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The green sea turtle *Chelonia mydas* (Testudines, Cheloniidae) in the Galapagos Islands, Ecuador: a literature review coupled with a population dynamics model

Trabajo de integración curricular presentado como requisito para la obtención del título de Bióloga

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Executive Summary

Sea turtles play an important role within marine ecosystems. Being considered sentinel species, they help us to determine the health of the environment in which they are found. According to the IUCN, most sea turtles fall into one of the endangered categories. In Ecuador, a country where five of the seven extant species have been observed, sea turtles are considered near threatened. Thanks to the marine turtle monitoring program on the Galapagos beaches, it has been possible to collect biological data on the distribution, abundance, and reproductive biology of the species *Chelonia mydas*, the green sea turtle. However, this information, although available, is still scarce and scattered. This is unfortunate considering that the Galapagos Islands are one of the main nesting sites for this species in the East Pacific. Further, the lack of data systematization hinders deeper research efforts such as those based on ecological theory (including population dynamics), and their application for decisions related to the conservation of *C. mydas* in Galapagos.

In the first part of this thesis, a synthesis of the available biological data of the *C. mydas* population in Galapagos is presented, to assess the current and historical status of the population and thus be able to contribute to the implementation of concrete conservation actions. Although *C. mydas* nests on almost all the beaches of the Galapagos Islands, the main nesting sites are: Quinta Playa and Bahía Barahona (Isabela Island), Las Bachas (Santa Cruz Island), Las Salinas (Baltra Island), Espumilla (Santiago Island), and Punta Cormorán (Floreana Island). Quinta Playa and Las Bachas are the beaches that have been the best monitored historically. The historical record shows a high number of nesting females in some seasons, but there are also seasons in which the abundance of nesting females was extremely low (e.g., in 1983, when a strong "El Niño" event occurred). During the nesting season, female turtles return to the beach more than once to lay their eggs, with an average interval of 14.7 days. Furthermore, females return to nesting sites every 4.7 years on average, unlike males who return almost every year; this difference in the rate of return between the sexes is possibly due to the greater energy expenditure that the entire mating and nesting process entails for a female. In addition, the growth rates of *C. mydas* in Galapagos, with a mean age of sexual maturity of 36 to 50 years, are considerably slower than those reported for this species elsewhere. Furthermore, the average percentages of hatching success (46.0%) and emergence success (45.6%) of hatchlings on Galapagos beaches are relatively low compared to other sites. Regarding conservation indicators, it is worth emphasizing that, apart from the omnipresent problem of natural and introduced predators, 85% of the beaches that serve as nesting sites are frequented by tourists and fishing boats, which could impact negatively in the population. In fact, 22% of the mortality of *C. mydas* in Galapagos is caused by boat strikes. It is therefore a priority to establish and reinforce the conservation actions of these nesting sites to ensure a healthy population of *C. mydas* in the Galapagos Islands in the long term.

In the second part of this thesis, a sex-structured continuous time model is presented to study the population dynamics of *C. mydas*, the green sea turtle. The model is parametrized using as a reference the available data on reproductive biology and local abundance of this species in Galapagos (summarized in the first part of the thesis). Stages of the life cycle of sea turtles in which they are not reproductively active were discarded, thus simplifying the mathematical model. In this sense, only two stages are considered: adults and eggs. In addition, the model makes a clear distinction between the sexes dividing the adult stage into males and females, resulting in a non-linear three-dimensional system of differential equations. Through the qualitative mathematical analysis of the model, the following is demonstrated: 1) The flow induced by the system is positively invariant in the region of biological interest (Ω); and 2) The condition ($R_0 > 1$) is necessary and sufficient for the only non-trivial equilibrium point (I^*) to be globally and asymptotically stable in that region. The condition ($R_0 > 1$) is derived from the linearization of the three-dimensional system and the use of the Routh-Hurwitz stability criterion for the analysis of local stability of the equilibrium points. For the study of global stability, the original system was reduced to a two-dimensional one to later apply the Bendixon's criterion and the Poincare-Bendixon's Theorem and conclude that the non-trivial equilibrium point is globally asymptotically stable. When implementing the estimated values for our parameters in the numerical simulations, it was observed that indeed the population of Galapagos green sea turtles complies with the conditions for which the non-trivial critical point (I^*) is globally asymptotically stable ($R_0 = 6.3$); that is, the asymptotic stability is maintained for any initial value within the set Ω. In contrast, when altering the estimated values of the parameters so that the established condition is not met, the trivial critical point (I_0) becomes globally stable, and the population falls towards extinction regardless of the values taken within the positively invariant Ω set. Therefore, based on the historical data of the nesting population records, together with the results of the qualitative analysis and the numerical simulations, it can be concluded that the green turtle nesting population in Galapagos is a healthy population, with a significant number of individuals.

Resumen Ejecutivo

Las tortugas marinas juegan un papel importante dentro de los ecosistemas marinos. Al ser consideradas especies centinela, nos ayudan a determinar la salud del ambiente en el que se encuentran. De acuerdo con la UICN, la mayoría de las tortugas marinas se encuentran en alguna de las categorías de amenaza. En Ecuador, un país donde se han registrado cinco de las siete especies conocidas, las tortugas marinas están consideradas casi amenazadas. Gracias al programa de monitoreo de tortugas marinas en las playas de Galápagos, se han podido recolectar datos biológicos sobre la distribución, abundancia y biología reproductiva de la especie *Chelonia mydas*, la tortuga marina verde. Sin embargo, esta información, aunque disponible, es aún escasa y se encuentra dispersa. Esto es lamentable considerando que las Islas Galápagos son uno de los principales sitios de anidación de esta especie en el Pacífico Oriental. Además, la falta de sistematización de los datos dificulta consolidar esfuerzos de investigación más profundos como aquellos basados en teoría ecológica (incluyendo la dinámica de poblaciones) y su aplicación para la toma de decisiones relacionadas a la conservación de *C. mydas* en Galápagos.

En la primera parte de esta tesis, se presenta una síntesis de los datos biológicos disponibles de la población de *C. mydas* en Galápagos, con el fin de evaluar el estado actual e histórico de la población y así poder coadyuvar a la implementación de acciones concretas de conservación. Aunque *C. mydas* anida en casi todas las playas de las Islas Galápagos, los principales sitios de anidación son: Quinta Playa y Bahía Barahona (Isla Isabela), Las Bachas (Isla Santa Cruz), Las Salinas (Isla Baltra), Espumilla (Isla Santiago) y Punta Cormorán (Isla Floreana). Quinta Playa y Las Bachas son las playas que históricamente han sido mejor monitoreadas. El registro histórico muestra un alto número de hembras anidadoras en algunas temporadas, pero también existen temporadas en las que la abundancia de hembras anidadoras fue sumamente baja (e.g., en el año 1983, cuando un fuerte fenómeno de "El Niño" ocurrió). Durante la temporada de anidación, las tortugas hembras regresan a la playa más de una vez para dejar sus huevos, con un intervalo promedio de 14.7 días. Además, las hembras regresan a los sitios de anidación cada 4.7 años en promedio, a diferencia de los machos que regresan casi todos los años; esta diferencia en la tasa de retorno entre sexos posiblemente se debe al mayor gasto energético que supone para una hembra todo el proceso de apareamiento y anidación. Por otra parte, las tasas de crecimiento de *C. mydas* en Galápagos, con una edad media de madurez sexual de 36 a 50 años, son considerablemente más lentas que las reportadas para esta especie en otros lugares. Además, los porcentajes promedio de éxito de eclosión (46.0%) y éxito de emergida (45.6%) de los neonatos en las playas de Galápagos son relativamente bajos en comparación con otros sitios. En cuanto a indicadores de conservación, vale recalcar que, aparte del problema omnipresente de predadores naturales e introducidos, el 85% de las playas que sirven de sitios de anidación se encuentran en playas que son frecuentadas por turistas y embarcaciones pesqueras, lo cual podría impactar negativamente en la población. De hecho, el 22% de la mortalidad de *C. mydas* en Galápagos es causada por golpes de embarcaciones. Es por tanto prioridad el establecer y reforzar las acciones de conservación de estos sitios de anidación para asegurar una población saludable de *C. mydas* en las Islas Galápagos a largo plazo.

En la segunda parte de esta tesis, se presenta un modelo matemático de tiempo continuo estructurado por sexos para estudiar la dinámica poblacional de *C. mydas*, la tortuga verde marina. El modelo se parametriza utilizando como referencia los datos conocidos sobre biología reproductiva y abundancia local de esta especie en Galápagos (resumidos en la primera parte de la tesis). Etapas del ciclo de vida de las tortugas marinas en las que no son reproductivamente activas fueron descartadas, simplificando el modelo matemático. En este sentido, se consideran únicamente dos etapas: adultos y huevos. Además, el modelo hace una clara distinción de sexos dividiendo la etapa adulta en machos y hembras, resultando en un sistema tri-dimensional no lineal de ecuaciones differenciales. A través del análisis matemático cualitativo del modelo se demuestra lo siguiente: 1) El flujo inducido por el sistema es positivamente invariante en la región de interés biológico (Ω); y 2) La condición ($R_0 > 1$) es necesaria y suficiente para que el único punto de equilibrio no trivial (I^*) sea globalmente y asintóticamente estable en esa región. La condicion ($R_0 > 1$) se deriva de la linearización del sistema tri-dimensional y el uso del criterio de estabilidad de Routh-Hurwitz para el análisis de estabilidad local de los puntos de equilibrio. Para el estudio de la estabilidad global, se redujo el sistema original a uno de tipo bi-dimensional para posteriormente aplicar el criterio de Bendixon y el Teorema de Poincare-Bendixon, y concluir que el punto de equilibrio no-trivial es global y asintóticamente estable. Cuando se implementa los valores estimados para nuestros parámetros en las simulaciones numéricas, se pudo observar que en efecto la población de tortugas verdes de Galápagos cumple con las condiciones para las cuales el punto crítico no-trivial (I^*) es global y asintóticamente estable ($R_0 = 6.3$); es decir, la estabilidad asintótica se mantiene para cualquier valor inicial dentro del conjunto Ω . En contraste, cuando se alteran los valores estimados de los parámetros de manera que no se cumpla la condición establecida R_0, el punto crítico trivial (I_0) se vuelve globalmente estable, y la población cae hacia la extinción independientemente de los valores tomados dentro del conjunto Ω positivamente invariante. Por lo tanto, en base en los datos históricos de los registros de población anidadora, junto con los resultados del análisis cualitativo y las simulaciones numéricas, se puede concluir que la población anidadora de tortuga verde en Galápagos es una población sana, con un número significativo de individuos.

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Abbreviations

ASTM Areas of Special Temporal Management 17

CBD Convention on Biological Diversity 16
CCL curved carapace length 6
CCRF Code of Conduct for Responsible Fisheries 16
CCW curved carapace width 6
CITES Convention on International Trade in Endangered Species of Wild Fauna and Flora 16
CMS Convention on Migratory Species 16
CPPS Permanent Commission for the South Pacific 16

DPS Distinct Population Segment xii, 3

ESD Environmental Sex Determination 3

FM Female-Male pattern 4
FMF Female-Male-Female pattern 4

GNP Galapagos National Park 6
GSD Genetic Sex Determination 3

HWM high-water mark 10

IAC Inter-American Convention for the Protection and Conservation of Sea Turtles 16
IATTC Inter-American Tropical Tuna Commission 16
IUCN International Union for Conservation of Nature 14

MAAE Ministerio del Ambiente y Agua del Ecuador 5
MARPOL International Convention for the Prevention of Pollution from Ships 16
MF Male-Female pattern 4
MNP Machalilla National Park 5

MNS mean nesting size 11
mtDNA mitochondrial DNA 2

Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat 16

SCL straight carapace length 7
SCW straight carapace width 7

TSD Temperature Sex Determination 4
TSP thermosensitive period 4

UNCLOS United Nations Convention on the Law of the Sea 16

WHMSI Western Hemisphere Migratory Species Initiative 16

1. Problem statement and objectives

Sea turtles fulfill essential functions in marine ecosystems. They maintain ecological interactions, help the functionality of beaches, and because of their long life and high degree of coastal fidelity, they serve as sentinel species or biological indicators. Despite the fact that five of the seven extant species of sea turtles visit Ecuador's maritime territory or nest on its beaches, few studies have been carried out on these ecologically valuable species. The green sea turtle, *Chelonia mydas*, is the only species that nests in the Galapagos Islands, considered one of the main nesting sites in the East Pacific. The scarce biological information about the green sea turtle in Galapagos is found disaggregated in published and unpublished documents, and there is no authoritative review at present that compiles and assesses the information obtained over the years. Yet, this information is essential to develop effective conservation actions.

In response to this reality, this thesis poses the following two objectives:

i) Compile and assess the biological knowledge and conservation status of the green sea turtle (*Chelonia mydas*) population in the Galapagos Islands.

ii) Formulate, analyze, simulate and biologically interpret a sex-structured continuous time population dynamics model of the green sea turtle (*Chelonia mydas*) population in the Galapagos Islands.

The fulfillment of these objectives will help in the decision-making processes for the integral management of the species in the Galapagos Islands, assuring its long term persistence.

2. Assessment of the biology and conservation status of the green sea turtle (*Chelonia mydas*) population in the Galapagos Islands

2.1 Global distribution and systematics of the green sea turtle

Only seven species of sea turtles are extant today: six of them are members of the Cheloniidae family (*Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata*, *Lepidochelys kempii*, *Lepidochelys olivacea*, *Natator depressus*), while one (*Dermocheleys coriacea*) is the only extant member of the Dermochelyidae family[1]. *Chelonia mydas* (Linnaeus, 1758) belong to the Cheloniidae family, in the Testudines order, class Reptilia. Linnaeus scientifically described the green sea turtle for the first time in 1758[2], although it was Schweigger in 1812 who first applied the scientific name *Chelonia mydas*[3], which is used today.

The green sea turtle is one of the most common sea turtles and is widely distributed throughout tropical and subtropical oceans around the world[4]. Analysis of the mitochondrial DNA (mtDNA) of the global matriarchal phylogeny has concluded the existence of a divergence in the population that resulted in two different geographical clusters of green sea turtles: the Indian-Pacific population and the Atlantic-Mediterranean population[5,6]. Each population is genetically distinct, with its own nesting and feeding territory[5]. Further studies, also based on mtDNA, but in combination with the nesting behaviour, have proposed that each local nesting population can be considered as Distinct Population Segments (DPSs), which represent independent demographic units[7]. These DPS are found in both the Indian-Pacific and the Atlantic-Mediterranean populations, geographically distributed within the ocean basins[4] (Table 2.1).

Table 2.1: Distinct population segments (DPSs) of the *Chelonia mydas* species as occurring in the Indian-Pacific and Atlantic-Mediterranean populations.

N°	**Indian-Pacific**	**Atlantic-Mediterranean**
1	Southwest Indian DPS	North Atlantic DPS
2	North Indian DPS	Mediterranean DPS
3	Central West Pacific DPS	South Atlantic DPS
4	East Indian - West Pacific DPS	
5	Southwest Pacific DPS	
6	Central South Pacific DPS	
7	Central North Pacific DPS	
8	East Pacific DPS	

The *C. mydas* population that occurs in Ecuador belong to the East Pacific DPS. Morphological and behavioral evidence suggests the presence of one subspecies in this DPS: *Chelonia mydas agassizii*[8,9], or *Chelonia agassizzi*[10], ranging from Baja California to Peru. However, as explained above, genetic evidence only recognizes two large and different geographical clusters: the Atlantic-Mediterranean and the Indian-Pacific, each with numerous DPSs[11] (Table 2.1). In 1997, Hirth established the green sea turtle as a "circumglobal, morpho-species...made up of several distinct populations and metapopulations"[12]. In 1994, Moritz recommended to adopt the concept of species over that of subspecies[11]. In this review, in the absence of a concluding genetic study of the *agassizii* form, the name of *Chelonia mydas* is adopted for the species present in the Galapagos Islands.

The East Pacific DPS extends from the California-Oregon border in USA to southern Chile[13]. The two largest nesting aggregations of the East Pacific DPS are located in Michoacan (Mexico) and in the Galapagos Islands (Ecuador)[13,14]. However, there are other relatively less crowded nesting sites throughout the Pacific Coast in Revillagigedos Archipelago (Mexico) and in the coasts of Costa Rica, Guatemala, Colombia, Peru, and Ecuador[4].

2.2 Temperature Sex Determination (TSD)

Sex-determination of offspring in vertebrates can be divided into two different mechanisms: Genetic Sex Determination (GSD) and Environmental Sex Determination (ESD). Most vertebrate species have a GSD mechanism, that is, males and females have different alleles or even genes that determine the sexual morphology of the offspring at the time of fertilization. On the other hand, ESD mechanism is defined as a system where the offspring sex is determined by post-fertilization environmental factors[15,16]. In the case of reptile taxa, both GSD and ESD mechanisms have been identified[17]. Temperature Sex Determination (TSD) system is the most common ESD in reptiles: more than 70 species have shown this mechanism[18]. In the TSD system, the temperature of an embryo's environment during incubation period dictates the embryo's sex development. Many species of turtles[19], tortoises[20], lizards[21], and crocodiles[22] that exhibit TSD have a thermosensitive period (TSP) during which the embryo sex is developed. For turtles, this period has been observed to take place during the mid-trimester of the embryo's incubation period[23].

Among TSD, there are three different possible patterns that a species uses for sex determination: Female-Male pattern (FM), Male-Female pattern (MF), and Female-Male-Female pattern (FMF) (Figure 2.1). In the FM-pattern, females are produced at low incubation temperature, while males are mostly produced at high temperatures; many lizard species show FM pattern[24]. Conversely, in MF-pattern, male eggs are developed under low hatching temperatures and female eggs under high temperatures; this pattern has been reported only in sea turtles[24]. The FMF-pattern dictates that female eggs develop at high and low incubation temperatures, while a medium range temperature results in male eggs; *Alligator mississippiensis* presents this kind of pattern[25]. The temperature that produces the same number of males and females is known as the pivotal temperature and can vary between populations with a range of 28–30.3°C.

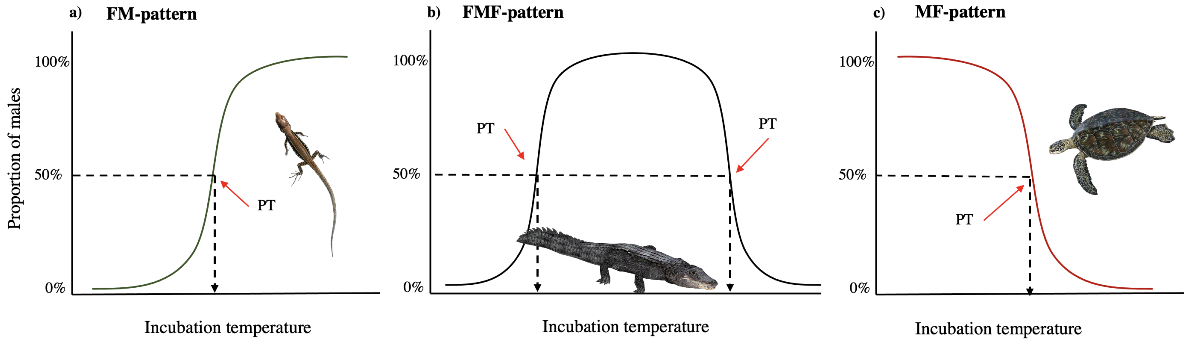


Figure 2.1: Temperature Sex Determination (TSD) patterns defined by proportion of males produced by different incubation temperatures: a) FM (female-male) pattern occurs mostly in lizards, b) FMF (female-male-female) pattern occurs mostly in crocodiles, and c) MF (male-female) pattern occurs just in sea turtles. PT = pivotal temperature.

Green sea turtle embryos follow the MF-pattern of TSD[24]. When the mean temperature of the nest is around the pivotal temperature an even distribution of male and female hatchlings occur[16,26]. Below the pivotal temperature, hatchling sex population will be mostly male; and above, mostly female[16,26,27]. For the green sea turtle population in the Galapagos there is not data or studies related to the pivotal temperature. However, studies carried out with the green sea turtle population of Suriname estimate that the pivotal temperature would be 29.2 or 29.3°C[28].

Climate change is one of the most important and threatening factors for the survival of sea turtles[29]. Sea level rise, as a consequence of climate change, causes accelerated beach erosion that results in loss of nesting sites and negative alteration of suitable habitat[30]. Furthermore, climate change can lead to higher average air and ocean temperatures, leading to the feminization of hatchlings, or even be lethal, resulting in the complete loss of the hatchling cohort[23].

With a trend towards increasing mean global temperature, species with TSD are particularly affected. The population of sea turtles is facing high egg mortality and feminization of the offspring[31,32]. In recent years a disproportionate ratio of female to male turtle eggs has been observed in a number of different studies[32], and has also been predicted to possibly lead to the extinction of sea turtles in the future[26,33,34]. The lack of males within the sea turtle population, as a consequence of the female-only offspring production, will eventually affect the entire population dynamics. In the Great Reef Barrier stock, considered as one of the largest green sea turtle populations in the world, a extremely female sex bias has been reported in foraging grounds (99.1% of juvenile, 99.8% of subadult, and 86.8% of adult-sized turtles)[32]. What is the minimum proportion of males sufficient to support the sea turtle population in such a way to avoid population collapse? This dilemma certainly requires a variety of studies. For instance, with the correct demographic data, sex-structured mathematical models can be used to evaluate and analyze population dynamics. Nevertheless, estimating sex ratios is a real challenge. Monitoring sex ratios in the nest involves a series of methodological and ethical complications. Studies in foraging areas of the Galapagos Islands have reported that the female:male sex ratio of juvenile and adult turtles is proportional 1:1, and has not significantly changed[35]. Yet, for the Galapagos Islands, to establish a technical protocol to determine and predict the proportion of males and females in a nest and foraging grounds is imperative in order to provide greater insight into the overall population sex ratio, and to assess how climate change or other factors are affecting the distribution of males and females in the environment.

2.3 Distribution in Ecuador

Galapagos Islands are considered one of the largest nesting aggregation of the East Pacific DPS. Even though there is nesting on almost all the beaches of the Galapagos Islands, the major nesting sites, considered as index beaches, are (Figure 2.2): Quinta Playa and Bahía Barahona southeast of Isabela Island, Las Bachas northeast of the coasts of Santa Cruz, Las Salinas on Baltra Island, Espumilla on the northern coast of Santiago Island, and Punta Cormorán on the north coast of Floreana Island[36]; in the Ecuadorian mainland, the main nesting beaches, although not as large as those in Galapagos[37] occur in Machalilla National Park (MNP): at Isla de la Plata, a continental island located 40 km off the coast, and at La Playita, on the mainland. The Ministerio del Ambiente y Agua del Ecuador (MAAE) has also reported nesting sites at San Lorenzo and La Botada beaches (Manabí province); at Tres Cruces and Punta Brava (Santa Elena province), and at Galerita (Esmeraldas province)[38]. The connectivity between the Galapagos Islands and the Ecuadorian mainland has been corroborated by genetic studies[38] and was confirmed after a female tagged in Isla de la Plata was found nesting in Quinta Playa[39].

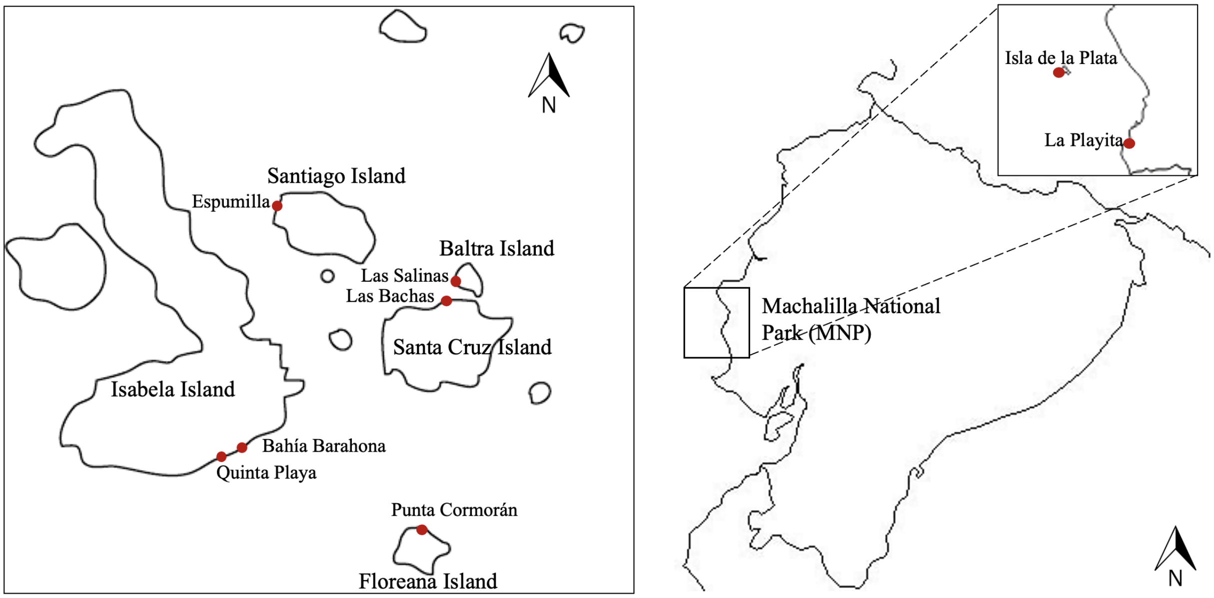


Figure 2.2: Main nesting sites of *Chelonia mydas* in Galapagos Islands and Ecuadorian mainland.

2.4 The green sea turtle nesting monitoring program in Galapagos

The breeding population of the Galapagos green sea turtle has been monitored at several beaches. In the 1970's, Pritchard established the foundations for the monitoring of the green sea turtle in the Galapagos Islands. As a result the first registry of nesting females in Galapagos was published in 1975[40]. The green sea turtle nesting program continued from 1976 to 1983 by researchers Derek Green and Mario Hurtado[36,41]. In the years to follow, however, no further efforts were made to monitor the abundance of nesting green sea turtles in Galapagos for almost two decades. In 2000/2001 the Charles Darwin Foundation officially began monitoring the nesting of green sea turtles in the Galapagos Islands, until 2007[42]. In 2009/2010 season, the monitoring program started to be conducted as a bi-institutional effort between the Charles Darwin Foundation and the Galapagos National Park (GNP)[43] (Figure 2.3).

The nesting monitoring of the green sea turtle in the Galapagos Islands is carried out annually since 2010 in two main nesting sites: Quinta Playa on Isabela Island and Las Bachas on Santa Cruz Island. The monitoring and study of the nesting sites allows the GNP to evaluate its conservation status, to establish an updated information base on the behavior of the nesting females during the breeding season, and to establish the hatching and emergence success of the nests deposited during each season. The monitoring is mainly done at night. The activities carried out to monitor nesting females are: tagging, external examination (identification of epibionts and damage), and morphometry (estimated by the curved carapace length (CCL) and curved carapace width (CCW)). In case the female makes a

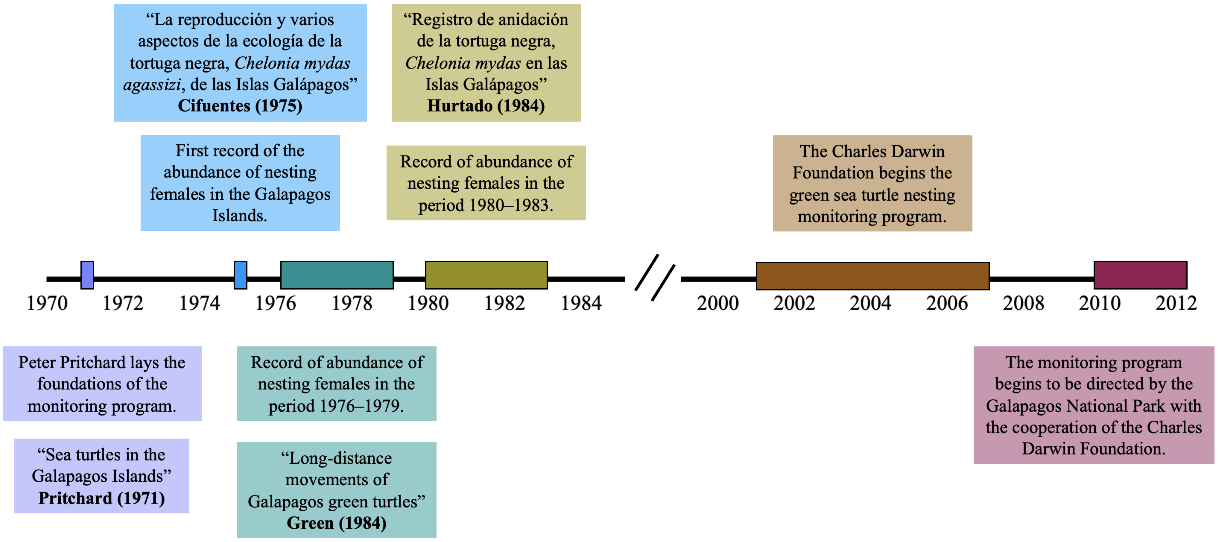


Figure 2.3: Timeline of the green sea turtle (*Chelonia mydas*) nesting monitoring program in the Galapagos Islands. The Galapagos National Park in coordination with the Charles Darwin Foundation are the entities in charge of the green sea turtle monitoring program in the Galapagos Islands at present.

nest and lays eggs, the nest is monitored, labeling it, recording geographical coordinates, and counting eggs (Figure 2.4). In addition, other related activities are carried out, such as: excavation and inventory of nests, counting and morphometry of hatchlings (estimated by straight carapace length (SCL) and straight carapace width (SCW)), and registration of native and introduced predators (Figure 2.5). In the mornings, a record of lost tracks is carried out and data on meteorological parameters is taken.

The methodology used by the GNP to monitor the green sea turtle offers a record of the trends and fluctuations of the nesting population and their possible causes. However, these techniques focus only on nesting sites, where females and males meet to breed. This facilitates the study of the abundance of females, nests and other demographic parameters on the beaches, but this information is insufficient to assess the population of green sea turtles as a whole, as females represent only a small component of the total population. To understand and predict trends in sea turtle populations, it is necessary to monitor juveniles, adult males and non-nesting females, which is a great challenge due to their migratory behavior. Establishing standardized monitoring techniques to assess the distribution and abundance of green sea turtles in foraging areas is necessary in the Galapagos Islands to estimate demographic parameters for population dynamics analysis.

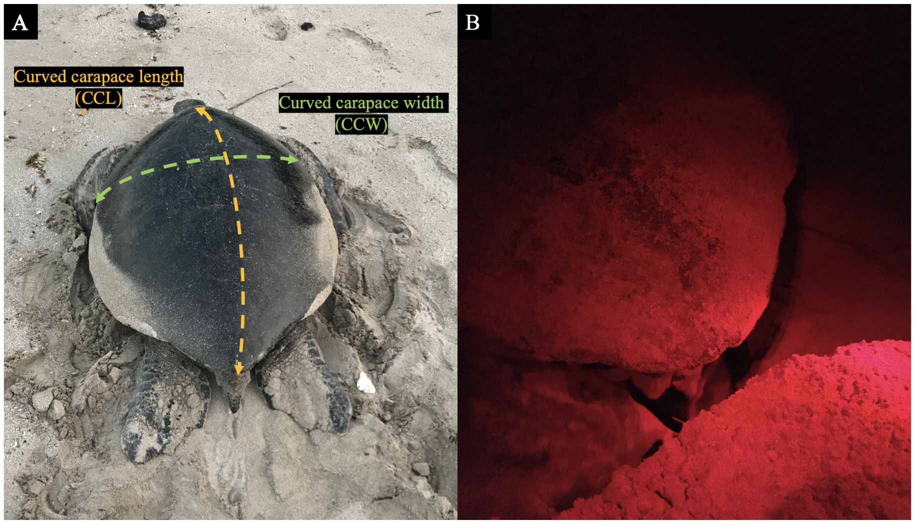


Figure 2.4: Green sea turtle nesting monitoring activities in Quinta Playa (Isabela Island), Galapagos Islands. A) Morphometry of a nesting female: curved carapace length (CCL) and curved carapace width (CCW). B) Nesting female laying eggs.

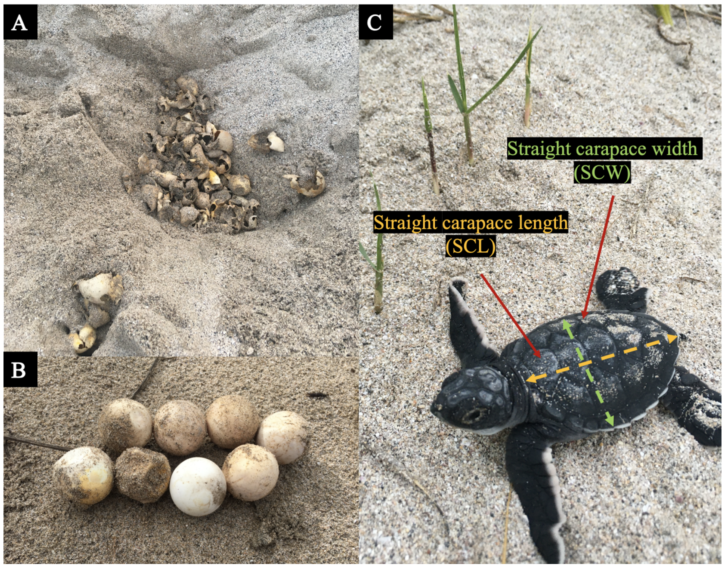


Figure 2.5: Eggs and hatchlings monitoring in Quinta Playa (Isabela Island), Galapagos Islands. Showing nest excavation and inventory. A) Shells of hatched eggs. B) Green sea turtle eggs that did not hatch. C) Morphometry of a hatchling: straight carapace length (SCL) and straight carapace width (SCW).

2.5 Local abundance in Galapagos Islands

In the Galapagos Islands, two morphotypes within the green sea turtle population are recognized: the typical dark form known locally as "*tortuga negra*" and an unusual sterile form with a yellowish carapace and a yellow-orange plastron, known locally as "*tortuga amarilla*"[44]. The yellow turtle, sometimes confused with the juvenile form of the green sea turtle, is an abnormal form of the green sea turtle where the gonads fail to develop and mature properly, producing sterile turtles.

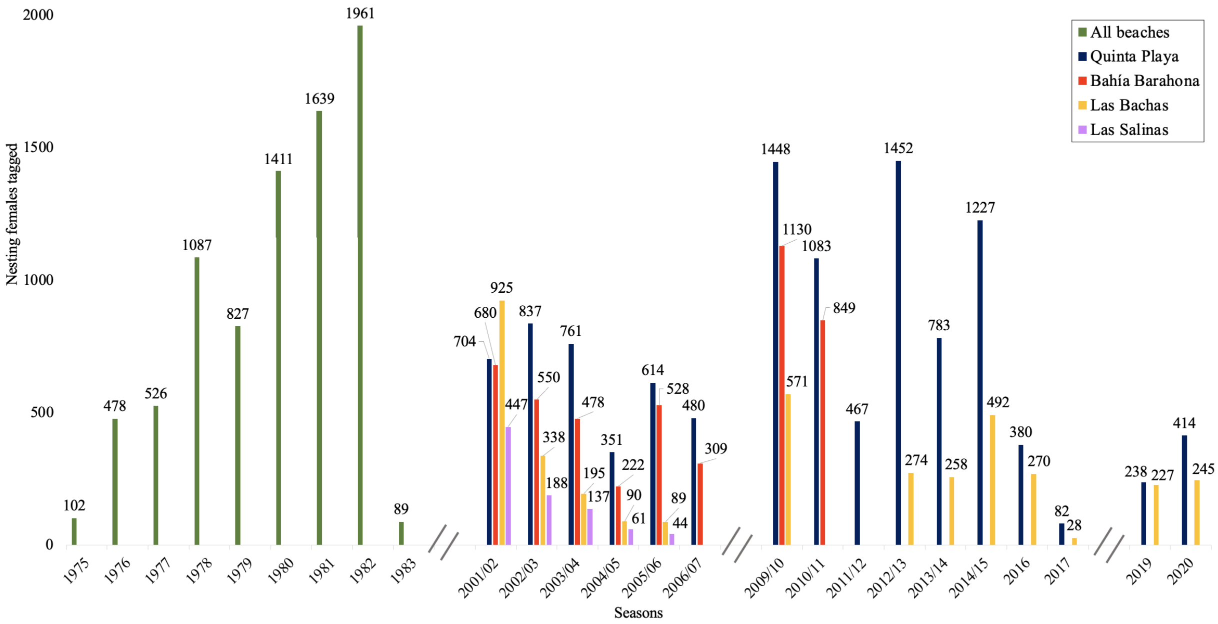


Figure 2.6: Abundance of nesting female green sea turtles tagged by site and by year in the Galapagos Islands. For the period 1975–1983, data per beach is unavailable; thus, the data only shows the total number of females monitored on the four beaches. Sources: 1975 by Cifuentes (1975), 1976–79 by Green (1984), 1980–1983 by Hurtado (1984), 2002–2007 Zárate (2007), 2010–2017, 2019–2020 Espinoza (IAC Annual Reports).

Despite registering high numbers of nesting females in some seasons, a pattern of decline has been observed over the years, in contrast to the studies conducted in the same nesting sites by Green and Hurtado, where the trend was towards the increase with the exception of the 1983 year where "El Niño" event was registered. The number of nesting females registered during the whole monitoring period (2001-2020) varies among different beaches and study periods (Figure 2.6). In general, the highest values of nesting females were recorded in Quinta Playa and Bahía Barahona (Isabela Island), and the lowest, in Las Salinas (Baltra Island) and Las Bachas (Santa Cruz Island). Factors such as the physical characteristics of the beaches and their level of conservation could have influenced the nesting process over the years. The large number of nesting females in Quinta Playa and Bahía Barahona may be due to the fact that they are isolated and protected sites. On the contrary, Las Bachas and Las Salinas receive daily visits as they are common sites for ecotourism[45]. Note that there is not always data available for all years and all beaches, as it could be ideal, because of logistical and economical hardships.

The dynamic fluctuation in the number of green sea turtles registered in the Galapagos Islands coincides with those registered in other populations[46]: there are years with high number of nesting females, followed by very low numbers (Figure 2.6). Some fluctuations can be related to "El Niño" events, because it affects physical, chemical, and nutritional conditions of the ocean, thus disrupting the migration, foraging and reproductive ecology of the green sea turtle[47]. In addition, alteration in the number of Galapagos green sea turtles is also conditioned by biotic factors as well as by the sampling conditions in the islands.

2.6 Breeding dynamics in the Galapagos Islands

2.6.1 Breeding cycle

In the Galapagos Islands, the breeding is quite marked and distinctly seasonal. Mating pairs can be seen almost year-round. At the beginning of September, cohorts of a female and several males can be observed copulating or in courtship behavior near nesting beaches[48]. In late September, copulating pairs increase noticeably, reaching a peak around mid-December, and then becoming sporadic during and after February[48]. After courtship, which can last several hours, the male, recognizable by his long tail that protrudes beyond the posterior edge of the carapace, mounts the female from behind and attaches himself to the anterior margin of the female's carapace with the claws of his front flippers. Mating can last up to six hours and throughout the process 1 to 6 "escort" males accompany them, attacking the successful male and trying to dislodge him and take his place in the copulation.

Mating and nesting behaviour in *C. mydas* has a higher energy cost for females compared to males. Post-mating, the female emerges from the sea, usually between 7 P.M. and midnight, when the tide is high, to nest. Females are rarely seen nesting during the day or at low tide. They are quite shy when emerging from the sea —any strange sound or light can scare them and make them return. Once the female reaches an area above the high-water mark (HWM), it begins to move the sand with her foreflippers forming a hole that allows her to be leveled with the surface of the beach. Then the female uses its hindflippers to excavate the chamber where the eggs will be deposited. While females are excavating the egg chamber, they become less sensitive to external stimuli and once they begin to lay their eggs, they will not stop, making them extremely susceptible to attack by predators[12]. Finally, the female, after laying the eggs, covers them and returns to the sea. All this process takes around 3 hours. There is no kind of paternal care for the eggs or hatchlings. Oviposition begins around early December, reaches a peak in late February to early March, coinciding with the hot season, and ends at the end of June. However, some turtles can be found nesting all year long[49,50]. The high energy expenditure is reflected in 4.7 yr average remigration intervals (N = 884 females)[51,52], unlike the males which remigrate to the nesting grounds every year[12].

The effort to lay the eggs on the beach is so great that not all landings are successful. Many females return to the sea without even having reached the HWM, while others excavate several chambers without laying an egg. During the nesting season, females return to the beach more than once to lay their eggs. The mean renesting interval for green sea turtles in Galapagos is 14.7±4.7 (±SD), with a range of 5–25 days, obtained by sampling 647 females[49].

2.6.2 Breeding adults

Sea turtles are recognized for their natal philopatry, which is the return of the species to their birthplace to breed. The data show considerably high site and temporal fidelity: around 85% of the females return to the same beach to nest[53]. The mean nesting size (MNS) of green sea turtles around the world has significant variation among nesting sites. In most populations, MNS varies from 95 cm to 110 cm of CCL[4]; however, there are some populations that have substantially larger or smaller MNS. The smallest turtles are found in the East Pacific DPS. In Galapagos the MNS is 86.7 cm CCL[49], slightly larger than the MNS in Michoacán, Mexico (82.0 cm CCL)[54]. The Galapagos colony is considered among those with the smallest MNS in the world[49].

The MNS of females reported in 2002 in Galapagos was similar to that reported in 1994[55]. In 2002, the smallest turtle observed nesting was 60.7 cm CCL. But note that Green in 1995[56] classified as immature any female smaller than 71.0 cm CCL. Table 2.2 summarizes nesting adults size and weight.

Table 2.2: *Chelonia mydas* mean nesting size (MNS) in Galapagos Islands as estimated by curved carapace length (CCL) in the year 2002. Note that nesting size is estimated by the female size measured by CCL.

	CCL (cm)				**Weight (kg)**				**References**
	N	**mean**	**SD**	**range**	**N**	**mean**	**SD**	**range**	
Females									49,55
Quinta Playa	701	86.1	6.2	66–104.3	-	-	-	-	
Bahia Barahona	677	85.6	6.1	60.7–105	-	-	-	-	
Las Bachas	899	87.8	7.9	62–109	-	-	-	-	
Las Salinas	432	87	6.1	61.3–102	-	-	-	-	
All	2709	86.7	6.2	60.7 –109	-	85.6	-	71–110.5	
Males	-	-	-	-	-	81.2	-	68.3–98	55

Growth rates of the Galapagos green sea turtle are considerably slower than those reported for green sea turtles elsewhere. The mean age of sexual maturity is estimated to be within the range of 36-50 years[44]. Growth rates help us determine the health of the population in general, therefore they are essential for the development of conservation strategies. Studying and monitoring this demographic parameter is fundamental for the Galapagos population as there are very few related studies[44,57].

2.6.3 Eggs and hatchlings

During mating season, a female green sea turtle may have multiple mates and lay several clutches of eggs at approximately 2-week intervals[49,58]. Table (2.3) summarizes the egg and nest parameters for the Galapagos green sea turtle.

Table 2.3: *Chelonia mydas* egg and nest parameters of Galapagos roockery.

Variable and year(s)	**N**	**mean**	**SD**	**range**	**References**
Clutches per season per female					
1980–1982	3405	0.86	-	-	[36]
2002	2756	1.37	-	-	[49]
Nest per year					
2013–2016	1039	1536.7	-	46–2769	[51]
Eggs per clutch					
2002	3790	82.9	-	10–157	[49]
Yolkless eggs per clutch					
2004–2007	1039	1.7	2.9	0–23	[59]
Nest depth (cm)					
2004–2007	679	34.7	7.6	16.6–75	[59]
Incubation period					
1975–1980	-	55	-	45–75	[48]

Hatchlings usually emerge at night around 6:00 to 9:00 P.M. after an incubation period of 45–75 days with an average of 55 days[48]. It takes them 3 to 7 days to reach the surface of the nest chamber. Hatchlings are extremely susceptible to the presence of artificial light in the vicinity of nesting beaches, as it can disturb and disorient the hatchlings, causing them to move away and lose their way to the sea[14,48]. As explained before, the sex of the offspring is determined by the prevailing temperature during the mid-trimester of the incubation period[31].

The survival of the hatchlings is a determining factor for the conservation of the species. The physical conditions of the beach greatly influence the successful emergence of the hatchlings. Mortality can be increased by very high or low temperatures, inefficient gas exchange or nest flooding[60–62]. Temperature is a determining factor in embryonic development, not only to determine the sexual differentiation of embryos, because temperatures outside the 25–33ºC range can lead to the death of embryos[63]. Two measurements are used to measure the survival of hatchlings: hatching success, and emergence success. Hatching success is the proportion (%) of eggs in the nest that produce live hatchlings; while emergence success is the proportion (%) of eggs in the nest chamber that hatch and reach the ocean. The mean hatching and emergence percentages reported for Galapagos beaches seen relatively low compared to other sites (Table 2.4), where they are on average 70 to 80%.

Given that the hatching and emergence success of hatchlings is directly related to biotic and abiotic factors, the

Table 2.4: Mean hatching and emergence success proportions (%) for the Galapagos green sea turtle population.

Variable and year(s)	**N**	**mean**	**SD**	**range**	**References**
Hatching success (%)					
2004-2007	1039	46.0	33.4	30.1-83.6	59
Emergence success (%)					
2002	19	89.0	-	-	49
2004-2007	1039	45.6	33.4	29.6-83.4	59

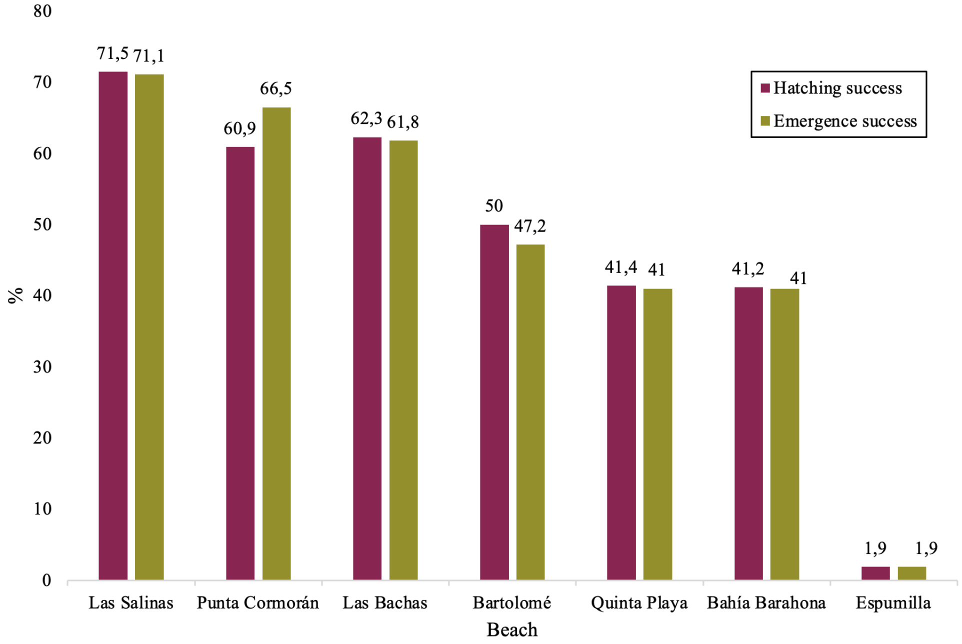


Figure 2.7: *Chelonia mydas*. Hatching and emergence success. Studies in Espumilla and Bartolomé are reported in 1982 by Green and Ortiz-Crespo[64], Punta Cormorán data is reported in 1984 by Hurtado[36], Quinta Playa, Bahía Barahona, Las Bachas, and Las Salinas are reported in 2013 by Zárate[59].

percentages shown in each beach (Figure 2.7) represent the interaction between human activity, predation of the eggs by a wide range of native and introduced predators (see section 2.7), due to the alteration of the structure and composition of the beach as a result of tidal changes, and the high density of nesting females (because the increase of nesting females on a beach, increases the probability that one female will excavate into another's nest).

2.7 Conservation and management of the green sea turtle in Ecuador

According to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, three of the seven extant species of sea turtles are classified as either endangered or critically endangered. Another three species are considered as vulnerable, and the conservation status for *Natator depressus* remains uncertain due to data deficiency[65]. *Chelonia mydas*, the green sea turtle, is listed as either endangered or threatened, depending on the scope of the assessment[4]. The conservation status of green sea turtle population in the Galapagos Islands and the Ecuadorian coast is considered near threatened by the IUCN Red List[66].

2.7.1 Threats

Threats to green sea turtle populations and their habitat are widespread, affecting both marine and nesting habitats. Among the most important threats include predation, incidental bycatch, egg and turtle harvest, boat strikes, pollution, and climate change (Figure 2.8). Nesting beaches are very dynamic and their morphology is severely affected by anthropogenic factors. Sand removal for construction purposes, coastal development, and vehicle traffic on the beach contributes to the destruction of nests, negatively impacting the nesting of the green sea turtle[4]. Light pollution in the vicinity of nesting beaches can disturb and disorient the hatchlings, causing them to move away and lose their way to the sea. Pollution, fishing activities, and climate change may result in the alteration of green sea turtle feeding habitat affecting forage quantity, quality and/or distribution. In foraging habitats, it is common to find turtles with injuries caused by boat propellers and shark bites[67]. Turtles have great difficulty avoiding boats at speeds higher than 40 km/h[67] so approximately 22% of the mortality of the green sea turtle in Galapagos is caused by boat strikes[68]. In nesting areas, the presence of this type of lesion is 5–20%, while at feeding sites is 31–51%[69]. All these dangers threaten the survival not only of the green sea turtle population, but also other marine fauna, who resides or visits Galapagos.

During the first life stages (eggs and hatchlings) the Galapagos green sea turtles are susceptible to native predators such as the ghost crab (*Ocypode gaudichaudii*), the land hermit (*Coenobita compressus*), the yellow-crowned night heron (*Nyctanassa violacea*), and the beetle (*Trox suberosus*), and to introduced predators such as feral cats and pigs, and black rats[48] (Table 2.5). Espumilla on Santiago Island used to have serious problems with feral pigs (*Sus scrofa*): they prey on the eggs and destroy the nests. The GNP began the introduced species eradication program to combat the problem of pigs and has almost completely eliminated this threat. Although, a new study on the survival of hatchlings on this beach is necessary to assess its current state.

Predators are undoubtedly one of the greatest problems to the survival of hatchlings: the beetle *Omorgus subeosus* and the feral pig have been reported on almost all beaches of the Islands. To determinate the factors that affect the survival of hatchlings and their impact is of utmost importance to generate and improve protection and conservation strategies in different beaches.

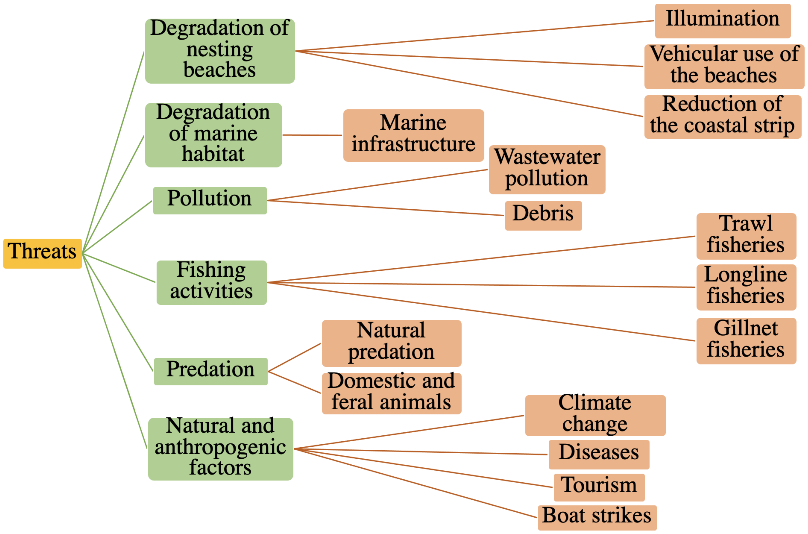


Figure 2.8: Main threats to the *Chelonia mydas* species in the Galapagos Islands.

Table 2.5: Native and introduced predators that affect eggs and hatchlings of green sea turtles in Galapagos Islands.

Predator	**Origen**	**Target**
Fregata minor	Native	Hatchlings
Fregata magnificens	Native	Hatchlings
Larus fuliginosus	Native	Hatchlings
Larus pipixcan	Native	Hatchlings
Ardea herodias	Native	Hatchlings
Pelecanus occidentalis	Native	Hatchlings
Nyctanassa violacea	Native	Hatchlings
Ocypode gaudichaudii	Native	Eggs/hatchlings
Coenobita compressus	Native	Hatchlings
Grapsus grapsus	Native	Eggs/hatchlings
Omorgus suberosus	Native	Eggs
Sus scrofa	Introduced	Eggs/hatchlings
Rattus rattus	Introduced	Eggs/hatchlings
Felis catus	Introduced	Eggs/hatchlings

2.7.2 Ecuadorian legislation on sea turtle conservation

Since sea turtles are highly migratory species, during their life cycle they remain in different environments in various countries. Therefore, it is necessary to consider an international policy for their conservation and proper management. Ecuador, through the MAAE, developed the Action Plan for the Conservation of Sea Turtles in Ecuador 2020-2030[45]. This is a tool that seeks to strengthen the state of conservation of sea turtles and their habitats, by implementing actions such: conservation of nesting, reproduction, migration and foraging sites, reduction of contamination and other threats, international cooperation, research, and technical training of personnel. Ecuador is part of a series of regional and international treaties that directly or indirectly protect sea turtles and their habitats (Table 2.6).

Table 2.6: Regional and International treaties of which Ecuador is part for the direct or indirect protection of sea turtles and their habitats.

Treaty	**Scope of action**
Global	
Convention on International Trade in Endangered Species of Wild Fauna and Floral (CITES)	International Trade
United Nations Convention on the Law of the Sea (UNCLOS)	Marine environment
Convention on Migratory Species (CMS)	Habitat / Ecosystems
Ramsar Convention	Habitat / Ecosystems
Convention on Biological Diversity (CBD)	Habitat / Ecosystems
International Convention for the Prevention of Pollution from Ships (MARPOL)	Marine environment
Code of Conduct for Responsible Fisheries (CCRF)	Incidental bycatch
Regional	
Inter-American Tropical Tuna Commission (IATTC)	Incidental bycatch
Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC)	Sea turtles (specifically) Habitat / Ecosystems
Western Hemisphere Migratory Species Initiative (WHMSI)	Habitat / Ecosystems
Permanent Commission for the South Pacific (CPPS)	Marine environment

The GNP plays a transcendental role in the study and conservation of the species, however, like any public institution, the activities of the GNP are limited by the state budget. Despite the fact that in 2016 the *Código Orgánico de la Economía Social de los Conocimientos, Creatividad e Innovación* was approved with the aim of regulating and promoting scientific research, technological development and innovation in the country, the established budget has not been met a fullness. In 2020, investment in science and technology constituted only 0.47% of the growth domestic product (GDP), which considerably limits scientific development and production. Without a doubt, public and private investment are necessary for research, science and technology to develop in the country.

2.7.3 Zoning conservation system in Galapagos

The zoning system established by the GNP is a tool that allows the integral management and conservation of the biodiversity of terrestrial and marine ecosystems through a regional model that links protected areas and populated areas. The coastal waters that surround each island or islet belong to Zone 2 (Limited Use), in which four sub-zones are recognized with the purpose of protecting environments, resources or activities that are notably susceptible to alterations.

- **Subzone 2.1** (Comparison and protection: Conservation subzone)
  These zones serve as control areas, i.e. areas to study biodiversity and ecology in the absence of human impacts. Only science and education are allowed in these areas. Fishing and tourism are not allowed.
- **Subzone 2.2** (Conservation and non-extractive use: Tourism subzone)
  The main use is water tourism, but it also includes science, conservation and education. In this subzone, some or all of the following activities can be allowed: snorkeling, diving, and whale watching from the boat.
- **Subzone 2.3** (Conservation, extraction and non-extractive use: Fishing subzone)
  Extractive use includes artisanal fishing, navigation, education, science, tourism, patrolling, and military maneuvers.
- **Subzone 2.4** (Temporary special handling areas: ASTM)
  Occasionally, along the established zones, special areas temporarily managed for experimental or recovery purposes may be determined, whose extension will be defined for each case by the *Junta de Manejo Participativo* and which will be approved by the *Autoridad Interinstitucional de Manejo*.

According to the current zoning scheme that governs the Galapagos National Park and Marine Reserve[70], Quinta Playa, Bahía Barahona, Las Bachas, Las Salinas and Espumilla beaches occur in subzone 2.3 (Conservation, extractive and non-extractive use), while, Punta Cormonán is located within subzone 2.2 (Conservation and non-extractive use) (Figure 2.9). It is estimated that almost half of the beaches in Galapagos present significant nesting potential for *Chelonia mydas*. The majority of these beaches (87.0%), however, are in sites that correspond to extraction areas (subzone 2.3), whereas 5.8% are in tourism sites (subzone 2.2), 4.3% in comparison and protection subzones (subzone 2.1) and 2.9% in temporary special management areas, close to populated centers (subzone 2.4). Of the total number of beaches, only 4.5% have been studied for *Chelonia mydas* presence as of today.[49,71].

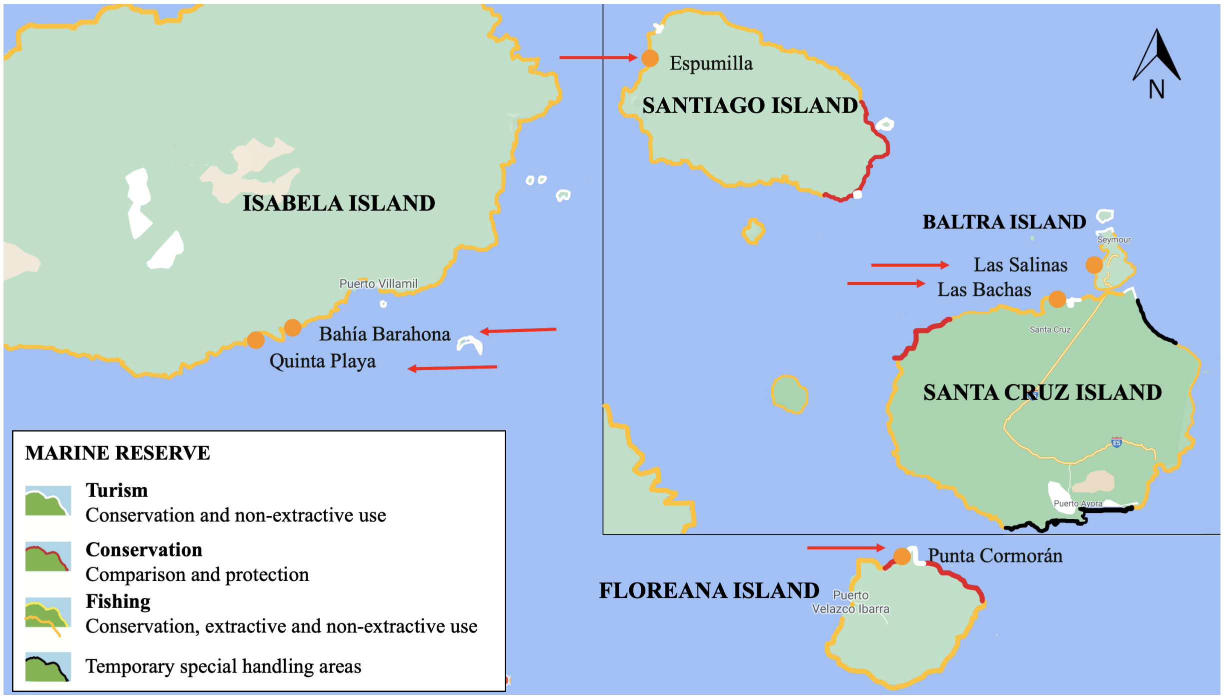


Figure 2.9: Galapagos National Park and Marine Reserve zoning system. The red arrows show the main nesting beaches: Quinta Playa, Bahía Barahona, Las Bachas, Las Salinas and Espumilla beaches, located in fishing subzones (yellow profile line). Punta Cormonán is located within the tourism subzone (white profile line).

3. A sex-structured continuous time population dynamics model of the green sea turtle (*Chelonia mydas*) population in the Galapagos Islands

In the realm of ecology, population dynamics is the area dedicated to understand and explain how the size of biological populations change through time. There is a long history reflecting the progressive development of population dynamics theory. Simple population models represented the starting point on the study of demographic processes. In the *Exponential model*, originally associated with Thomas Robert Malthus[72], the assumption of a constant per-capita growth rate leads population growth in a geometric progression. In the *Logistic model*, published by Pierre-François Verhulst[73], as a generalized expression of the exponential growth, a maximum population size was set. These simple models helped to understand the basics of *idealized* demographic phenomena, but did not incorporate many of the factors influencing the complex demographic processes of populations.

Many factors that influence population dynamics have been incorporated to explain the complex population dynamics. Age-structure of a population is one factor that potentially affects population growth. Using a continuous-time model, James Lotka[74] determined the relation between age-specific birth and death rates, that served as a basis to model several species interactions such as competition, mutualism, and predator-prey interactions (the Lotka-Volterra model[75,76]). In 1948, Patrick Holt Leslie proposed the use of matrices in age-structured populations[77], thus adapting Lotka's continuous-time model to a discrete-time approach. Sex-structured models were described by Iannelli et al.[78], arising after it was realized that the one-sex stable population theory was insufficient to answer questions related to existence and demographic interrelations of the sexes.

For the present work, we will use the basic concepts of some of the most widely used models to interpret population dynamics. A sex-structured-continuous-time model will be developed to represent the population dynamics of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands.

3.1 Model Formulation

The green sea turtle, like other sea turtles, has a remarkable life cycle. Individuals inhabit widely separated localities during the course of their lives. These habitats include foraging, migration, breeding, and nesting areas (Figure 3.1). After hatchlings emerge from their nests, they immediately travel to the sea. Once in the ocean, hatchlings are washed away by ocean currents, live a pelagic phase in the open ocean, and they are not seen again until they appear as juveniles in foraging areas, probably a decade later[79]. This period of time between the hatchling and juvenile stages is known as the "lost years" because migratory route taken by the hatchlings and their behavior remains a mystery[79,80]. In the foraging areas, they continue to mature until they become subadults. Subadults are occasionally seen foraging in the open ocean[79]. Once the turtles reach sexual maturity, males and females return to their home beach, shallow waters, to mate and nest. This behavior is known as philopatry and has been documented for several species[81].

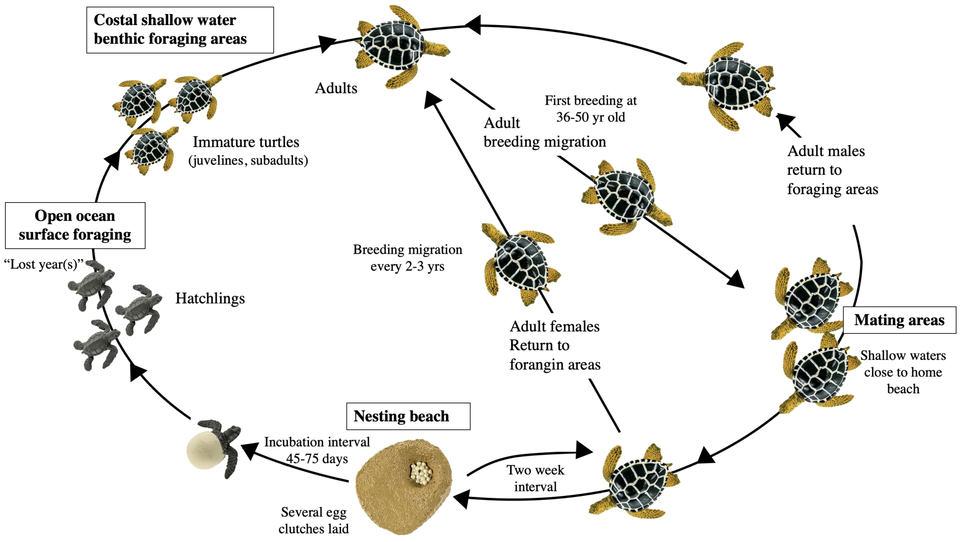


Figure 3.1: Schematic diagram of the *Chelonia mydas* life cycle.

Because during the early stages of the turtle life cycle, hatchlings, juveniles, and subadults are not reproductively active, we can simplify the life cycle of the green sea turtle and consider only two main stages: adults and eggs. In turn, the adult stage can be divided into two populations: female adults and male adults, which are interesting to analyze by themselves. An schematic diagram of the simplified life cycle of the green sea turtle is shown in Figure 3.2.

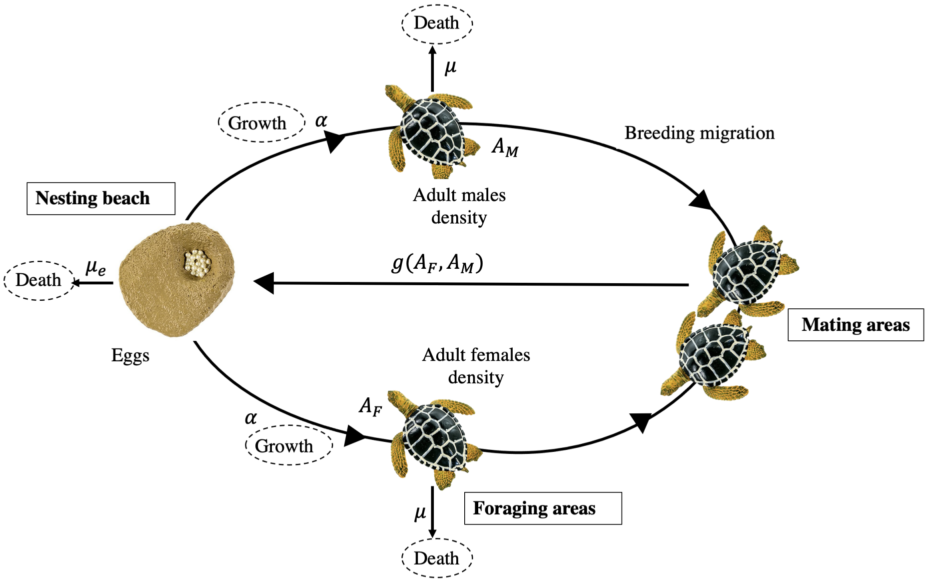


Figure 3.2: Schematic diagram of the mathematical model, which represents a simplification of the green sea turtle life cycle.

This scheme of the life cycle (Figure 3.2) makes a clear distinction between adult males and females, focusing on their interaction during mating process that eventually will result in the production of eggs. After an incubation period of 45-75 days[82] the eggs develop into either female or male sea turtles. It also shows the outflows of each stage: the death of adult females, males, and eggs. Successful mating of males and females will produce and increase the egg population which in turn will develop into males and females. What determines the proportion of eggs that develop as males or females is the incubation temperature of the eggs.

The reproductive biology and nesting behavior of male and female sea turtles comprises a number of aspects that make modeling this interaction truly challenging. The interaction itself between males and females involves a variety of factors that can strongly affect the birth rate of the population and therefore the long-term dynamics. For instance, density of adult female (A_F) and male populations (A_M), the behavioral responses during mating process, and searching efficiency[58], are some of the variables to take into account for a successful mating.

This study is particularly concerned on the proportion of eggs allocated to males and females in the population.

At time t, we denote, the egg population as $E(t)$ and adult population for males and females as $A_M(t)$ and $A_F(t)$, respectively. The dynamics of the egg population is governed by the following first order ordinary differential equation:

$$\frac{dE}{dt} = g(A_F, A_M) - (\alpha + \mu_e)E, \tag{3.1}$$

where α is the maturity rate of eggs that become adult males or females. μ_e is the mortality rate of the egg stage. The function $g(A_F, A_M)$ is the successful mating interaction that results in egg production and is represented by:

$$g(A_F, A_M) = \hat{f}(A_M + A_F)\left(1 - \frac{A_M + A_F}{K}\right),$$

where $\hat{f}$ is the fecundity rate, K is the environmental carrying capacity, i.e. the maximum population size that the environment can sustain indefinitely. When the adult population approaches the carrying capacity, then the per-capita egg production approaches zero.

To model the changes in adult male and female population over time, linear ordinary differential equations were developed:

$$\frac{dA_M}{dt} = q\alpha E_M - \mu A_M, \tag{3.2}$$

$$\frac{dA_F}{dt} = (1-q)\alpha E_F - \mu A_F, \tag{3.3}$$

where the proportion of male and female eggs are given by q and $1 - q$ respectively. μ is the death rate for adult stage. As there is not evidence of different maturity and death rates for males and females, α and μ remains the same for both sexes.

Based on (3.1) to (3.3), the next system of differential equations is proposed:

$$\begin{cases} \dfrac{dA_M}{dt} = q\alpha E - \mu A_M \equiv F_1(A_M, A_F, E) \\ \dfrac{dA_F}{dt} = (1-q)\alpha E - \mu A_F \equiv F_2(A_M, A_F, E) \\ \dfrac{dE}{dt} = \hat{f}\,(A_F + A_M)\left(1 - \frac{A_M + A_F}{K}\right) - (\alpha + \mu_e)\,E \equiv F_3(A_M, A_F, E). \end{cases} \tag{3.4}$$

Our parameters α, μ, $\hat{f}$, μ_e, K, and q are positive constants. For a detailed description of the parameters see Table 3.2.

3.2 Qualitative analysis of the model

In the next sections, a complete qualitative description of the dynamics of system (3.4) will be given. The region where the system is positively invariant is characterized and the local and global stability of the equilibrium points are described.

Since the vector field of system (3.4) is continuously differentiable, the first result follows from the fundamental existence-uniqueness theorem (see for instance[83,84]).

Theorem 1. For any initial condition $A_M(0) \geq 0$, $A_F(0) \geq 0$, and $E(0) \geq 0$, there exists $\beta > 0$ such that the corresponding solution of system (3.4) is unique on $[0, \beta)$.

3.2.1 Region of biological interest

The region of biological interest is given by the set Ω, defined as:

$$\Omega = \left\{ (A_M, A_F, E) \in \mathbb{R}^3_+ : 0 < A_M < K, 0 < A_F < K - A_M, 0 < E < \frac{\mu K}{2\alpha} \right\}. \tag{3.5}$$

The following theorem guarantees that the system (3.4) is biologically well posed and that the dynamic of the system is concentrated on a bounded region of $\mathbb{R}^3_+$.

Theorem 2. Suppose that $1 > \frac{\hat{f}\alpha}{2\mu(\alpha+\mu_e)}$, then the region Ω is positively invariant under the flow induced by (3.4).

Proof. In order to prove this theorem, The vector field defined by (3.4) is analyzed on the boundary of Ω, denoted by $\partial\Omega$. Figure 3.3 shows the surface given by $\partial\Omega$. Note that the prism given by Ω has five faces and six vertices.

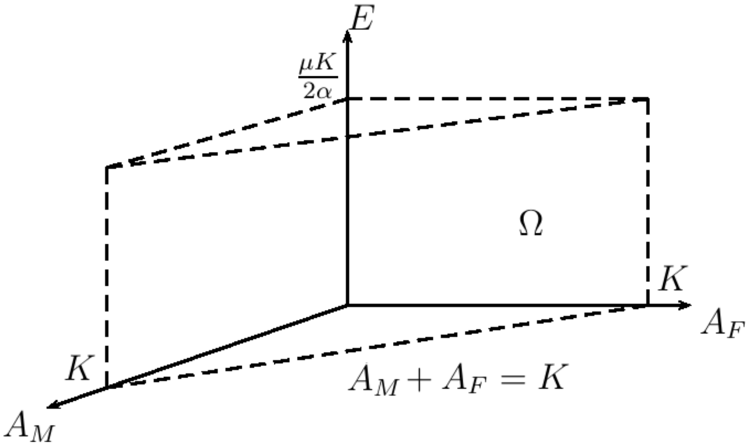


Figure 3.3: The positively invariant Ω region for the system (3.4).

The vector field given by the right side of system (3.4) on the boundary of Ω is directed to the interior of the set Ω (see Table 3.1). In consequence, solutions with initial data in Ω remain there for all $t \geq 0$, and therefore they have biological meaning. This concludes the proof.

Table 3.1: Vector field analysis on $\partial\Omega$ for system (3.4).

i) $A_M \in (0, K), A_F = 0, E = 0$	ii) $A_M = 0, A_F \in (0, K), E = 0$	iii) $A_M = 0, A_F = 0, E \in (0, \frac{\mu K}{2\alpha})$
$A'_M = -\mu A_M < 0,$ $A'_F = 0,$ $E' = \hat{f}\left(1 - \frac{A_M}{K}\right)A_M > 0$	$A'_M = 0,$ $A'_F = -\mu A_F < 0$ $E' = \hat{f}\left(1 - \frac{A_F}{K}\right)A_F > 0$	$A'_M = q\alpha E > 0$ $A'_F = (1-q)\alpha E > 0$ $E' = -(\alpha + \mu_e)E < 0$
iv) $A_M = K, A_F = 0, E \in (0, \frac{\mu K}{2\alpha})$	v) $A_M = 0, A_F = K, E \in (0, \frac{\mu K}{2\alpha})$	vi) $A_M = 0, A_F \in (0, K), E = \frac{\mu K}{2\alpha}$
$A'_M = -\mu K + q\alpha E \leq -\frac{\mu K}{2} < 0,$ $A'_F = (1-q)\alpha E > 0,$ $E' = -(\alpha + \mu_e)E < 0,$	$A'_M = -q\alpha E > 0,$ $A'_F = -\mu K + (1-q)\alpha E \leq -\frac{\mu K}{2} < 0$ $E' = -(\alpha + \mu_e)E < 0,$	$A'_M = \frac{q\mu K}{2} > 0,$ $A'_F =$ no matter sign $E' = -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\left(1 - \frac{A_F}{K}\right)A_F$ $\leq -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\frac{K}{4} < 0$
vii) $A_M \in (0, K), A_F = 0, E = \frac{\mu K}{2\alpha}$	viii) $A_M \in (0, K), A_F = K - A_M,$ $E = 0$	ix) $A_M \in (0, K), A_F = K - A_M,$ $E = \frac{\mu K}{2\alpha}$
$A'_M =$ no matter sign $A'_F = (1-q)\frac{\mu K}{2} > 0$ $E' = -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\left(1 - \frac{A_M}{K}\right)A_M$ $\leq -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\frac{K}{4} < 0$	$A'_M = -\mu A_M < 0$ $A_F = -\mu A_F < 0$ $E' = 0$	Note that $\langle 1, 1, 0\rangle$ is a normal vector of the plane $A_M + A_F = K$. Therefore, $\langle F_1, F_2, F_3\rangle \cdot \langle 1, 1, 0\rangle = -\frac{\mu K}{2} < 0$, and $E' = -(\alpha + \mu_e)\frac{\mu K}{2\alpha} < 0$. So, $\langle F_1, F_2, F_3\rangle$ is directed to the interior of Ω
x) $A_M \in (0, K), A_F = 0, E \in (0, \frac{\mu K}{2\alpha})$	xi) $A_M = 0, A_F \in (0, K),$ $E \in (0, \frac{\mu K}{2\alpha})$	xii) $A_M \in (0, K), 0 < A_F < K - A_M,$ $E = 0$
$A'_M =$ no matter sign $A'_F = (1-q)\alpha E > 0$ $E' =$ no matter sign	$A'_M = q\alpha E > 0$ $A'_F =$ no matter sign $E' =$ no matter sign	$A'_M =$ no matter sign $A'_F =$ no matter sign $E' = \hat{f}\left(1 - \frac{A_M + A_F}{K}\right)(A_M + A_F) > 0$
xiii) $A_M \in (0, K), 0 < A_F < K - A_M,$ $E = \frac{\mu K}{2\alpha}$	xiv) $A_M \in (0, K), A_F = K - A_M,$ $E \in (0, \frac{\mu K}{2\alpha})$	
$A'_M =$ no matter sign $A'_F =$ no matter sign $E' = -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\left(1 - \frac{A_M + A_F}{K}\right)$ $(A_M + A_F) \leq -(\alpha + \mu_e)\frac{\mu K}{2\alpha} + \hat{f}\frac{K}{4} < 0$	This case is analogous to (ix)	

□

3.2.2 Equilibrium points

Remark. From Theorem 2, it can be deduced that the solutions of system (3.4) are defined for all $t \geq 0$. Henceforth the condition $1 > \frac{\hat{f}\alpha}{2\mu(\alpha + \mu_e)}$ is assumed.

The equilibria of system (3.4) are given by the solutions of the following system of algebraic equations.

$$\begin{cases} q\alpha E - \mu A_M = 0 \\ (1-q)\alpha E - \mu A_F = 0 \\ \left(1 - \frac{A_M + A_F}{K}\right) \hat{f}\,(A_F + A_M) - (\alpha + \mu_e)\,E = 0. \end{cases} \tag{3.6}$$

Solving (3.6) we obtain one trivial critical point $I_0 = (0,0,0)$, that always exists, and a unique nontrivial critical point $I^* = (A_M^*, A_F^*, E^*)$ which exists if the following condition is true:

$$R_0 = \frac{\hat{f}\alpha}{\mu(\alpha + \mu)} > 1. \tag{3.7}$$

In this case, we have:

$$A_M^* = qK\left(1 - \frac{\mu\,(\alpha + \mu_e)}{\hat{f}\alpha}\right), A_F^* = (1-q)K\left(1 - \frac{\mu\,(\alpha + \mu_e)}{\hat{f}\alpha}\right), E^* = \mu K\left(1 - \frac{\mu\,(\alpha + \mu_e)}{\hat{f}\alpha}\right).$$

I_0 equilibrium point represents the extinction of the species, this is the moment when all the components of the system of differential equations are zero. Whereas I^* is the equilibrium point where the population persist, in this case, all the components of the system of differential equations coexist in a balanced way, allowing the subsistence of the species. Then a necessary and sufficient condition for I^* to have biological sense is if and only if $R_0 > 1$. This result is summarized in the following theorem.

Theorem 3. Model (3.4) admits the two equilibrium points I_0 and I^* contained in Ωif $R_0 > 1$. Whereas, if $R_0 \leq 1$ the system (3.4) only admits the I_0 equilibrium.

3.2.3 Local stability of equilibrium points

In this subsection we shall discuss the local stability properties of the equilibria I_0 and I^*. To determine the stability of our equilibria, we can linearize our system in the matrix form $\dot{x} = Jx$. Where J is the so-called Jacobian matrix, whose entries are the partial derivatives of the right hand sides of the differential equations of system (3.4), taken with respect to the different state variables of the model (A_M, A_F and E).

$$\begin{pmatrix} \dot{A_M} \\ \dot{A_F} \\ \dot{E} \end{pmatrix} = \begin{pmatrix} \frac{\partial F_1}{\partial A_M} & \frac{\partial F_1}{\partial A_F} & \frac{\partial F_1}{\partial E} \\ \frac{\partial F_2}{\partial A_M} & \frac{\partial F_2}{\partial A_F} & \frac{\partial F_2}{\partial E} \\ \frac{\partial F_3}{\partial A_M} & \frac{\partial F_3}{\partial A_F} & \frac{\partial F_3}{\partial E} \end{pmatrix} \begin{pmatrix} A_M \\ A_F \\ E \end{pmatrix}, \tag{3.8}$$

For the tri-dimensional system the corresponding Jacobian matrix at an arbitrary point is given by

$$J = \begin{pmatrix} -\mu & 0 & q\alpha \\ 0 & -\mu & (1-q)\,\alpha \\ \gamma & \gamma & -\alpha - \mu_e \end{pmatrix} \tag{3.9}$$

where

$$\gamma = \hat{f}\left(1 - \frac{2}{K}(A_M + A_F)\right).$$

The linearized model gives us a very good description of the behaviour of the nonlinear model, at least in the neighborhood of the equilibrium. If the real part of the eigenvalues are non negative, then the behaviour of the system near the equilibria is qualitatively the same as the behaviour of the linear approximation.

To establish the stability of our equilibrium points, the Jacobian matrix (3.9) associated to the system (3.4) is evaluated in I_0 and I^*.

Theorem 4. If $R_0 \leq 1$ the system (3.4) has only the I_0 critical point and is locally asymptotically stable. If $R_0 > 1$, I_0 becomes unstable.

Proof. The Jacobian matrix associated to system (3.4) about the equilibrium point I_0 is given by

$$J(I_0) = \begin{pmatrix} -\mu & 0 & q\alpha \\ 0 & -\mu & (1-q)\,\alpha \\ \hat{f} & \hat{f} & -\alpha - \mu_e \end{pmatrix}. \tag{3.10}$$

The characteristic polynomial associated to (3.10) is

$$\begin{aligned} P(\lambda) &= \lambda^3 + (\mu_e + \alpha + 2\mu)\lambda^2 + \left(2\mu_e\mu + 2\alpha\mu + \mu^2 - \alpha\hat{f}\right)\lambda + \alpha\mu^2 + \mu_e\mu^2 - \alpha\mu\hat{f} \\ &= a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 \end{aligned}$$

where $a_0 = 1$, $a_1 = \alpha + \mu_e + 2\mu$, $a_2 = -\hat{f}\alpha + \mu(\alpha + \mu_e) + \mu(\alpha + \mu + \mu_e)$, and $a_3 = \mu(-\hat{f}\alpha + \mu(\alpha + \mu_e))$. To determine the conditions on the parameters for the trivial equilibrium (I_0) to be local asymptotically stable we will use Routh-Hurwitz stability criterion[85]. This give us a necessary and sufficient condition for stability. Let

$\phi(\lambda) = a_0\lambda^n + a_1\lambda^{n-1} + \cdots a_{n-1}\lambda + a_n$ and consider the following diagram known as the Routh array:

$$\begin{array}{cccc} a_0 & a_2 & a_4 & \cdots \\ a_1 & a_3 & a_5 & \cdots \\ b_1 & b_3 & b_5 & \cdots \\ c_1 & c_3 & c_5 & \cdots \end{array}$$

where the elements b_i and c_i are obtained from the following expressions

$$b_1 = -\tfrac{1}{a_1}\begin{vmatrix} a_0 & a_2 \\ a_1 & a_3 \end{vmatrix}, \quad b_3 = -\tfrac{1}{a_1}\begin{vmatrix} a_0 & a_4 \\ a_1 & a_5 \end{vmatrix}, \quad \cdots$$

$$c_1 = -\tfrac{1}{b_1}\begin{vmatrix} a_1 & a_3 \\ b_1 & b_3 \end{vmatrix}, \quad c_3 = -\tfrac{1}{b_1}\begin{vmatrix} a_1 & a_5 \\ b_1 & b_5 \end{vmatrix}, \quad \cdots$$

$$\vdots \qquad\qquad \vdots \qquad\qquad \vdots$$

with the agreement of adding zeros to each row to make the calculation possible, and where the number of rows equals $n + 1$. Now the equilibrium point (I_0) is local asymptotically stable for system (3.4) if the roots of (3.10) have negative real part.

CRITERION OF ROUTH-HURWITZ: *All the roots of the real polynomial* $\phi(\lambda) = a_0\lambda^n + a_1\lambda^{n-1} + \cdots a_{n-1}\lambda + a_n$, $(a_0 \neq 0)$ *have negative real parts if and only if by using the Routh algorithm all the elements of the first column of the Routh array are different from zero and have the same sign.*

Now, for the polynomial $P(\lambda)$, we have that the first column of the Routh array is

$$a_0 = 1, \quad a_1 = \mu_e + \alpha + 2\mu, \quad b_1 = \frac{1}{a_1}(a_1a_2 - a_3), \quad c_1 = a_3 = \mu(-\hat{f}\alpha + \mu(\alpha + \mu_e)).$$

Since a_0, a_1, and a_3 are positive and $a_1a_2 - a_3 = (\alpha + \mu + \mu_e)(-\hat{f}\alpha + \mu(\alpha + \mu_e) + \mu(\alpha + \mu_e + 2\mu)) > 0$. $I_0 = (0, 0, 0)$ is locally asymptotically stable if and only if $R_0 \leq 1$, otherwise, it is unstable. This concludes the proof.

□

Theorem 5. If $R_0 > 1$ the system (3.4) admits the nontrivial equilibrium point I^* and is locally asymptotically stable. If $R_0 \geq 1$, I^* becomes an unstable point.

Proof. The Jacobian matrix of system (3.4) about the equilibrium point I^* is given by

$$J(I^*) = \begin{pmatrix} -\mu & 0 & q\alpha \\ 0 & -\mu & (1-q)\,\alpha \\ \gamma^* & \gamma^* & -\alpha-\mu_e \end{pmatrix}, \tag{3.11}$$

where

$$\begin{aligned}
\gamma^* =&\hat{f}\left(1-\frac{2}{K}(A_M^*+A_F^*)\right)\\
=&\hat{f}\left(1-\frac{2}{K}\left(qK\left(1-\frac{\mu\,(\alpha+\mu_e)}{\hat{f}\alpha}\right)+(1-q)K\left(1-\frac{\mu\,(\alpha+\mu_e)}{\hat{f}\alpha}\right)\right)\right)\\
=&\hat{f}\left(1-2\left(1-\frac{\mu\,(\alpha+\mu_e)}{\alpha\hat{f}}\right)\right)\\
=&\hat{f}\left(1-2\left(1-\frac{1}{R_0}\right)\right)\\
=&\hat{f}\left(\frac{2}{R_0}-1\right).
\end{aligned}$$

The characteristic polynomial associated to (3.11) is

$$\begin{aligned}
P(\lambda) &= \lambda^3+(\mu_e+\alpha+2\mu)\lambda^2+\left(2\mu_e\mu+2\alpha\mu+\mu^2-\alpha\hat{f}\left(\frac{2}{R_0}-1\right)\right)\lambda\\
&+ \alpha\mu^2+\mu_e\mu^2-\alpha\mu\hat{f}\left(\frac{2}{R_0}-1\right)=a_0\lambda^3+a_1\lambda^2+a_2\lambda+a_3,
\end{aligned}$$

where $a_0 = 1$, $a_1 = \mu_e + \alpha + 2\mu$, $a_2 = \hat{f}\alpha + \mu^2$, and $a_3 = \mu(\hat{f}\alpha - \mu(\alpha + \mu_e))$. Now, the equilibrium point I^* is local asymptotically stable for system (3.4) if the roots of (3.11) have negative real part, which is equivalent by the Routh-Hurwitz stability criterion[85] to $a_0, a_1, a_3 > 0$ and $a_1a_2 - a_3 > 0$. Since a_0, a_1, and a_3 are positive and $a_1a_2 - a_3 = (\mu_e + \alpha + 2\mu)(\hat{f}\alpha + \mu^2) - \mu(\hat{f}\alpha - \mu(\alpha + \mu_e)) > 0$, then the equilibrium point I^* exist and is locally asymptotically stable for system (3.4) if and only if $R_0 > 1$; otherwise, it is unstable. This concludes the proof. □

3.2.4 Global stability analysis

Now, I proceed to prove that under some conditions the nontrivial equilibrium point is globally asymptotically stable. The global stability of the equilibrium solutions can be proved by transforming system (3.4) into a planar system and then using two fundamental results of bi-dimensional systems, namely Bendixon's criterion and Poincare Bendixon's Theorem[83]. After that, we can go back to system (3.4) and prove the global asymptotic stability of the three dimensional equilibrium point.

Theorem 6. Suppose that $1 > \frac{\hat{f}\alpha}{2\mu(\alpha+\mu_e)}$. If $R_0 > 1$, then the equilibrium point I^* is global asymptotically stable in Ω; otherwise I_0 is global asymptotically stable.

Proof. Let $(A_M(0), A_F(0), E(0))$ be an arbitrary initial data on Ω. If we make the change of variable $A = A_M + A_F$, then system (3.4) can be reduced to the following bi-dimensional system:

$$\begin{cases} \dfrac{dA}{dt} = \alpha E - \mu A \equiv G_1(A, E) \\ \dfrac{dE}{dt} = \left(1 - \frac{A}{K}\right) \hat{f}(A) - (\alpha + \mu_e) E \equiv G_2(A, E) \end{cases} \tag{3.12}$$

Since the vector field of system (3.12) is directed to the interior of the region

$$\tilde{\Omega} = \left\{ (A, E) \in \mathbb{R}^2 : 0 < A < K, 0 < E < \frac{\mu K}{2\alpha} \right\},$$

we have that $\tilde{\Omega}$ is positively invariant (Figure 3.4).

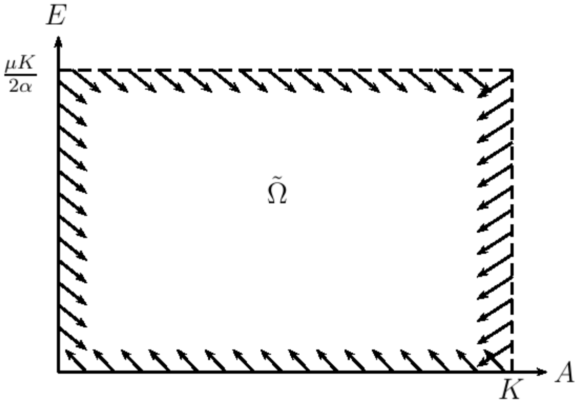


Figure 3.4: Vector field of system (3.12) on the boundaries of $\tilde{\Omega}$.

Suppose that $R_0 > 1$, and consider $I^* = (A_M^*, A_F^*, E^*)$ the nontrivial equilibrium point of system (3.4). Note that $(A_M(0) + A_F(0), E(0)) \in \tilde{\Omega}$ and the system (3.12) has the equilibrium points $\tilde{I}_0 = (0, 0)$ and $\tilde{I}_* = (A^*, E^*)$ where

$A^* = \frac{\alpha}{\mu}E^*$. Since

$$\operatorname{div}(G_1, G_2) = -(\mu + \alpha + \mu_e) < 0,$$

we get, by using the Bendixon's criterion[83], that system (3.12) has not periodic solutions in $\tilde{\Omega}$. On the other hand, the eigenvalues of the linearized system around $\tilde{I}_*$ associated to (3.12) are given by

$$\lambda = \frac{1}{2}\left(-(\mu + \alpha + \mu_e) \pm \sqrt{(\mu + \alpha + \mu_e)^2 - 4\alpha\hat{f}}\right),$$

which have negative real part ($\Re(\lambda) < 0$). So, $\tilde{I}_*$ is locally asymptotically stable, and applying Poincare-Bendixon's Theorem[83], it can be concluded that the equilibrium point $\tilde{I}_*$ is globally asymptotically stable on $\tilde{\Omega}$. That is to say,

$$\lim_{t\to\infty} A(t) = A^* \quad \text{and} \quad \lim_{t\to\infty} E(t) = E^*.$$

Now, by using the first equations of system (3.4), we get that

$$A_M(t) = A_M(0)e^{-\mu t} + e^{-\mu t}\int_0^t q\alpha E(s)e^{\mu s}ds.$$

On the other hand, given $\epsilon = E^*/2$, there exists $\tau > 0$ such that $E(t) > E^*/2$ for $t > \tau$; hence

$$\begin{aligned}\int_0^t q\alpha E(s)e^{\mu s}ds &= \int_0^\tau q\alpha E(s)e^{\mu s}ds + \int_\tau^t q\alpha E(s)e^{\mu s}ds\\ &\geq \int_0^\tau q\alpha E(s)e^{\mu s}ds + \int_\tau^t q\alpha\frac{E^*}{2}e^{\mu s}ds \to \infty \text{ as } t \to \infty.\end{aligned}$$

Therefore, by using the L'Hospital rule, we have that

$$\lim_{t\to\infty} A_M(t) = \lim_{t\to\infty} A_M(0)e^{-\mu t} + \lim_{t\to\infty} e^{-\mu t}\int_0^t q\alpha E(s)e^{\mu s}ds = \frac{q\alpha}{\mu}E^* = A_M^*.$$

Analogously, we obtain that

$$\lim_{t\to\infty} A_F(t) = \frac{(1-q)\alpha}{\mu}E^* = A_F^*.$$

So, the equilibrium point $I^* = (A_M^*, A_F^*, E^*)$ is globally asymptotically stable in Ω.

If $1 \geq R_0$, then I_0 is the unique point of equilibrium of system (3.4). Following an analogous reasoning to the one above, we have that I_0 is globally asymptotically stable. This concludes the proof. □

The methodology applied here to study the dynamics of the population of green sea turtles on the Galapagos Island, can be applied to study the dynamics of other types of reptiles. In all these cases, the region of biological interest will be of the polyhedral type, which allows us to study the vector field on each face of the region, and the invariance of this region can be achieved in the same way we did it with the prism in this work. After that, we can study the local stability of the equilibrium points by linearizing the differential equation around them, and looking at the sign of the eigenvalues; then reduce the system to a two-dimensional one and apply Bendixon's criterion, and finish it with the Poincare-Bendixon theory to conclude that the non-trivial equilibrium point is globally asymptotically stable. From the foregoing comments, it is clear that our method can be used to study a broad class of similar problems.

3.3 Numerical simulations and biological interpretation

The sex-structured continuous time model used to evaluate the Galapagos green sea turtle population dynamics comprised five demographic parameters, which are summarized in Table 3.2. The above results are applied to show numerical examples using open-source numerical tool XPPAUT and data from the literature review presented in Chapter 2.

Table 3.2: Parameters values used for the simulation of a sex-structured population dynamics model of the green sea turtle in Ecuador (Galapagos Islands).

Parameter	Description	Estimated values	Reference
α	Maturity rate of green sea turtle	0.54 ±0.45	[44]
μ	Per capita death rate for adults	0.052 ± 0.005	[86]
μ_e	Per capita death rate for eggs	0.79 ± 0.19	[59]
q	Proportion of eggs that become male	0.5	[35]
$\hat{f}$	Fertility rate	0.35 ± 0.15	(Estimated)

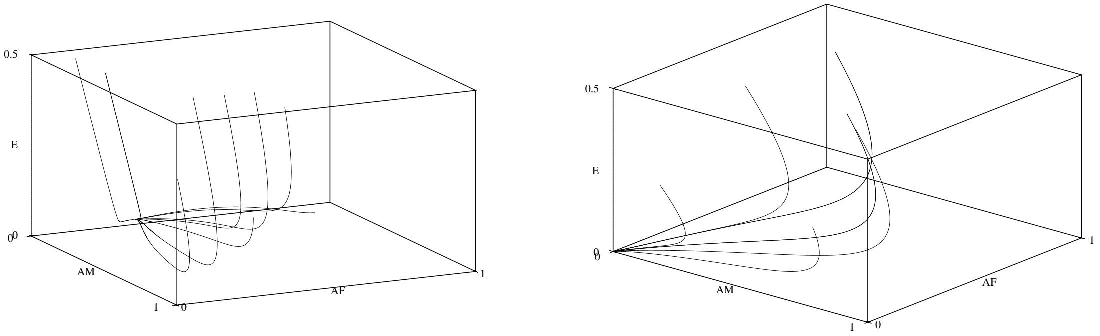
The fertility rate $\hat{f}$ is derived from:

$$\hat{f} = \text{fecundidy} \cdot \mu_e$$

where: fecundity= (PBF)(EPC)(CPS)(RMI)$^{-1}$(MR); PBF, probability of being female; EPC, mean eggs per clutch; CPS, mean number of clutches per season per female; RMI, remigration interval (breeding probability (RMI)$^{-1}$); and MR, maturity rate. There are no specific studies that determine the hatchling sex ratio in the Galapgos Islands, even so, studies carried out in foraging areas report a ratio between males and females of 1:1, therefore, we will assume that, as the probability of being female (PBF = 0.5)[35], .

By implementing the estimated values for our parameters within the model (3.4) we can observe that indeed, the population of Galapagos meets the conditions for which the nontrivial critical point is globally asymptotically stable

($R_0 = 6.3$) (Figure 3.5(a)). That is, the asymptotic stability is maintained for any initial value within the Ω set. On the other hand, by altering the estimated values of the parameters, such that the established condition R_0 is not met, the trivial critical point becomes globally asymptotically stable (Figure 3.5(b)). That is, the population falls towards extinction regardless of the values taken within the positively invariant Ω set.



(a) Global stability for the nontrivial I^* equilibrium point

(b) Global stability for the trivial I_0 equilibrium point

Figure 3.5: Numerical simulations for global stability for the a) nontrivial (I^*) and b) trivial (I_0) equilibrium points.

As mentioned previously, R_0 establish the condition that ultimately determine the extinction of the species or its persistence in the environment. In terms of the biological significance of the parameters defining this number, R_0 can be interpreted as the basic reproduction number of the green sea turtle population. The average number of individuals that reaches successfully adulthood, produced by a typical female during mating interaction. As is expected biologically $R_0 > 1$ implies population persistence, otherwise population tends to extinction.

Table (3.3) resumes the dynamical behavior of system (3.4). R_0 represents the reproductive potential of the population. If R_0 is greater than 1.0, there is a net surplus of offspring produced, and the population increases. If R_0 is less than 1.0, the mortality is too high and therefore the population cannot replace itself, therefore it decays to extinction.

Table 3.3: Existence and stability conditions of the equilibria of model (3.4).

Equilibrium	**Biological existence**	**Stability**
I_0	Always exists	$R_0 \leq 1$
I^*	$R_0 > 1$	$R_0 > 1$

3.4 Advantages and drawbacks of the model

The dynamic behavior of a population could be studied through a mathematical model that describes the system under certain considerations such as: birth, death, immigration and emigration rates, etc. The way in which the population dynamics is represented depends largely on how it is structured, on the variables selected to represent the population dynamics, and the availability of demographic data corresponding to the species being studied.

Populations such as the green sea turtle are usually structured by physiological stages, that is, they are classified taking into account the stages through which the individual passes in its life cycle. In the case of green sea turtle: eggs, hatchlings, juveniles, sub-adults, and adults. This division in the life cycle of the species gives rise to mathematical representation by means of discrete matrix systems[87]. Discrete matrix systems consider the growth and survival of individuals and their reproductive capacity for each of the stages. In this sense, developing a matrix model of population dynamics requires the presence of these demographic data for each stage. In populations that have been studied for decades with a solid and stable monitoring protocol such us the Great Barrier Reef green sea turtle population[88], it has been possible to obtain demographic data through observation and parameter estimation[89], which has been very useful for the development of discrete matrix models for population dynamics.

In the case of the Galapagos green sea turtle population, this information is not yet available for each stage. That is why a different approach is needed. By implementing a mathematical model of continuous ordinary differential equations, the population structure is simplified, resulting in fewer necessary demographic parameters. In this way, the information that is available can be used and a mathematical model that interprets part of the population's reality can be generated. On the other hand, the disadvantage of the model also lies in its simplicity, since the assumptions on which it is based are not very rigorous.

Unlike conventional discrete age-structured models, which only take into account the female nesting population, this mathematical appreciation of the population dynamics of the *Chelonia mydas* species makes a clear distinction between sexes through a sex-structured continuous time model. This allows us to include a greater part of the green sea turtle population in the analysis. Of course, more extensive analyzes of the model are necessary e.g. a sensitivity analysis on the R_0 condition to determine which of the parameters that compose it mainly influence the stability of the nontrivial equilibrium point I^*. Despite this, the model can be used as a basis for a more complex models and include a series of parameters, which can offer us a better appreciation of population dynamics and how it is affected or distorted by the influence of new parameters, such as temperature.

Stage-structured continuous time models have included TSD by considering the proportion of male eggs as a function of temperature $q(T)$ and adding details about other stages of the turtle life cycle[90], and have concluded that low temperatures are not as harmful as high temperatures. Incorporate these new parameters in the model proposed in this thesis could reveal new stability conditions, which can help to envision the population situation and take actions for the conservation of the species.

In the construction of models there is great freedom in the selection of the assumptions with which investigations are governed and it is precisely this freedom that makes biological models so useful, since the researcher can easily alternate these assumptions and explore their consequences.

4. Conclusions and outlooks

The information of this study summarizes the data obtained during the different research projects developed around the *Chelonia mydas* species in the Galapagos Islands. Despite the fact that the Galapagos Islands are home to one of the largest green sea turtle nesting populations in the East Pacific, there are few published studies on this independent demographic unit. Demographic data, such as population abundance in nesting and foraging sites, growth rates and sexual maturity, lifespan, sex ratios, and survival rates of the different stages are necessary to have a better understanding of the current state of the species and to be able to predict the population dynamics long term and take pertinent conservation actions.

The importance of the GNP in the conservation and preservation of the *Chelonia mydas* species is evident. The efforts made by the GNP in the study and monitoring of the green sea turtle provide valuable information that helps to analyze the current state of the population, the main threats of nesting beaches, the influence of anthropogenic factors on the survival of the species, and the various strategies or action plans that can be taken to protect and guarantee the conservation of the green sea turtle and its habitat.

Even though most of the beaches of the Galapagos Islands have significant nesting potential for the *Chelonia mydas species*, 87.0 % of these beaches are in subzone 2.3 (Conservation, extractive and non-extractive use), so the current zoning system is partially protecting the nesting green sea turtle population in Galapagos. It is a priority, then, that greater efforts be established and maintained regarding the conservation of these sites to ensure a healthy maintenance of the population.

The continuity of the green sea turtle nesting monitoring project in the Galapagos Islands is essential to generate relevant scientific information that helps to the conservation of the species. But, in addition, technical protocols for foraging sites must be established and standardized, since in this way more information on the general status of the population can be gathered. Favoring the development of new and better mathematical models that study and analyze the dynamics of the population.

The model developed in this thesis represents the population dynamics of green sea turtles through a sex-structured continuous time model. Through the distinction between sexes, this thesis seek to determine how different parameters can influence population dynamics and its stability. The qualitative analysis of the model showed that the average number of individuals that reaches successfully adulthood, produced by a typical female during mating interaction determine the persistence of the green sea turtle population, or its extinction. Biologically, the number of offspring a female individual produces over time should be higher than the outflow rates of the population stages, in order for the population to persists.

Based on the historical data of the nesting population records, together with the results of the qualitative analysis and the numerical simulations carried out, it can be concluded that the nesting green sea turtle population in Galapagos is presented as a healthy population, with a significant number of individuals, which is an important factor because the population that nests in Galapagos is considered one of the main in the East Pacific.

The analysis provided in this manuscript is only a small part of all that can be studied from models with similar characteristics, without leaving doubts, it is necessary to carry out many and more detailed analyzes that allow evaluating the population status of the green turtle, but this model establishes a start for more complex models.

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