmontel et al. 1997, Jiménez-Pérez 1998, Heinsohn et al. 2004), this model did not assume density dependence in reproduction.

Life history parameters

Parameters included in the model were: reproductive system, age at first reproduction (hereafter, age at first offspring, FO), maximum age at reproduction, maximum age, maximum number of broods per year, maximum number of progeny per brood, percentage of 1 progeny and twins per brood, sex ratio, percentage of adult females breeding, percentage of males in the breeding pool, and natural mortality rates (Table 2).

Table 2. *Trichechus manatus manatus*. Life history and environmental parameters used for the baseline model. Data were extrapolated from the sources indicated. EV: variation due to the environment. See 'Methods' for details. na: not applicable

Parameter	Reported range	Value used	Source
Reproductive system	Polygynous	Polygynous	Marmontel et al. (1997)
Age at first reproduction (yr)	3–6	6	O'Shea & Hartley (1995)
Maximum age at reproduction (yr)	27–39	39	Marmontel et al. (1997)
Maximum age (yr)	na	60	Marmontel et al. (1996)
Maximum no. of broods yr ⁻¹	na	1	Marmontel et al. (1997)
Maximum no. of progeny brood ⁻¹	1–2	2	Marmontel et al. (1997)
One progeny per brood (%)	na	98.6	Rathbun et al. (1995)
Twins per brood (%)	na	1.4	Rathbun et al. (1995)
Sex ratio at birth in % of males	na	50	Marmontel et al. (1997)
% female adults breeding	na	33	Marmontel et al. (1997)
% males in breeding pool	na	45	Marmontel et al. (1997)
Natural mortality rates (%)			Jiménez-Pérez (1998)
Age 0–1	na	18 (EV=1.8)	Jiménez-Pérez (1998)
Age 1	na	5 (EV=0.5)	Jiménez-Pérez (1998)
EV correlation between subpopulations (%)	na	75	Jiménez-Pérez (1998)
Negative environmental effect on survival (%)	na	10	Marmontel et al. (1997)
Negative environmental effect on reproduction (%)	na	5	Marmontel et al. (1997)
Carrying capacity (<i>K</i> ; no. of individuals)	na	13 400	Present study
Frequency of hurricanes			
Subpops. 1, 2, 3 (%)	na	0.5	Marmontel et al. (1997)
Subpops. 4, 5, 6 (%)	na	0.1	Present study

Although there has been no study specifically devoted to mating behavior, scramble promiscuity—implying polygyny and androgyny—has been securely established as the manatee mating pattern (Rathbun et al. 1995, Anderson 2002). Long-term photo-identification studies show that adult manatees have an annual survival rate of about 96% in the Florida population, with relatively low human-related mortality (Langtimm et al. 2004). Analysis of growth layers in the earbone indicates that manatees can live up to 60 yr in the wild (Marmontel et al. 1996), so we took 60 as the oldest age. Captive manatees are known to live up to 63 yr or more (R. K. Bonde pers. comm.)

Age at FO was determined as follows. The median age at first reproduction for females is about 5 yr, with some individuals giving birth at Age 4 and most by Age 7 (Marmontel 1995, O'Shea & Hartley 1995, Rathbun et al. 1995). Although males undergo spermatogenesis as young as 2 to 3 yr of age (Hernández et al. 1995), the age at which they sire and produce their first offspring is unknown. Therefore, we assumed the age at FO to be 6 yr for both females and males.

Gestation lasts between 11 and 13 mo (Rathbun et al. 1995, Reid et al. 1995, Pomeroy 2011). The typical litter size is one, with twins reported rarely (Marmontel 1995, Odell et al. 1995, O'Shea & Hartley 1995, Rathbun et al. 1995). Values for single (98.6%) and twin (1.4%) births were adopted from Rathbun et al. 1995. Calves have been observed feeding on plants just after birth (Hartman 1979), but dependence on milk can last up to 18 mo or more (O'Shea & Hartley 1995, Rathbun et al. 1995, Reid et al. 1995). Inter-birth intervals average 2.5 to 3 yr, when the calf survives to weaning (Marmontel 1995, Rathbun et al. 1995, Reid et al. 1995). Thus, we used 33% of adult females breeding each year. There is no conclusive evidence on reproductive senescence in manatees, but free-ranging females are known to continue reproducing at least into their thirties (Marmontel 1995). Therefore, we used 39 yr as the maximum age at reproduction.

It is recognized that rates and causes of mortality are likely to differ between Florida and Antillean manatees. Florida manatees are at the northern part of the range of distribution and they are naturally affected by diseases (Buergelt et al. 1984), starvation, and complication during parturition (Ackerman et al. 1995). Cold stress and red tides could cause massive death of individuals, especially young and calves (Walsh et al. 2007). In contrast, in the tropics, water temperature remains in the optimal range for manatees,

which is probably $>20^{\circ}\text{C}$ (Irvine 1983), and provides no risk to the manatee population. However, physiological changes have been observed in manatees that inhabit very warm water temperatures ($>35^{\circ}\text{C}$, see Bossart et al. 2003). The massive death of manatees reported in Florida due to exposure to neurotoxins produced by the dinoflagellate *Karenia brevis* has not been reported in the tropics. Instead, disease, perinatal death (Mignucci-Giannoni et al. 2000), and, in a small proportion, predation (Falcon-Matos et al. 2003) could be the most common natural causes of mortality of the Antillean manatees. Thus, our model used similar values of natural mortalities reported for the manatee *Trichechus manatus manatus* population in Costa Rica (Jiménez-Pérez 1998); data are summarized in Table 2.

Environmental effects

Sources of environmental variation (e.g. weather, predator and prey population densities, parasite loads) can affect reproduction and survival independently or simultaneously (Miller & Lacy 2005). We assumed a random environmental effect on reproduction and survival rates, and an environmental correlation of 75% between subpopulations (Jiménez-Pérez 1998). Although discontinuous, the entire metapopulation is located in the tropical range, and large environmental phenomena could affect it as a whole. There are no estimates of carrying capacity (K ; no. of individuals) for Antillean manatees, either because the population is too small for resources to become limiting, or because of the absence of monitoring programs powerful enough to detect such change. However, the current extended availability of suitable habitats for manatees along the distribution area, such as seagrass beds (Short et al. 2007) and mangrove ecosystems (Giri et al. 2011), indicates that Antillean manatee populations are currently below their carrying capacities. Therefore, K was set at double the current estimated metapopulation size. Nevertheless, habitat loss is considered one of the main threats to the species, and in the future it could become a relevant issue. No environmental variation was added to K . The variation on mortality rates due to natural environmental variation was set to 10% of the mean of the mortality rates (Jiménez-Pérez 1998).

Empirical evidence suggests that manatee survival may be affected by severe storm events. Hurricanes and tropical storms can cause manatee mortality by wounding, beaching (due to storm surge or injury

from debris in turbulent water), or displacing manatees by storm currents into areas unsuitable for their survival (Langtimm & Beck 2003, Langtimm et al. 2006). Those environmental phenomena might also affect survival through the destruction or removal of vegetation, as has been the case with dugongs (Heinsohn & Spain 1974, Preen & Marsh 1995). Hurricanes were included in the model as global catastrophes (i.e. hurricanes have the potential to affect all manatee subpopulations). However, the probability that these will affect manatees varies from one subpopulation to another. Hurricanes have a greater effect in the Gulf of Mexico, Caribbean, and Mesoamerica than on the coast of South America. For example, in Colombia, the possibility of hurricanes affecting the mainland is quite small because the Sierra Nevada de Santa Marta, north of Colombia, acts as a barrier that reduces the force of the winds (Ortiz-Royero 2007). Furthermore, the South American coast is rarely affected by hurricanes, since most are formed in the north Atlantic, off the coast of Africa. Therefore, the frequency of hurricane occurrence was set to 0.5% for subpopulations 1, 2, and 3 (to be consistent with Marmontel et al. 1997) and to 0.1% for the other subpopulations. The negative effect of hurricanes on reproduction and survival was set to 5 and 10%, respectively (Marmontel et al. 1997).

Anthropogenic causes of mortality

Poaching of Antillean manatees for human consumption has prehistoric origins (McKillop 1985), and has been reported in almost all of the areas where the subspecies is distributed (Quintana-Rizzo & Reynolds 2010). In some floodplain areas, incidental drowning of the Antillean manatee in fishing nets is the main cause of mortality (Castelblanco-Martínez et al. 2009). Other causes of mortality, such as collisions with motor boats, have been reported, but they are uncommon (Mignucci-Giannoni et al. 2000, Borges et al. 2007).

We use the term 'human-related mortality' to refer to hunting, entanglement, and collisions with boats. There is inconsistent information about general human-related mortality of the metapopulation, although some local reports exist. For example, in Chetumal Bay, Mexico, 0.31% of manatee deaths per year between 1990 and 2007 were attributed to anthropogenic causes (Morales-Vela et al. 2002, Morales-Vela & Padilla-Saldívar 2009). This means that 1 manatee died every 2 yr due to human factors. For the Orinoco Basin (Colombia, Venezuela), studies

report a human-related death range from 1 to 10 manatees yr^{-1} from 1980 to 2004 (Castelblanco-Martínez et al. 2009), on average 3.8 ind. yr^{-1} (around 1.2% of the assumed Orinoco population). Assuming that all subpopulations experience approximately the same human pressure, we arbitrarily set the baseline model to 1% of each subpopulation dying from anthropogenic causes every year. We assumed that females and males have the same probability of being caught. Poachers prefer to hunt adults over calves because adults have more meat for consumption. However, young and juveniles are more frequently caught in fishing nets, as large animals can usually break through the nets (Castelblanco-Martínez et al. 2003). Since adults are more vulnerable to hunting, and young animals to entanglement, in the input model we assumed the same probability of human-related mortality for all age classes. The occurrence of orphan calves as a collateral consequence of separation from the mother was not included as a mortality source, because no estimates were available about the percentage of calves that die due to this factor.

Simulation parameters

Sensitivity test of the baseline model

Models can be more sensitive to some parameters than others; therefore, sensitivity tests were conducted to identify areas of uncertainty in several of the parameter values (mortality rates, K ; no. of individuals, age at FO, initial population size, and maximum age), allowing us to estimate how large an error in these parameters could affect the simulation results. We ran 500 simulations for each separate parameter to test model sensitivity, and ran the model for 200 yr (Table 3).

Modeling

Different scenarios were simulated by modifying specific parameters simultaneously for human-related mortality, habitat fragmentation, and catastrophic events (Table 4). Additionally, a series of models combining several levels of those parameters was developed. The worst- and best-case scenarios were simulated and compared with the baseline model. VORTEX ran 500 iterations in a simulated period of 500 yr. The quasi-extinction level was defined as $N < 670$ ind., i.e. 10% of the inferred current population (Heinsohn et al. 2004).

Table 3. *Trichechus manatus manatus*. Variation/modification in selected parameters used to evaluate the sensitivity of the model. Baseline values are in **bold**. Baseline parameters were taken from data collected on the Florida manatee (Table 2), except the initial metapopulation size (Table 1) and the carrying capacity (K ; no. of individuals; Table 2)

Parameter	Values
Mortality rates	Half of baseline parameters, baseline parameters , double baseline parameters
Carrying capacity	13 400 , 6700
Age at first reproduction (yr)	3, 5, 6
Max. reproductive age (yr)	27, 35, 39
Initial metapopulation size (no. ind.)	1675, 3350, 6700 , 13400
Max. age (yr)	50, 60 , 65

Table 4. *Trichechus manatus manatus*. Variation in the factors used to evaluate the viability of the metapopulation. Human-related mortality (%) is based on the number of individuals dying in each population per year; habitat fragmentation shows the % survival of transients; and catastrophic events the % frequency of hurricanes. Baseline values are in **bold**

Factor	Definition	
1. Human-related mortality (% ind. pop.⁻¹ yr⁻¹)		
Level 0	No human-related mortality	
Level 1	1	
Level 2	2	
Level 3	3	
Level 4	4	
Level 5	5	
Level 6	10	
Level 7	30	
2. Habitat fragmentation (% survival)		
Level 1	95	
Level 2	70	
Level 3	50	
Level 4	30	
Level 5	10	
3. Catastrophic events (% frequency)		
	Subpops. 1, 2, 3	Subpops. 4, 5, 6
Level 0	0	0
Level 1	0.5	0.1
Level 2	1	0.6
Level 3	2	1.2

Human-related mortality

In order to model variations in the intensity of human-related mortality, we simulated several levels of this parameter: 0% (the ideal situation), 1% (baseline), and 2, 3, 4, 5, 10, and 30% to simulate different rates of human pressure and their impact on survival.

These rates were applied to all subpopulations equally, since we did not have information on precise differences between subpopulations.

Habitat fragmentation

Habitat fragmentation is defined as the process of creation of habitat 'islands' of different sizes, with important consequences for the physical environment as well as for the biota (Saunders et al. 1991). The major effect of habitat fragmentation on a metapopulation is the disruption of biological corridors and, therefore, a decrease in connectivity (Saunders et al. 1991). Corridors are strips of habitat with a biologically designed or incidental function of increasing dispersal among populations (Akçaya et al. 2007). Functional connectivity, understood as the degree to which landscapes actually facilitate or impede the movement of organisms and processes (e.g. reproduction: Uezu et al. 2005), can be inferred by the survival of transient manatees moving between adjacent subpopulations. We modeled 5 different levels of survival of transients: 95% (baseline), and 70, 50, 30, and 10%, to simulate the effects of habitat fragmentation.

Catastrophic events

Global climate change is expected to affect temperature and precipitation patterns, oceanic and atmospheric circulation, rate of sea level rise, and the frequency, intensity, timing, and distribution of hurricanes and tropical storms (Michener et al. 1997). Hurricanes can decrease the viability of manatees due to direct mortality, indirect mortality, and emigration from the region as a consequence of storms. Also, important seagrass communities can be severely damaged by tropical storms, affecting the feeding resource for manatees (Langtimm & Beck 2003). For the baseline model we assumed a hurricane frequency of 0.5% (Subpopulations 1–3) and 0.1% (Subpopulations 4–6). Thus, we arbitrarily modeled frequencies of 0% for all subpopulations (deterministic model), 1 and 0.6%; and 2 and 1.2%, for Subpopulations 1 to 3 and Subpopulations 4 to 6, respectively.

RESULTS

The baseline model describes a metapopulation with an estimated initial size of 6700 ind. and positive

growth ($r = 0.032$; Table 5). This is the average metapopulation growth expected based on mean fecundity and mortality rates in the absence of inbreeding, with low human pressure and relatively low frequency of stochastic processes (e.g. occurrence of hurricanes and tropical storms). All subpopulations showed the same growth pattern (Fig. 2A), with the number of individuals increasing until K was reached. The probability of extinction for all the subpopulations was 0. Mesoamerica (Subpopulation 3) has the largest population size and was predicted to have the highest number of extant individuals after 500 yr.

In the sensitivity tests, when the natural mortality values were reduced by half (Fig. 2B, Mortality 1), the metapopulation maintained a pattern similar to the baseline-value simulation (Mortality 2). However, when the natural mortality was increased to twice the baseline (Mortality 3), the metapopulation showed a strong break, reaching extinction after only 100 yr. Because the natural mortality of Antillean manatees seems to be lower than that of Florida manatees, reaching levels of Mortality 3 (double the baseline parameters) may be unlikely. A decrease to half of K leads to a non-growing population maintaining the initial population size over time.

Sensitivity tests to changes in the age at FO, the maximum reproductive age (MRA), and maximum age (MA) (data not shown) revealed some differences in the time that K is reached. However, they were not sensitive to possible errors in the estimation of those parameters. Several initial population sizes (IPS) were used to identify how an error in this parameter could affect the simulations. The obtained curves varied slightly, but the growth rate remained positive in all cases (Table 6). We believe that the population size cannot be outside the tested range (IPS = 1675 to 13400), and we consider that $N = 6700$ is a reasonable value.

A reduction in human-related mortality to 0 did not result in a substantial growth of the population, compared with the 1% baseline model (Fig. 3). This is due to the assumed K

of the system, which limits the increase in manatee numbers. Similar curves were obtained with 2, 3, and 4% values. However, the population showed negative growth ($r = -0.001$) when the human-related mortality was 5% (Table 7). This means that the population would be unable to withstand any annual human-related mortality $>5\%$. However, the estimated time to extinction was >500 yr. Human-related mortality simulations of 10 and 30% accelerated the extinction process, with times to extinction of 307 and 283 yr, respectively.

Concerning habitat fragmentation, the population showed positive growth with values of transient survival of 95% (baseline value) and 70% (Table 7, Fig. 4). For a survival probability of 50%, the r -value was still positive, but lower. However, 30 and 10% survival probabilities led to a negative growth of the population, with time to extinction

Table 5. *Trichechus manatus manatus*. Predictions of the baseline model for the Antillean manatee, including mean annual rate of population change across the simulations under deterministic (det- r) and stochastic (stoc- $r \pm$ SD) models; final number of individuals (N-final \pm SD). Probability of extinction was 0 in all cases. Values for the metapopulation are shown in **bold**

Subpopulation	det- r	stoc- r	N-final
1. Greater Antilles	0.428	0.026 \pm 0.027	2595.51 \pm 19.11
2. Gulf of Mexico	0.428	0.046 \pm 0.027	2499.22 \pm 11.46
3. Mesoamerica	0.428	0.006 \pm 0.027	4537.97 \pm 156.17
4. Colombia	0.124	0.1 \pm 0.028	999.96 \pm 10.19
5. Venezuela	0.124	0.082 \pm 0.027	799.72 \pm 8.06
6. Brazil	0.124	0.021 \pm 0.023	1994.37 \pm 15.14
Metapopulation	0.276	0.032 \pm 0.021	13426.74 \pm 165.31
Within subpopulations		0.047 \pm 0.026	2237.79 \pm 36.69

Table 6. *Trichechus manatus manatus*. Sensitivity tests with varying mortality, carrying capacity (K ; no. of individuals), age at first offspring (FO), maximum reproductive age (MRA), and initial population size (IPS), including deterministic and stochastic mean annual rate of population change across the simulations (det- r and stoc- $r \pm$ SD), probability of quasi-extinction over 500 yr (PE), and the mean final population size (N-final \pm SD). The mean time to quasi-extinction was 0 yr in all cases except Mortality 3 (68.8 yr). Mortality 1 and 3 are half of and double the baseline parameters, respectively

Scenario	det- r	stoc- r	PE	N-final
Mortality 1	0.308	0.063 \pm 0.02	0	13 600.1 \pm 31.39
Mortality 3	0.209	-0.034 \pm 0.028	1	0
$K = 6700$	0.276	0.032 \pm 0.021	0	6704.66 \pm 98.99
FO = 3 yr	0.305	0.055 \pm 0.024	0	13 590.05 \pm 41.56
FO = 6 yr	0.284	0.038 \pm 0.022	0	13 541.93 \pm 93.16
MRA = 27 yr	0.269	0.024 \pm 0.021	0	12 638.78 \pm 386.65
MRA = 39 yr	0.276	0.032 \pm 0.021	0	13 420.99 \pm 170.79
IPS = 1675	0.276	0.032 \pm 0.021	0	13 426.97 \pm 176.13
IPS = 3350	0.276	0.032 \pm 0.021	0	13 420.27 \pm 167.59
IPS = 13 400	0.276	0.032 \pm 0.021	0	13 426.14 \pm 171.39

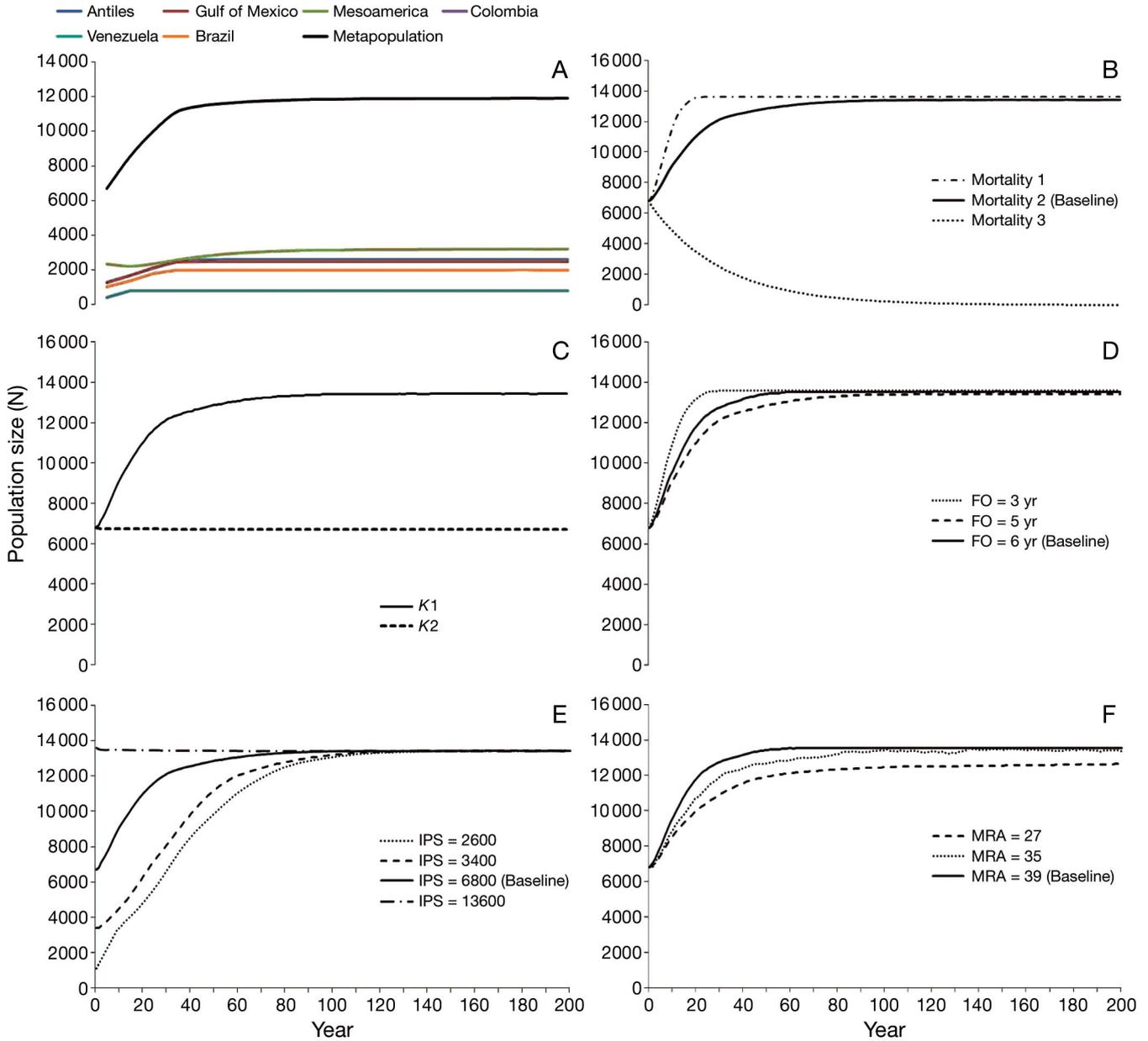


Fig. 2. *Trichechus manatus manatus*. Models showing the growth of Antillean manatee populations in number of individuals. (A) Model obtained for the 6 subpopulations and the metapopulation using baseline parameters. (B–F) Parameters of the baseline model varied during sensitivity testing for the metapopulation: (B) natural mortality, where Mortality 1 and 3 are half of and double the baseline parameters, respectively; (C) carrying capacity (K ; $K1$: 13 400; $K2$: 6700 individuals); (D) age at first reproduction (FO); (E) initial metapopulation size (IPS); and (F) maximum reproductive age (MRA). Simulation tests were repeated 500 times and performed for 200 yr

estimated at 229.3 and 104 yr, respectively. With regard to natural catastrophes, variation in the intensity and frequency of hurricanes did not lead to any important change in the population growth curves (data not shown). Human impact and habitat fragmentation were the main factors that drastically caused changes in the simulated extinction process of the population (Table 7).

We varied 3 levels of both factors (human-related mortality and habitat fragmentation) in combined models (Fig. 5). The optimistic baseline scenario (Model 1) showed a positive growth of the population and an extinction time equal to 0. Increasing human-related mortality led to extinction in all cases (Models 2, 3, 5, 6, 8, and 9), but time to extinction was variable. A reduction in the survival probability of tran-

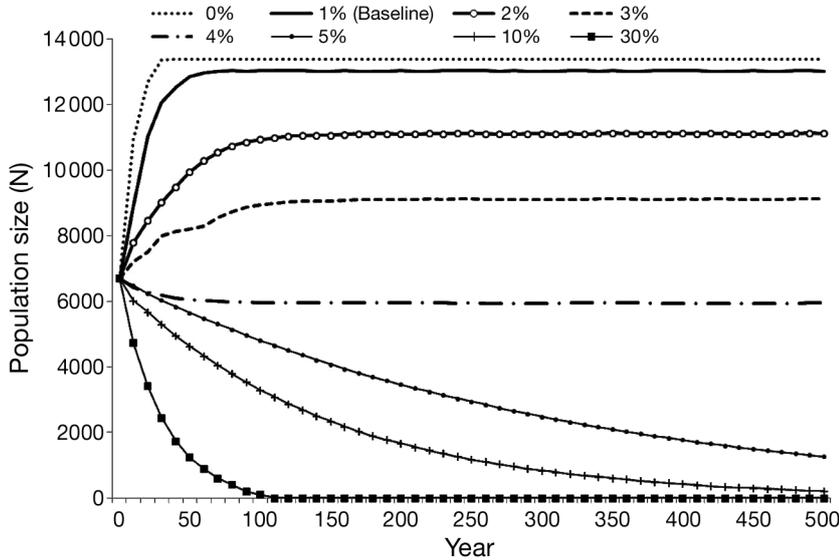


Fig. 3. *Trichechus manatus manatus*. Effect of several levels (%) of human-related mortality on the Antillean manatee metapopulation over the next 500 yr; 1% is the assumed level for the baseline model

sients could be tolerable, if the human-related mortality is kept below 1% (Model 4). However, a small increase in this rate (5%) produced extinction of the population in 208.9 yr (Model 5). The worst-case scenario occurred when 30% of the population was extracted every year, and just 30% of the transients between subpopulations survived (Model 9), with a

calculated extinction time of only 41.5 yr.

DISCUSSION

In the case of the manatee, a PVA can be powerful for several reasons. First, the possibility of extinction highlights the necessity for adaptive management plans or the monitoring of current plans. Second, the PVA involves reviewing published and unpublished information. This process is helpful to identify gaps in the biology and conservation knowledge that need to be filled. Lastly, the PVA can lead us to detect particular cases or demographic processes that require urgent attention, e.g. countries where manatee populations are decreasing or their status is unknown (Table 1).

There are also some caveats for the use of this model. Its main weakness is the lack of certainty about the demographic characteristics, primarily regarding the estimated size of the population. The most robust data have been obtained in the Caribbean region, where habitat characteristics make it

Table 7. *Trichechus manatus manatus*. Predictions for Antillean manatees, with varying human-related mortality (% of deaths per year due to human causes) and habitat fragmentation (% survival of transients; see Fig. 4). The results include deterministic and stochastic mean annual rates of population change across the simulations (det-r and stoc-r ± SD), probability of quasi-extinction over 500 yr (PE), mean final population size (N extant ± SD), and the mean time (yr) to quasi-extinction (mean TE). Predictions of Levels 3 and 4 of human-related mortality are not shown. Values of the baseline model are in **bold**

Combined model	Human-related mortality (%)	Survival of transients (%)	det-r	stoc-r	PE	N extant	Mean TE
1 (baseline)	Level 0 (0)	Level 1 (95)	0.28	0.04 ± 0.02	0.00	13 349.40 ± 77.98	0.00
	Level 1 (1)	Level 1 (95)	0.28	0.04 ± 0.02	0.00	13 573.00 ± 0.00	0.00
	Level 2 (2)	Level 1 (95)	0.28	0.04 ± 0.02	0.00	13 348.80 ± 84.38	0.00
2	Level 5 (5)	Level 1 (95)	0.24	0.001 ± 0.02	1.00	199.47 ± 21.30	>500
	Level 6 (10)	Level 1 (95)	0.24	-0.01 ± 0.03	1.00	931.50 ± 229.81	307.00
3	Level 7 (30)	Level 1 (95)	0.24	-0.01 ± 0.03	0.99	732.67 ± 16.50	283.00
	Level 1 (1)	Level 2 (70)	0.26	0.02 ± 0.02	0.00	11 127.81 ± 308.00	0.00
4	Level 1 (1)	Level 3 (50)	0.28	0.00 ± 0.02	0.00	7098.74 ± 926.35	0.00
5	Level 5 (5)	Level 3 (50)	0.26	-0.01 ± 0.02	1.00	0.00	208.90
6	Level 7 (30)	Level 3 (50)	0.24	-0.04 ± 0.05	1.00	0.00	55.80
7	Level 1 (1)	Level 4 (30)	0.28	-0.01 ± 0.02	1.00	0.00	229.30
	Level 1 (1)	Level 4 (30)	0.28	-0.01 ± 0.02	1.00	0.00	226.00
8	Level 5 (5)	Level 4 (30)	0.26	-0.02 ± 0.03	1.00	0.00	97.90
9	Level 7 (30)	Level 4 (30)	0.24	-0.06 ± 0.05	1.00	0.00	41.50
	Level 1 (1)	Level 5 (10)	0.28	-0.02 ± 0.02	1.00	0.00	104.00

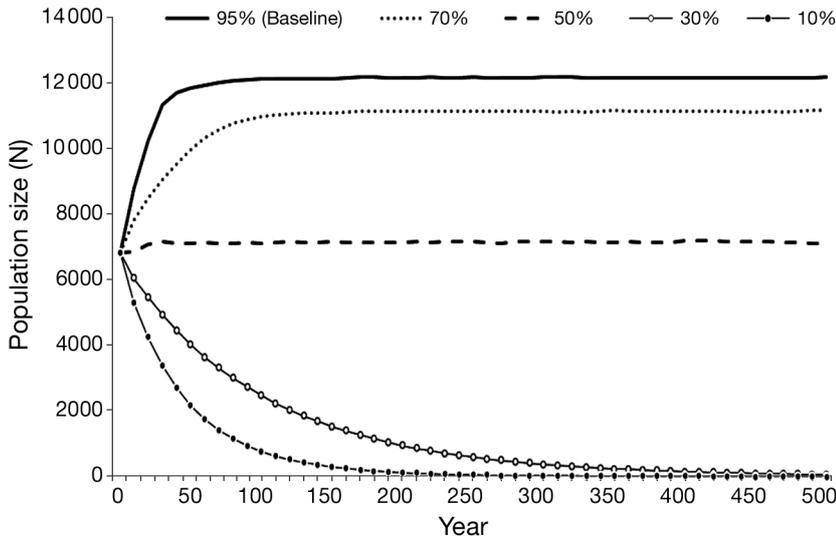


Fig. 4. *Trichechus manatus manatus*. Effect of several habitat fragmentation levels (% survival of transients moving between subpopulations) on the Antillean manatee metapopulation over the next 500 yr; 95% survival is the assumed level for the baseline model

possible to detect and count manatees using aerial surveys. Aerial surveys are useful to determine minimum population size, but they are probably not sufficient to assess a population size. Also, almost one half of the *Trichechus manatus manatus* population inhabits lagoons, streams, and floodplains. In this type of habitat, it is very difficult to detect manatees from the air, due to the low water transparency, dense vegetation, and access constraints. For those cases, it is important to develop new economic, practical, and suitable alternatives in order to estimate the manatee population size.

Our model did not take into account the trends of local populations (increase, decrease, stable, or unknown), because no quantitative data are avail-

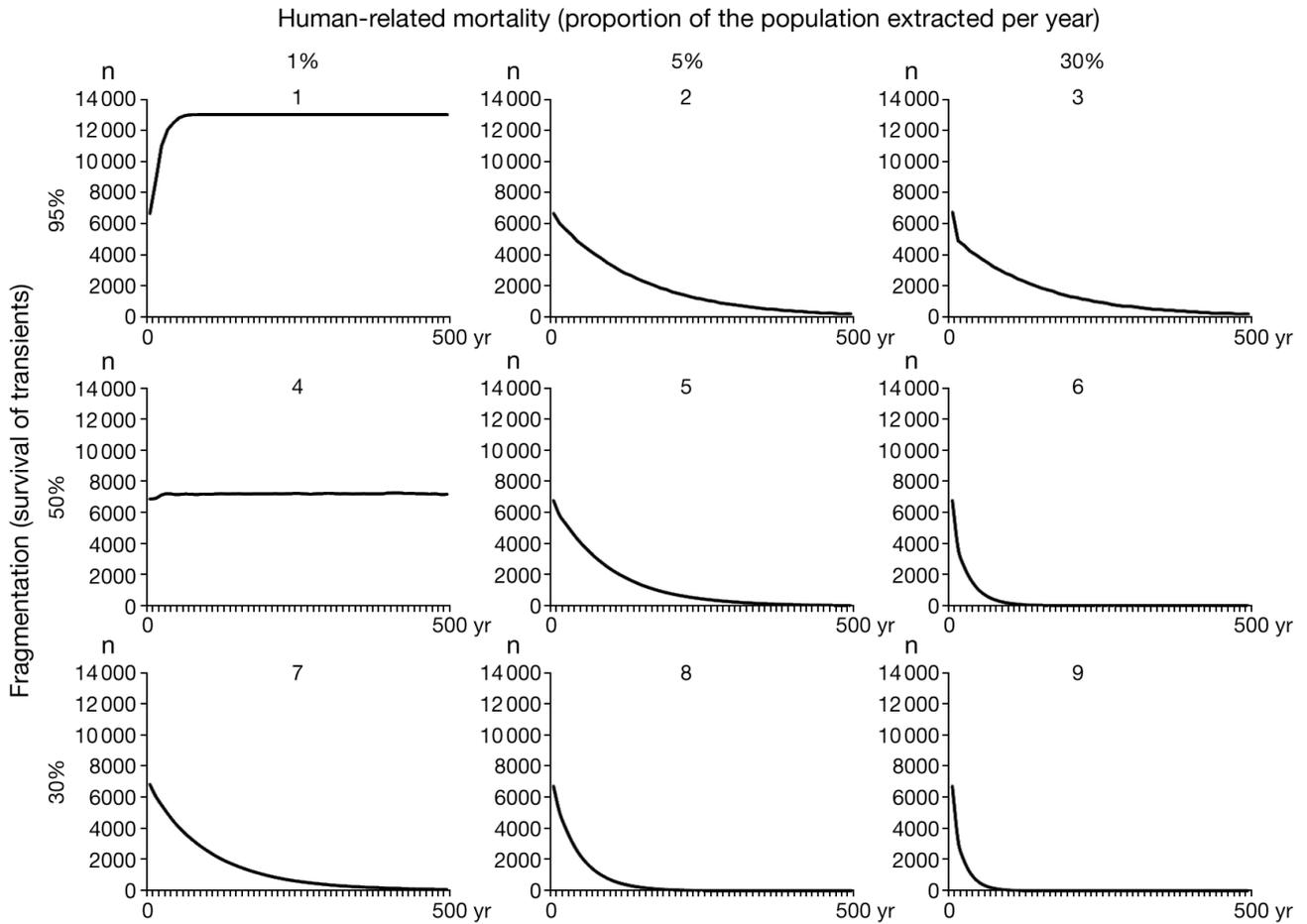


Fig. 5. *Trichechus manatus manatus*. Models 1 to 9, showing the combined effects of 3 levels of human-related mortality and 3 levels of fragmentation on Antillean manatee population dynamics. y-axes show the population size (number of individuals, n); x-axes show the simulation time (yr)

able. However, it is important to emphasize that experts and local people throughout the region agree that the number of manatees sighted per year has decreased over time (information obtained by D. N. Castelblanco-Martínez in structured and semi-structured interviews). The present model also assumes that all threats that affect Antillean manatees are equal between subpopulations. Further information is needed to refine the intensity of human pressure at several scales. As more information can be included in the model, predictions can be improved and the uncertainty reduced.

Another important source of uncertainty could be the parameter values for the life history of the Antillean manatee that were extrapolated from data on the Florida manatee. Studies on captive Antillean manatees show that the reproductive information is similar for both subspecies (Marmontel et al. 1992), and thus we expect that some values used for the Antillean subspecies are similar to the well-studied Florida manatee. The sensitivity tests showed that any slight differences between the values of the 2 subspecies parameters would not drastically affect the results of the model.

Our baseline model describes a metapopulation with a positive growth. The population dynamics of sirenians are such that mortality must be low in order to maintain a maximum potential annual rate of increase on the order of 5% (Marsh et al. 1984). Therefore, the observed baseline model growth rate is reasonable. In Florida, a viability analysis using VORTEX revealed negative growth of the population for all possible scenarios tested (Marmontel et al. 1997). The difference between Florida and our study could be related to intrinsic variations between subspecies and also differences in the values used in the model parameters, such as population size and mortality rates. A major difference between the Florida and Antillean manatee models is the estimated population size, about 7 times smaller for Florida. The population size is a determining parameter of the population dynamic model. In a smaller population, the number of interacting stochastic processes can decrease population growth and stability (Lacy 2000a).

Another important difference between Florida and Antillean manatees is the massive mortality associated with cold fronts and red tide episodes, which has a strong impact on the population. Florida manatees can experience over 300 to 400 deaths a year, as a result of cold stress or red tide exposure (Walsh et al. 2007). This is not the case for Antillean manatees, which inhabit the warm waters of tropical

America. No red tides affecting this subspecies have been documented.

Boat collisions account for about 25% of manatee deaths annually in Florida (Aipanjiguly et al. 2003). Although it is known that Antillean manatees are also affected by boat collisions (Mignucci-Giannoni et al. 2000, Borges et al. 2007), boat densities in developing countries seem to be remarkably lower than in Florida, and the overlap of manatees and human activities areas is less frequent and less invasive. For instance, in Kings Bay, Florida, the mean number of boats per day in a manatee area was 32.7, ranging from 1 to 79 (Buckingham et al. 1999), while on the Orinoco River, the mean number was 4.28 boats per day, ranging from 0 to 32 (Castelblanco-Martínez 2004). For Antillean manatees, resource availability appears to determine habitat use, more than the boat traffic variable itself (Jiménez-Pérez 2005, Hamilton 2009). Although human populations in countries where Antillean manatees live are increasing (Wittemyer et al. 2008), there are not many areas yet where an intensive overlapping between manatees and boats occurs, as happens in Florida. This can be due to a lower density of manatees and/or a lower density of humans occupying the coasts, with a conversely lower level of boating activity.

Although variation in natural catastrophes did not affect population growth, climate change can still affect manatees through habitat fragmentation, loss of suitable feeding areas, and general landscape modifications. Global climate change will affect the physical, biological, and biogeochemical characteristics of the oceans and coasts, affecting manatees living in estuaries and coastal ecosystems (Würsig et al. 2002). Furthermore, an important part of the Antillean manatee population lives in freshwater river systems and streams. Because the flooding regime is strongly related to large-scale climatic phenomena, there might be a perilous connection between climate change and the future prospects for those freshwater subpopulations (Arraut et al. 2010). Effects on the aquatic environment are especially difficult to predict because of the complex interactions between aquatic systems and climate, and will vary greatly between areas. Therefore, predictions of the effects of climate changes on species and populations are speculative (Würsig et al. 2002) and deserve deeper analysis.

There are other important effects of climatic change that were not taken into account because of the lack of sufficient information about their effect throughout the region. Identification of food resources, temporal dietary patterns, and foraging

locations is necessary to detect changes in the feeding ecology of the species due to global warming. Long-term studies of individually identifiable animals can be expensive and require a long-term commitment for funding (Quintana-Rizzo & Reynolds 2010). Furthermore, marking and tracking methods are generally too expensive for developing countries, and low-cost and practical monitoring strategies need to be identified to address multiple research objectives simultaneously (Quintana-Rizzo & Reynolds 2010).

Antillean manatees still die as a direct result of human-related factors in all subpopulations. It is difficult to estimate accurately the current level of such deaths, but it is important to ensure that it is maintained below 5% of the estimated population size annually. Also, it should be noted that the model did not include another source of extraction from the natural population, such as orphaned calves as a collateral consequence of boat collision, hunting, entanglement, or natural death of the mother. Manatees have a long period of maternal care, and the mother's death directly implies the death of the dependent calf, if artificial care is not provided. There are relatively few manatee rehabilitation centers throughout the distribution area, and an unknown number of orphan calves still die due to the lack of appropriate detection, recovery, and subsequent care. Furthermore, most of the rehabilitated manatees remain in captivity, and in the majority of the cases there are no formal projects to reintroduce them back to the wild, as has been successfully done in Brazil (Lima et al. 2005, 2007) and Belize (N. Auil pers. comm.). Improving and/or creating rehabilitation facilities to attend to emergencies is recommended (Quintana-Rizzo & Reynolds 2010). Also, it is important to strengthen plans and actions to rehabilitate and release rescued manatees when their condition is appropriate for those actions.

In the majority of countries in which Antillean manatees occur, motorized boat traffic is currently relatively low (e.g. Castelblanco-Martínez 2004, Hamilton 2009), and except for Puerto Rico and Belize, collisions with boats do not represent the main threat to the subspecies. However, boat traffic is expected to increase in the future as local users increasingly abandon traditional dugout dories in favor of motor boats (Hamilton 2009). Recreational areas, often placed in shallow waters, should be carefully planned to avoid lethal encounters between manatees and boaters.

The survival of individuals moving between subpopulations is a success indicator of biological corri-

dors, and therefore of habitat fragmentation levels. This model shows that not only the protection of areas intensively used by manatees, but also the maintenance of connectivity among subpopulations is necessary. The survival probability of transients can be increased by promoting and conserving natural corridors, thereby guaranteeing long-distance movements of some individuals each year. In this regard, some critical areas, including Panama and the Holbox region in Mexico, deserve particular attention. Panama represents the bridge between South America and Mesoamerica, and its preservation could be relevant to facilitate genetic exchange. The Holbox region (northeastern Yucatan Peninsula, Mexico) is very interesting in terms of genetic dispersion between the Gulf of Mexico and Caribbean region. Manatees have been reported in both Panama (Schad et al. 1981, Mou-Sue et al. 1990, Viquez 1993) and the Holbox areas (B. Morales-Vela pers. comm.), but there is no available information on their current conservation status or population size. Habitat fragmentation does not only impact the survival of manatees per se, but also has collateral effects. For example, fragmentation of rivers by dams might affect plant dispersal along river corridors (Jansson et al. 2000), and it could have an impact on the manatees' food resources. Additionally, pollution, environmental noise, boat traffic, and other factors are also important indirect collateral effects of fragmentation that can affect the viability of manatees. This aspect should be taken into account during the planning of ports, dams, bridges, channels, and any other alterations of the coastal shoreline and flow of rivers. Also, it is important to avoid fragmentation within subpopulations.

The review of published and unpublished literature about Antillean manatees raised an important issue: studies of the subspecies have been mostly addressed on a country-by-country basis. This is due to the fact that some countries have more governmental support for research and biological conservation than others. Countries such as Mexico, Belize, and Brazil have developed important long-term research projects on manatees, including genetics, radio tracking, and ecology. Those experiences should be communicated, and if possible, replicated in other countries with similar conditions. Antillean manatees can use extended areas and perform transboundary displacements (Morales-Vela & Padilla-Saldívar 2009). This wide use of habitat implies the need for international collaboration and must receive attention by scientists, governments, and managers of natural protected areas, in order to design conser-

vation strategies not limited by national borders. We recommend establishing a multinational committee for regional Antillean manatee population monitoring, including conducting demographic censuses, establishing stranding networks, and providing environmental education.

Management decisions are based not only on whether the proposed strategy is sufficient to achieve recovery, but also on whether the likely benefit will justify the expenditure (Brook et al. 2000). Decisions by managers should take into account other factors that this study did not address, such as the economic and social costs of protecting Antillean manatees. However, this work provides information on critical points that will have to be further investigated in order to protect this endangered subspecies.

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Editorial responsibility: Brendan Godley,
University of Exeter, Cornwall Campus, UK

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