

POPULATION ASSESSMENT AND MANAGEMENT NEEDS OF A GREEN
TURTLE, *Chelonia mydas*, POPULATION IN THE WESTERN CARIBBEAN

By

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by

Cathi Lynn Campbell

This dissertation is dedicated to my mother, Georgianna Carbin, and my grandmother, Martha Bazemore, who have always supported my endeavors and helped me face many challenges throughout my life.

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May 2003

Chair: Michael P. Moulton

Major Department: Wildlife Ecology and Conservation

In this study I estimated survival rates of large juvenile and adult female green turtles (*Chelonia mydas*) from mark-recapture data from the Nicaragua foraging ground and from band recovery analysis. I used these data to estimate the long-term growth rate of a simulated population to assess the current status of the Tortuguero, Costa Rica green turtle population. I also examined potential changes to current harvest levels in Nicaragua to estimate sustained yield.

Based on band recovery analysis, large juvenile and adult green turtles tagged at Nicaragua turtle fishing sites and adult females tagged on the nesting beach exhibit low mean annual survival probabilities, $O = 0.55$ (SE = 0.04) and, $O = 0.82$ (SE = 0.12), respectively. Based on a series of matrix population projections simulations using these survival rate estimates, there is evidence that the Tortuguero population is probably declining. The severity of the threat, however, depends in part on the proportion of large juveniles from this population that are exposed to the Nicaragua turtle fishery. Based on

simulations in which this issue was explored, possibly 41% of large juveniles could be exposed to the Nicaragua fishery and still maintain a stable population, provided the survival rate of the remaining large juvenile population is at least 0.90. These results were based on the model with the most optimistic demographic parameters; other models revealed that 0 or 9% may be exposed to the Nicaragua turtle fishery. It is likely that more than 41% of large juveniles from the Tortuguero population are exposed to the Nicaragua turtle fishery because no other major foraging habitat for large juveniles has been identified.

Estimates of sustained yield ranged from 1,027 to 2,912 large juvenile and adult turtles/yr based on the most conservative model (model with the least optimistic demographic parameters). These results suggest that considerable reductions in the green turtle harvest of between approximately 8,080 and 9,970 turtles/yr are needed based on a current harvest level of 11,000 turtles/yr. Potential mechanisms to reduce the Nicaragua harvest include: a closed season, harvest quotas, size and/or sex restrictions, and zoning fishing areas for variable use.

Resumen de Disertación Presentada a la Escuela de Postgrado
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EVALUACIÓN DE LA POBLACIÓN Y NECESIDADES DE MANEJO DE UNA
POBLACIÓN DE TORTUGA VERDE, *Chelonia mydas*, DEL CARIBE OCCIDENTAL

Por

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Mayo 2003

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En este estudio estimé las tasas de sobrevivencia de juveniles grandes y adultos de tortuga verde (*Chelonia mydas*) a partir de datos de marcado-recaptura de las áreas de forrajeo en Nicaragua y de análisis de recuperación de marcas. Usé estos datos para estimar la tasa de crecimiento a largo plazo de una población simulada para evaluar la situación actual de la población de tortugas verdes de Tortuguero, Costa Rica. También examiné los cambios potenciales de los actuales niveles de captura en Nicaragua para estimar el rendimiento sostenible.

Con base en el análisis de recuperación de marcas, los juveniles grandes y adultos de tortuga verde marcados en los sitios de pesca en Nicaragua y las hembras adultas marcadas en la playa de anidación exhiben bajas probabilidades promedio de sobrevivencia anual, $O = 0.55$ (SE = 0.04) y, $O = 0.82$ (SE = 0.12), respectivamente. Con base en una serie de simulaciones por matrices de proyecciones poblacionales usando estas estimaciones de las tasas de sobrevivencia, existe evidencia de que la población de

Tortuguero está probablemente declinando. Sin embargo, la severidad de la amenaza depende en parte de la proporción de juveniles grandes de esta población que están expuestos a la pesquería de tortugas en Nicaragua. Con base en simulaciones en las que se exploró este tema, posiblemente el 41% de los juveniles grandes pudieron ser expuestos a la pesquería de Nicaragua y aún mantener una población estable, siempre y cuando la tasa de sobrevivencia del resto de la población de juveniles grandes es de al menos 0.90. Estos resultados se basaron en el modelo con los parámetros demográficos más optimistas; otros modelos revelaron que 0 ó 9% pueden estar expuestos a la pesquería de tortugas en Nicaragua. Es probable que más del 41% de los juveniles grandes de la población de Tortuguero están expuestos a la pesquería de tortugas en Nicaragua ya que no se ha identificado otro hábitat de forrajeo importante para los juveniles grandes.

Estimaciones del rendimiento sostenible variaron de 1,027 a 2,912 juveniles grandes y tortugas adultas/año en el modelo más conservador (modelo con los parámetros demográficos menos optimistas). Estos resultados sugieren que se necesitan reducciones considerables en la captura de tortugas verdes de entre aproximadamente 8,080 y 9,970 tortugas/año, con base en un nivel actual de captura de 11,000 tortugas/año. Los mecanismos potenciales para reducir la captura en Nicaragua incluyen: una temporada de veda, cuotas de captura, restricciones por tamaño y/o sexo, y restringir áreas de pesca para uso variable.

CHAPTER 1 INTRODUCTION

Conservation Issue

On a nesting beach in Costa Rica, the green turtle (*Chelonia mydas*) life cycle begins when females deposit their eggs on a stretch of beach called Tortuguero, the largest remaining rookery for endangered green turtles in the Atlantic basin (Carr et al. 1978). The hatchlings that emerge from these nests (approximately 9 weeks later) will already have survived numerous predators of sea turtle eggs (Fowler 1979) and will face other predators as they rush across the beach to the ocean. During this short journey, some of these hatchlings will not survive the vultures (*Coragyps atratus*, *Cathartes aura*), coatis (*Nasua narica*), and other predators that await them. Those that reach the surf will attempt to make it to offshore currents that will take them to convergences where they can find food resources and refuge (Carr 1987, Hirth 1997). But some of these tiny turtles will fall victim to predatory sea birds, sharks, and fishes. Those that survive the days or weeks it will take to reach the convergent zones will spend the next few years feeding as they passively drift to unknown areas. Survivors of this pelagic, oceanic stage (lasting 1-6 years, Ehrhart and Witherington 1992, Zug and Glor 1998) will shift habitats when they reach roughly 25 cm in carapace length and move to shallow seagrass flats (such as those in the Bahamas, Bermuda, and southeastern U.S.) where they become herbivorous and continue their development. Large predators such as sharks and large fish will take more of these small juvenile green turtles in the estimated 12 years (Bjorndal et al. 2000) it will take for them to attain a size large enough to shift habitats

again and avoid most predators. Once they attain a size of about 70 cm, many of these still immature turtles will join adult turtles that forage on the deeper seagrass beds found in the coastal waters of Caribbean Nicaragua, among the largest in the world (Roberts and Murray 1983). The size of these immature and adult turtles ensures that they will have few natural predators, and so natural mortality for these turtles is low. However, it is in Nicaragua that the Tortuguero population, and possibly other smaller rookeries, face extensive commercial harvesting of large juvenile and adult turtles. Green turtles have been harvested for centuries in the coastal waters of Nicaragua; however, previous levels were likely much lower than current levels. Today, along Nicaragua's Caribbean coast more than 11,000 green turtles are harvested annually (Lagueux 1998). Since the end of the civil war in 1990, coastal inhabitants on Nicaragua's Caribbean coast have moved back to their communities. These growing communities, in one of the poorest countries in the Western Hemisphere (Central Intelligence Agency 2002), and their need to function in a cash economy are driving this renewed turtle fishery.

Recent results from long-term studies on turtle demography show that turtles are characterized by low survival of young, high survival rates of large juveniles and adults, longevity, delayed maturation, and iteroparity (Gibbs and Amato 2000). These characteristics make them vulnerable to overexploitation and thus, poor candidates for sustained harvesting (Congdon et al. 1993, 1994). Ideally, before an endangered population of sea turtle is subjected to such intense harvesting, an assessment of its current state would be conducted so that species recovery and potential use can be properly managed. Unfortunately, no such assessment has been conducted for the Tortuguero green turtle population.

How is the resurgence of this turtle fishery in Nicaragua affecting the depleted Tortuguero population today, and possibly other depleted rookeries in the region? Is a harvest sustainable? Should any large-scale harvesting be permitted or at what stage of population recovery? These questions must be answered to avoid further depletion of the Tortuguero population. Since this intense harvesting in Nicaragua restarted approximately 10 years ago, efforts to assess the status of the Tortuguero green turtle population and evaluate management options are seemingly long overdue. Such information is essential so that stakeholders can make informed decisions and agreements about the future of this valuable resource. Without information on the status of the resource and the impact of the Nicaragua turtle fishery on the resource, the future of the Tortuguero green turtle population is uncertain. The purpose of this study is to assess the status of the resource and to evaluate management options for the turtle fishery in Nicaragua.

Background Information

Nearly 50 years ago, Archie Carr (1954) wrote “The Passing of the Fleet,” in reference to the decline of Caribbean green turtles. He spoke of the role of green turtles in history, the demise of several major rookeries in the wider Caribbean, and his concern for the future of the remaining populations. But optimistically, he believed that intervention was clearly possible and that cooperation among governments that share this resource could save the green turtle. Largely through his efforts, the green turtle rookery at Tortuguero, Costa Rica, was afforded some protection by the Costa Rica government in the 1960's (Carr 1969, Carr et al. 1982), and finally, almost complete protection through the establishment of the Tortuguero National Park in 1975. However, these efforts protect only breeding adults and eggs, and conservation of the entire population

depends on cooperation among several nations. Unfortunately, cooperation has been sparse; thus in 1969, while Costa Rica was implementing conservation measures for the Tortuguero rookery, Nicaragua established three turtle canneries on its Caribbean coast to process juvenile and adult turtles for export. Pritchard (1969) stated that the Tortuguero rookery was threatened by this recent expansion of exploitation in Nicaragua, the main feeding ground for the colony. This threat subsided when the processing plants were closed in 1976 as a result of outside pressure on the Nicaragua government brought on by declines of green turtles on the foraging grounds in Nicaragua (Nietschmann 1979). The resulting decreased demand for turtles from the foraging ground in Nicaragua, combined with *de facto* protection resulting from a civil war in Nicaragua from 1981 to 1990, protection of nesting females and eggs since 1963 in Costa Rica, and establishment of the Tortuguero National Park in 1975, provided a reprieve for the green turtle population and it began to show signs of increase on the nesting beach (Bjorndal et al. 1999).

The question arises as to why it is necessary to revisit conservation and management issues for the Tortuguero green turtle population now. The depleted status of many green turtle populations was recognized decades ago in the form of regulations, treaties and conventions at both national and international levels. The purpose of identifying species threatened with extinction is to bring attention to their perilous status and promote conservation (IUCN 1996). Green turtles, like many other species, were listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 1992) in order to curtail trade of the species among nations; however, this convention has no bearing on domestic trade of wildlife products. Yet such domestic trade in wildlife species for meat is said to be the main problem for

half of the world's threatened animals (Caughley and Gunn 1996). Many countries in the Caribbean have regulations to conserve green turtles within their borders (e.g., Belize, Nicaragua, Costa Rica); however, they rarely provide complete protection (with restrictions of take by size, season, or within specific boundaries), and enforcement of these regulations is often inadequate (e.g., Smith et al. 1992, pers. obs.). Curtailment of trade in green turtles by national and international listings and conventions has aided the conservation of some green turtle populations that have not already been lost to overexploitation, e.g., the Florida, USA (Meylan et al. 1995) and Tortuguero, Costa Rica (Bjorndal et al. 1999) rookeries. However, an apparent lack of cooperation among governments and inappropriate and unenforced regulations continue to plague the still depleted Tortuguero population of green turtles today.

Since the 1960s, governments of some nations with green turtles from the Tortuguero population have taken the job of managing this resource more seriously than others. For example, on one extreme of the management continuum, Costa Rica fully protects nesting female green turtles and their eggs from harvesting (albeit with pressure from conservation groups) and has developed a lucrative non-consumptive use of nesting turtles (turtle watching) on the beach at Tortuguero. At the other extreme, Nicaragua has allowed the renewal of an uncontrolled commercial harvest (effectively no management) of both adult and large juvenile animals on the foraging grounds of more than 11,000 turtles per year since the mid-1990s) without an evaluation of the status of the resource. In addition, some take of green turtles from the Tortuguero population still occurs in Panama (A. and P. Meylan pers. comm.) and most likely in Honduras (C. Molinero pers. comm.) and Belize (Smith et al. 1992), although at a much smaller scale than in

Nicaragua. The Tortuguero green turtle population may thus be facing a serious threat from overexploitation due primarily to the green turtle fishery in Nicaragua. An evaluation of the status of this population is needed to determine if current levels of harvest exceed the population's ability to maintain itself.

Determining Population Status

A simple method to evaluate the status of a population is to analyze trends in population size and determine population growth rate. However, the size of sea turtle populations is nearly impossible to determine because obtaining direct counts of animals that spend almost their entire life in the ocean at numerous developmental and foraging habitats is not feasible. An index of population size that is commonly employed to evaluate sea turtle populations is nesting activity, usually nesting emergences or nest densities. Unfortunately, nesting activity of marine turtles can fluctuate widely from year to year and marine turtles are slow to mature, making it difficult to use nesting activity as an index of population status over relatively short time intervals. Regardless, since the mid-1970s nesting emergences at Tortuguero have shown a general increasing trend (Bjorndal et al. 1999). However, this relatively recent increase may be somewhat misleading because it only gives us a glimpse of nesting females and tells us nothing about the immature life stages or the adult male segment of the population. The majority of green turtles harvested in the turtle fishery in Nicaragua are large juvenile females (Lagueux 1998), and since some Caribbean green turtles may take as many as 36 years to reach sexual maturity (Frazer and Ladner 1986), it would take many years before the impact of the Nicaragua fishery is felt on the nesting beach at Tortuguero. Additionally, by the time a decline in the nesting population can be detected using nesting emergences as an index, the population as a whole could be in a serious state of depletion and take

many years to recover, if it can recover at all. Based on current information the impact of the Nicaragua turtle fishery on the Tortuguero population is unclear, although speculation from scientists is that of a detrimental outcome for the turtle population (Seminoff In Press, Lagueux 1998). Thus, other methods are needed to assess the current state of the population so that the turtle fishery may be regulated based on sound scientific evidence.

A variety of other methods can be used to determine animal abundance and changes over time (e.g., see Seber 1982, Hilborn and Walters 1992, Caughley and Gunn 1996). In fisheries management, changes in capture per unit effort (CPUE) have often been used to estimate abundance from commercial catches and assess the impact of fishing (Hilborn and Walters 1992). A basic assumption of using CPUE as a measure of abundance is that abundance is directly proportional to catch rate. For this relationship to hold, fishing effort must be distributed randomly with respect to the target species, meaning that fishermen fish at random, which is not the case (Hilborn and Walters 1992). Two other possible relationships between CPUE and abundance are hyperdepletion and hyperstability, the latter being far more common and likely more applicable to the harvest of sea turtles on their feeding grounds (Hilborn and Walters 1992). Hyperstability is the situation in which capture effort remains high while abundance may actually be decreasing (Hilborn and Walters 1992). Hyperstability can occur when fishers seek out their target species (rather than fishing randomly) and share information that makes their search more efficient (Hilborn and Walters 1992). Species that aggregate are especially vulnerable to hyperstability (Hilborn and Walters 1992). Green turtles in Nicaragua apparently aggregate nocturnally at what turtle fishers call “sleeping rocks,” and these are the very sites that are used by turtle fishers. With little knowledge of the behavioral

dynamics of green turtles that use these sleeping areas and the potential for hyperstability, capture effort is probably not a good index for detecting trends in sea turtle abundance.

Recently, there has been an increase in the use of matrix population models to assess sea turtle populations. Population models can provide a useful tool to determine important life-history components and direct management efforts (Heppell et al. 1996*b*). Crouse et al. (1987) reported that changes in survival rates of the older life stages of a loggerhead population in the U.S. had the most impact on population growth rate. Their results made it clear that efforts to protect sea turtle eggs would not likely result in the most effective conservation of loggerhead sea turtles, and that reducing mortality in the large juvenile and adult stages was needed for the population to increase.

Several studies have used population models to evaluate various management options for sea turtles such as the use of turtle excluder devices (Crouse et al. 1987, Crowder et al. 1994), headstarting (Heppell et al. 1996*a*), and harvesting (Heppell et al. 1996*b*, Siddeek and Baldwin 1996). Matrix models have also been used to assess the current state of some sea turtle populations (Heppell et al. 1996*b*, Turtle Expert Working Group 2000). In addition, evaluation of age- or stage-class contributions to population growth is frequently used to better understand population dynamics and direct management efforts (e.g., Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996*a*, *b*). Thus, matrix population models can be used to estimate the status of a population under current conditions, identify important life stage parameters to focus research efforts, and evaluate management options, making this an appropriate tool to evaluate the potential threat facing green turtles in the western Caribbean today.

Current Study

The marine turtle fishery in Nicaragua probably affects green turtle populations originating from several nesting grounds in the Caribbean. The current study, however, will focus on the Tortuguero, Costa Rica, population since the majority of turtles in the foraging aggregation in Nicaragua are produced at the Tortuguero rookery (Bass et al. 1998), and it is the principal foraging site for Tortuguero adult females (Carr et al. 1978). The primary goals of the study are to 1) assess the status of the Tortuguero green turtle population as a whole (not only the nesting population), and 2) identify harvest strategies for the Nicaragua turtle fishery that will reduce its impact on the Tortuguero green turtle population. I hypothesize that the current rate of harvest of green turtles in Nicaragua has led to low survival probabilities in large juvenile and adult turtles, and this could result in a serious decline in the Tortuguero, Costa Rica, population. To test this hypothesis, I incorporate current demographic data on Caribbean green turtles (whenever possible data from the Tortuguero rookery are used) into matrix population models and provide a range of possible population growth rates. To determine a management strategy that would be effective at improving population growth, I use matrix population models to evaluate reductions in fishing mortality rates attributed to the Nicaragua turtle fishery and strategies to reduce harvest levels.

The dissertation is divided into 7 chapters. A description of the study area is provided in Chapter 2. In Chapter 3, I provide an overview of the ecology of green turtles in the western Caribbean, including what is known about their life history, the connections between relevant foraging aggregations and nesting populations, and a review of their use by humans in the relatively recent past. Band recovery methods (which for sea turtles involves the recovery of numbered flipper tags from harvested

animals) are used in Chapter 4 to estimate survival rates for large juvenile and adult green turtles. These estimates are for large juvenile and adult green turtles marked on the Nicaragua foraging ground in areas that are used by Nicaragua turtle fishers, and for adult females marked on the nesting beach at Tortuguero. Survival and fertility estimates, some derived from Chapter 4, are compiled in Chapter 5 and used in matrix population models to simulate the Tortuguero green turtle population under current conditions. In Chapter 6, I use population modeling to evaluate potential management options that might be applied to the Nicaragua turtle fishery. Recommendations are presented in Chapter 7.

CHAPTER 2 STUDY AREA

The study focuses on a population of green turtles (referred to as the Tortuguero population) that nest at the rookery at Tortuguero, Costa Rica, but occurs throughout the Caribbean in multiple developmental and foraging habitats during its life cycle. While foraging in Nicaragua, some proportion of the Tortuguero population, especially large juveniles and adults, is subjected to a marine turtle fishery; in addition, females from the nesting population can be exposed to turtle fishing throughout the Caribbean. Specific studies on survival of animals tagged on the foraging grounds in Nicaragua and tagged at the nesting beach at Tortuguero, Costa Rica, were conducted for this study to provide demographic data for population modeling. Thus, the study area descriptions focus on these two areas and do not include all areas in which green turtles from the Tortuguero population might occur.

Caribbean Nicaragua

One study area was located in the coastal waters of Caribbean Nicaragua. This area is well known for the broad continental shelf that extends some 200 km offshore at its widest point in the northern region. This continental shelf habitat is characterized by vast seagrass beds, among the largest in the world (Roberts and Murray 1983), that provide the primary food source, *Thalassia testudinum*, for green turtles in this region (Mortimer 1981). In addition to seagrass beds, coral reefs, offshore cays, and mangrove forests are found throughout most of this coastal zone.

From the north to the south Caribbean coast, annual rainfall increases from 2,500 to 5,500 mm (Murray et al. 1982). Winds are generally from the east and northeast (Murray et al. 1982), although periodically throughout the year winds can persist from any direction (pers. obs.).

The commercial artisanal marine turtle fishery along the Caribbean coast occurs primarily in the northern and central coastal regions from north of the Miskito Cays to just south of the Pearl Cays, although some harvest does occur seasonally further south when green turtles migrate to and from the Tortuguero, Costa Rica, rookery. The turtle fishery is described in more detail by Lagueux (1998). This study was conducted primarily in the Pearl Cays area, although one site north of the Pearl Cays (east of Río Grande Bar) was also used. The Pearl Cays are located off the mainland near the coastal community of Set Net (Figure 2.1). The Pearl Cays consist of a group of 18 sand and rock cays scattered amongst seagrass beds, fringe and patch reefs, as well as deeper coral reef systems (Figure 2.2). Turtle fishing locations in the Pearl Cays are usually found in deeper waters on the outskirts of the small islands. The turtle fishing areas are generally banks of relatively shallower water (approximately 9 to 15 m deep) surrounded by deeper water (approximately 18 to 21 m deep). These banks usually consist of large coral outcroppings that may have shelves or crevices that can be used by green turtles to “sleep” under or within. Presumably this provides the turtles with some protection against non-human predators (which are most commonly sharks).

The turtle fishing grounds in the Pearl Cays area are used by inhabitants of several communities; they include (with their approximate population sizes in parentheses) Awas (108), Kakabila (368), Haulover (1,469), Marshall Point (254), Orinoco (719), Pearl

Lagoon (2,552), Raitipura (371), and Set Net (103) (population data collected by Acción Medica Cristiana in 2002). Most of these communities are primarily Miskitu¹ Indian; however, Pearl Lagoon and Orinoco are primarily Creole and Garifuno, respectively. In addition, Rama Indians in the south harvest turtles as they migrate to and from the nesting beach at Tortuguero.

Tortuguero, Costa Rica

Tortuguero is located on the northeast Caribbean coast of Costa Rica (Figure 2.1). The nesting beach is approximately 35 km long and is bordered to the north by the Tortuguero River mouth and to the south by the Parismina River mouth. The Tortuguero beach is a high-energy, black sand beach, with little continental shelf extending off the mainland, and thus no foraging habitat for green turtles. The inshore current has a southeast trend during the nesting season, and a counter-clockwise gyre of the Caribbean circulation farther offshore (Carr et al. 1978). Lowland tropical rainforest borders the nesting beach, and the region is classified by Holdridge (1959) as very wet tropical forest. In 2000, rainfall ranged from more than 100mm/month to more than 600 mm/month (Mangel and Troëng 2001).

Three species of sea turtles--green, leatherback (*Dermochelys coriacea*), and hawksbill turtles (*Eretmochelys imbricata*)--nest at the Tortuguero rookery. Green turtles nest primarily from July to September, with less dense nesting also occurring in other months of the year (Carr et al. 1978). The northern 8 km of the nesting beach has been intensively studied by Archie Carr and others during the green turtle nesting season since the mid-1950s. Various aspects of the nesting ecology of Tortuguero green turtles have

¹The Miskitu Indians have also been referred to in some literature as the Miskito Indians; however, based on my experience working in the region, this indigenous group refers to themselves as the Miskitu, and thus I refer to them as such.

been described in numerous papers by A. Carr and colleagues (e.g., Carr and Giovannoli 1957, Carr and Ogren 1960, Carr et al. 1978, Bjorndal and Carr 1989, Bjorndal and Bolten 1992, Bjorndal et al. 1999). The annual tagging and research program is conducted by the Caribbean Conservation Corporation.

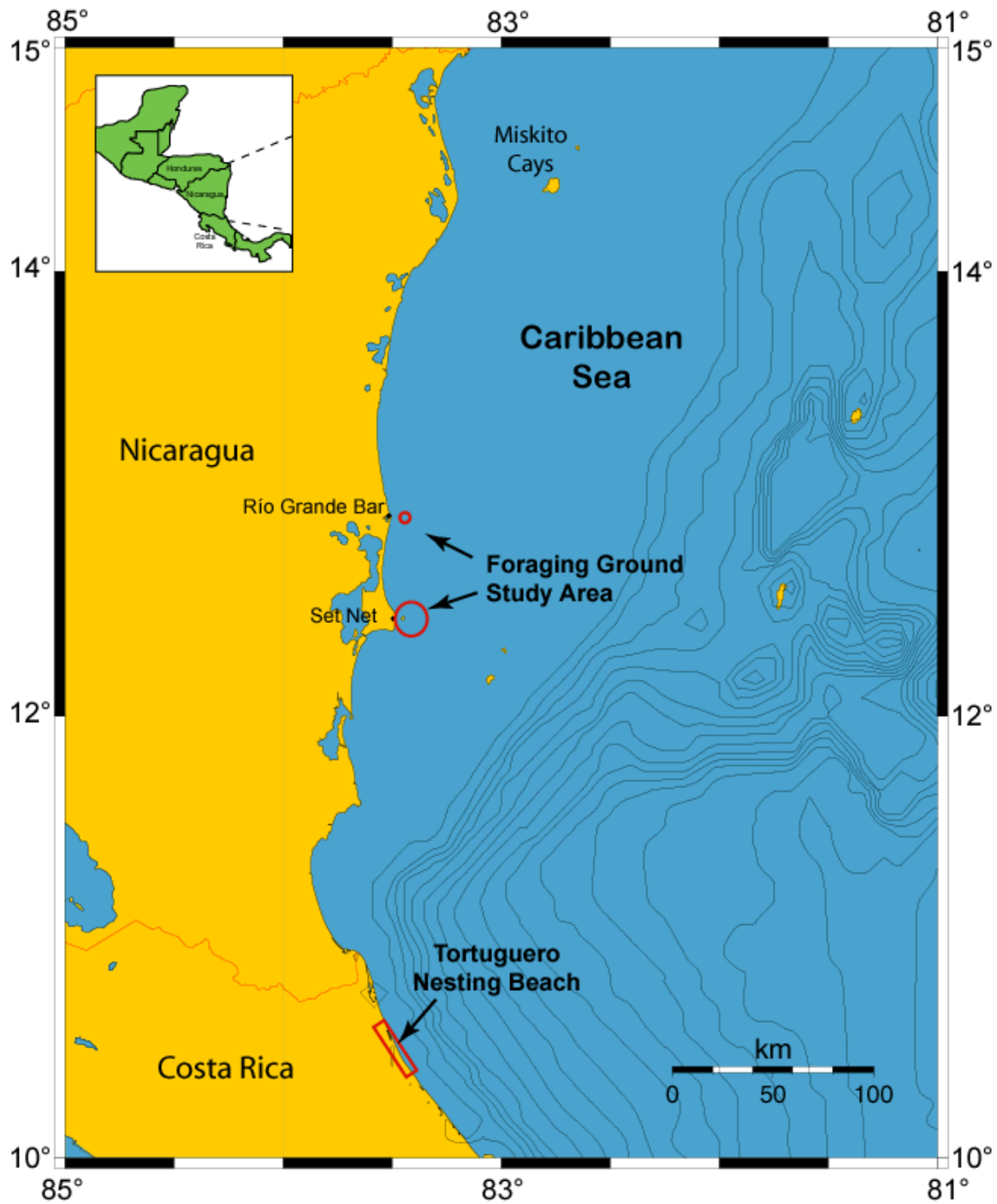


Figure 2.1. Study areas on the foraging ground in eastern Nicaragua and the nesting beach at Tortuguero, Costa Rica. Bathymetry lines represent contour intervals of 200 m.

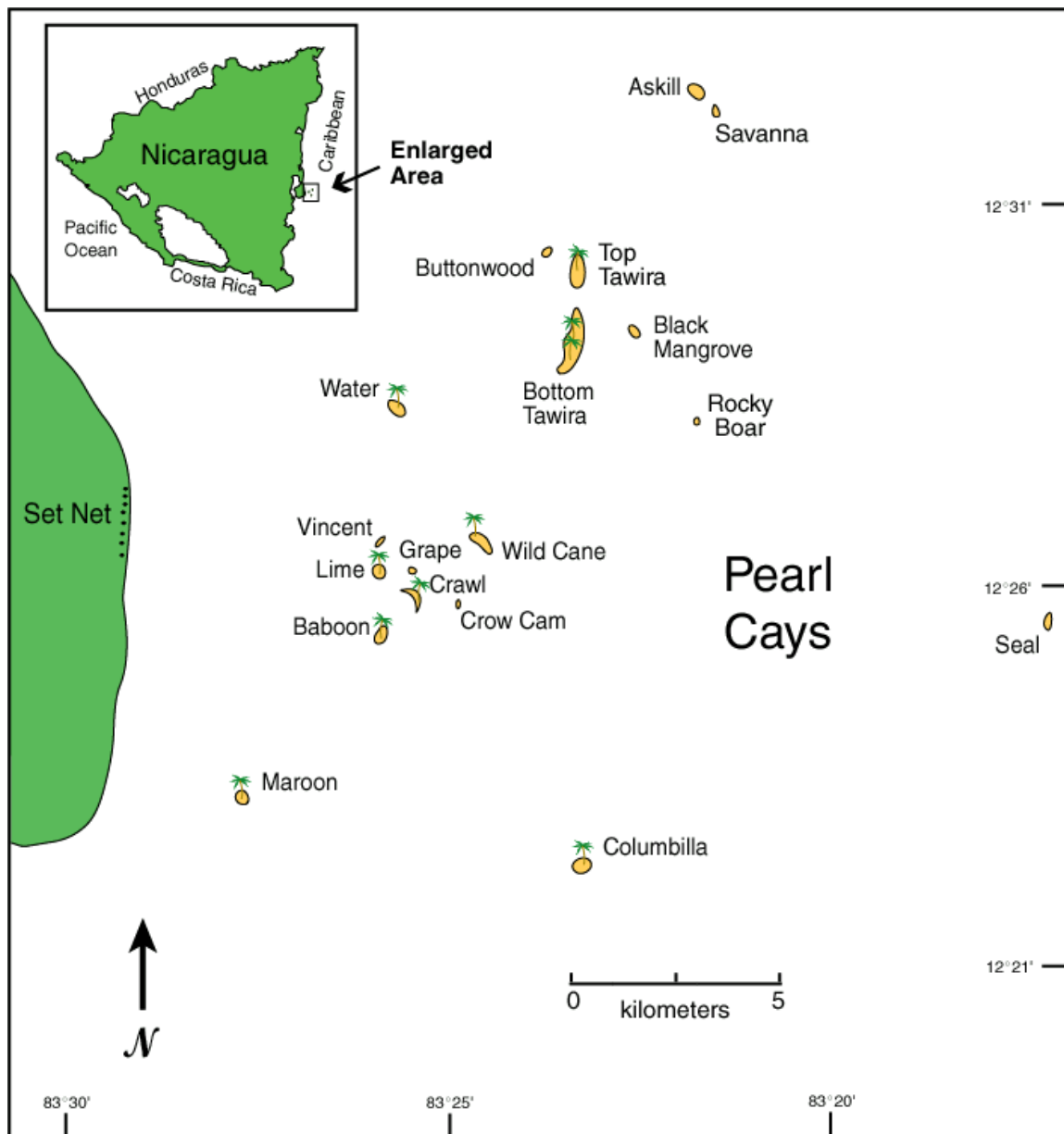


Figure 2.2. Map of the Pearl Cays, primary study area on the Nicaragua foraging ground.

CHAPTER 3 ECOLOGY AND HUMAN USE OF CARIBBEAN GREEN TURTLES

This chapter is divided into two sections, one on the ecology of green turtles and the other on the patterns and extent of human use of green turtles in the western Caribbean. Background information on the ecology of green turtles provides some of the demographic data necessary for population modeling and will help the reader understand the extent of habitat used by this species throughout its life cycle. This in turn will put into context the relationships among the foraging, developmental, and reproductive habitats of Caribbean green turtles, with an emphasis on the Tortuguero, Costa Rica, green turtle population. A general understanding of their life cycle and habitats, combined with background knowledge of the variable pressure on green turtles in the Caribbean from harvesting, provides a conceptual framework to understand the state of western Caribbean green turtle populations, particularly the Tortuguero population, today.

Ecology of Green Turtles in the Caribbean with Emphasis on the Tortuguero Population

Green turtles spend most of their lives in tropical and subtropical marine habitats around the world, emerging from the ocean only periodically as adults to deposit their eggs on coastal sandy beaches. They are unique in that they are the only herbivorous marine turtle, and among only a few herbivorous marine reptiles. Green turtles, like other marine turtles, have been well studied on their nesting beaches, providing a wealth of information on their nesting ecology. Nesting represents only a small part of their life

cycle, however, and many gaps in their life history remain. Long-term in-water studies are only beginning to fill the gaps about their developmental stages and foraging habitats. An overview of their life cycle, with specific demographic information used in later chapters to model population dynamics, and how it relates to the western Caribbean and specifically the Tortuguero, Costa Rica, green turtle population follows.

Life Stages

Eggs/hatchlings. Green turtles deposit their eggs in a flask-shaped hole they excavate between the water's edge and the vegetation of the upper beach platform (Bjorndal and Bolten 1992). The eggs are pliable and average diameter is 44 mm with a range of 39 to 48 mm (Bjorndal and Carr 1989). Average clutch size for Tortuguero green turtles is 112 eggs with a range of 3 to 219 (Bjorndal and Carr 1989). The incubation period ranges from 53 to 81 days, with an average of 62 days (Fowler 1979). Hatchling gender is determined by substrate temperature during incubation, and the temperature during the third trimester is particularly crucial. Hatching success varies somewhat; Horikoshi (1992) reported hatching successes of 51%, 49%, and 67% over 3 different seasons at Tortuguero. Hatchling emergence is usually at night and synchronous within a clutch. When the hatchlings emerge they move rapidly down the beach to the water, where they actively swim through the surf and, it is thought, they continue away from land until they encounter convergence zones (Hirth 1997). The principal predators of eggs and hatchlings on the beach at Tortuguero are coatis, vultures, ghost crabs, and at one time dogs (Fowler 1979). Once hatchlings reach the water, they may become prey to a variety of birds and fish species.

Pelagic post-hatchlings. This early developmental stage, once commonly referred to as the "lost-year" by many sea turtle scientists, is still the least well known for all

species of sea turtles. Post-hatchling green turtles are believed to use floating mats of sargassum in pelagic habitats of the open ocean (Carr 1987). Although believed to be omnivorous, they seem to have a tendency for carnivory (Bjorndal 1985). The duration spent in this stage is the least well known, however, estimated durations vary from one to six years (1 to 3 yr, Ehrhart and Witherington 1992; and 3 to 6 yr, Zug and Glor 1998).

Small juveniles. In the western Atlantic, small juveniles first appear in the shallow seagrass beds at a size of 20 to 25 cm carapace length (Bjorndal and Bolten 1988). Here they shift permanently to an herbivorous diet, although they also consume animals such as sponges and jellyfish (Bjorndal 1997). Their diet primarily consists of seagrasses, especially turtle grass, and algae (Mortimer 1981). In the Bahamas, small juveniles used grazing plots, thus gaining access to the more nutritious new growth of the turtle grass plants (Bjorndal 1980). Turtles may spend many years feeding and growing in the same area during this developmental stage, 12 yr was estimated for juvenile green turtles in the Bahamas (Bjorndal et al. 2000). When these juveniles attain a size of around 70 to 75 cm, they shift habitats again, and move to deeper benthic feeding areas.

Large juveniles/adults. Large juveniles/subadults are generally from 70 to 95 cm carapace length and adult females at Tortuguero range in size from about 95 to >115 cm carapace length, although nesting females smaller than 95 cm do occur. When large juvenile green turtles shift from shallow to deeper foraging habitats they continue to feed primarily on plants. Adult and large juvenile green turtles apparently use the same foraging habitats in some areas, e.g., Nicaragua. There is evidence for both resident and transient (emigration) behavior of green turtles in these later life stages on their foraging grounds (e.g., Chapter 4 this study, Carr et al. 1978, A. and P. Meylan pers. comm.), but

it is unclear if the transient behavior is due primarily to temporary emigration for reproduction. Mature males and females migrate, sometimes long distances (more than 2000 km), between foraging and nesting habitat, and Carr et al. (1978) suggested that subadults may also migrate with the reproductive animals.

Growth and Maturation

Growth rates. For pelagic post-hatchlings, no growth rate data are available for wild green turtles, however, since they are estimated to take from one to six years to complete this stage and they arrive in the benthic feeding habitat at about 25 cm, one could extrapolate that growth rates for post hatchlings could range from 3 to 20 cm/year (or 6.7 cm/yr for a three year stage duration). Numerous studies have provided data on annual growth rates of wild small juvenile green turtles (25 to 70 cm carapace length). For the 20 to 30 cm size class, annual averages of 3.6, 6.9, and 9.0 cm were reported for Puerto Rico (Collazo et al. 1992), Virgin Islands (Boulon and Frazer 1990), and Texas (Shaver 1994), respectively. For 30 to 40 cm size class, averages of 5.0 to 8.9 cm/yr were reported for various locations around the wider Caribbean (Bjorndal and Bolten 1988, Boulon and Frazer 1990, Collazo et al. 1992, Mendonça 1981). Growth rates are lower for the 40 to 50 cm size class, with averages ranging from 4.7 to 6.0 cm/yr for three locations (Bjorndal and Bolten 1988, Boulon and Frazer 1990, Collazo et al. 1992). Most averages reported for the 50 to 60 cm size class are from 3.1 to 3.8 cm/yr (Bjorndal and Bolten 1988, Boulon and Frazer 1990, Collazo et al. 1992, Mendonça 1981), however, an average of 6.6 cm was reported for green turtles in Texas (Shaver 1994). For 60 to 70 cm greens, averages of 1.8 to 3.9 cm annual growth were reported (Bjorndal and Bolten 1988, Boulon and Frazer 1990, Collazo et al. 1992, Mendonça 1981). Bjorndal and Bolten (1988) estimated it would take 17 years for turtles in the southern Bahamas to

grow from 30 cm to 75 cm, the approximate size range of juvenile turtles found in this shallow benthic habitat. Little data are available for growth of large juvenile/subadult green turtles (> 70 cm), however, there are sufficient data to suggest a very slow growth rate for these animals. Annual growth rates of 1.2 and 2.2 cm/yr were reported for the 70 to 80 cm size class in the Bahamas (Bjorndal and Bolten 1988) and Florida (Mendonça 1981), respectively. Growth rates of green turtles in the 80 to 90 cm size class are not available for the Caribbean, however, two turtles recaptured during this study showed annual growth rates of 1.5 and 2.6 cm/yr straight carapace length and are similar to those reported for the previous size class. Once females reach sexual maturity growth slows considerably. Carr (1971) reported average growth rates for Tortuguero nesting females to be 0.25 cm/yr. Published data on growth rates of adult male green turtles for this region are also not available.

Age at maturity. Age at maturity for green turtles has been estimated using growth rates of primarily small juvenile turtles and minimum or average size of nesting adult females. For the wider Caribbean region, estimates of age at maturity range from 12 to 36 years. Mendonça (1981) estimated age at maturity between 25 and 30 years. Burnett-Herkes et al. (1984) estimated age at maturity for green turtles in Bermuda at 27 years. Estimates by Frazer and Ehrhart (1985) ranged from 18 to 27 years based on the minimum and average size of nesting females in Florida. Frazer and Ladner (1986) estimated age at maturity for several Atlantic populations based on the minimum and average size of nesting females at each site: 27 to 33 years (U.S. Virgin Islands), 17 to 35 years (Ascension Island), 12 to 26 years (Costa Rica), and 24 to 36 years (Suriname), and

suggested that the upper estimates were more indicative of mean age at maturity. Ehrhart and Witham (1992) estimates range from 19 to 23 years for green turtles in Florida.

Longevity. The life-span of wild green turtles, or any other sea turtle species is unknown. However, data from tagged nesting females combined with estimates of age at maturity can provide some minimal estimates of longevity. Hirth (1997) reports an observation of a nesting green turtle at Tortuguero with a reproductive life span of at least 23 years, and females with reproductive life spans of at least 18 years are not uncommon (Caribbean Conservation Corporation unpubl. data). Thus, assuming an age at maturity of 33 years, these turtles were at least 51 to 56 years of age.

Reproduction

Breeding. Females rarely breed annually (Carr et al. 1978), and there is evidence that adult males in the Caribbean also tend not to be annual breeders (Lagueux 1998). The onset of reproductive activity occurs over several months prior to migration to the nesting beach (Lagueux 1998). Green turtles mate in Nicaragua (pers. obs.) and Panama (P. Meylan et al. 1992) during reproductive migrations, and in the waters adjacent to the nesting beach (Carr and Giovannoli 1957, Carr and Ogren 1960). Females mate numerous times with multiple males during a single season, but mating activity drops off about mid-way through the nesting season (Carr and Ogren 1960). And not too surprising, it has been shown that multiple paternity occurs within a single clutch (Peare et al. 1994).

Nesting ecology. Green turtles excavate a deep, flask-shaped hole in which they deposit their eggs and then carefully cover and camouflage the location of the clutch. There are several distinct nesting stages that are similar among the sea turtle species: emergence, approach crawl, body pitting, nest excavation, covering the nest chamber,

camouflaging the nest site, and return crawl. Tortuguero green turtles take about two and half hours to complete the nesting process (Hirth 1980). They are capable of laying multiple clutches during a single season, from one to seven clutches at Tortuguero (roughly averaging three clutches), with a mean renesting interval of 12 days (Carr et al. 1978). During the nesting season, females remain in the nearshore waters of the nesting beach with regular movements parallel to the shore (Meylan 1995). Individuals vary in their remigration intervals, usually females return to nest after two, three, and four-year intervals, with most exhibiting a three-year interval (Carr et al. 1978).

Distribution

Rookeries. Small remnant nesting populations of green turtles occur throughout the wider Caribbean, however, only a few relatively large rookeries still occur. The largest rookery by far is the green turtle nesting population at Tortuguero, Costa Rica (Carr et al. 1978, Groombridge and Luxmoore 1989). The size of this population is unknown but estimates of annual numbers of nesting females ranged from about 5,000 to 50,000 from 1971 to 1981 (Carr et al. 1982). Groombridge and Luxmoore (1989) estimate global annual nesting of greens to be from 100,000 to 200,000, making the Tortuguero female population about 1/6 of the world's remaining nesting females.

The other major rookeries in the greater Caribbean today are those found in Suriname and Aves Island, Venezuela. In the Suriname colony, from 1,400 to 2,100 females were estimated to nest annually from 1983 to 1987 (Ogren 1989), this is the only population in the region that appears to be stable and not significantly depleted (Groombridge and Luxmoore 1989). The somewhat smaller colony at Aves Island has fewer than 500 females nesting annually (Ogren 1989). A few other small rookeries can be found in Mexico (Carr et al. 1982), with about 500 females nesting annually on all

beaches combined (Groombridge and Luxmoore 1989). Sparse nesting occurs on many other beaches throughout the Caribbean, including numerous islands and mainland beaches, and are only remnants of populations that were once much larger. Other large rookeries may have occurred previously, such as the Cayman Islands and Bermuda rookeries, but were extirpated by many years of overexploitation by humans (King 1982, Groombridge and Luxmoore 1989).

Developmental habitats. Being herbivorous, Caribbean green turtles require seagrasses and algae to meet their dietary needs. Well-known developmental foraging habitats in the Caribbean have been identified in the southern Bahamas, southern Costa Rica, Lesser Antilles, Yucatan Peninsula, Mexico, northern and central Nicaragua, and northern and central Panama (Carr et al. 1982). Other developmental foraging areas can be found in Belize (Carr et al. 1982), Bermuda (A. Meylan et al. 1992), Cuba (Moncada and Nodarse 1998), Florida (Mendonça and Ehrhart 1982), Honduras (Carr et al. 1982), Jamaica (Carr et al. 1982), Puerto Rico (Collazo et al. 1992), and Texas (Shaver 1994). Aggregations of small green turtles in at least some of these developmental habitats are of mixed stock (Lahanas et al. 1998, Bass and Witzell 2000), i.e., multiple rookeries are represented in a foraging area. Also, juveniles from a single population are dispersed into multiple foraging habitats; for example, juvenile green turtles from the Tortuguero rookery have been identified in developmental foraging habitat in eastern Florida (Bass and Witzell 2000), the Bahamas (Lahanas et al. 1998), and likely occur in many other areas in the Caribbean. In addition, habitat shifts from the Bahamas (Bjorndal and Bolten 1996), Bermuda (Burnett-Herkes et al. 1984, Meylan et al. In prep.), Cuba (Moncada et

al. 2002), and Florida (D. Bagley pers. comm.) to the coastal waters of Nicaragua have been documented through tag recoveries.

Adult foraging habitats. Dispersal of adults from their rookeries indicates that adults from a single nesting population may use different foraging areas (Carr et al. 1978). Adult green turtles are known to co-occur with large juveniles in some areas of the Caribbean, e.g., Nicaragua, however, they appear to use deeper foraging areas than small juveniles. In the Caribbean, foraging habitat for adult green turtles is scattered throughout the region, although not all areas have been adequately surveyed (see Carr et al. 1982). Particularly important green turtle foraging habitats in the Caribbean are located in the coastal waters of Nicaragua, Mexico, Colombia/Venezuela, and in some of the Lesser Antilles, although some areas have not been adequately surveyed (Carr et al. 1982, Groombridge and Luxmoore 1989). In fact, Carr et al. (1978) reported that 86% of the tag recoveries of adult females tagged on the nesting beach at Tortuguero, Costa Rica, were from animals captured on the foraging grounds in Nicaragua. Like juvenile developmental foraging sites, adult foraging sites are also comprised of mixed stocks. For example, female green turtles have been captured on the Nicaragua foraging ground that were tagged on nesting beaches at Tortuguero, Costa Rica (Carr et al. 1978), and Aves Island, Venezuela (Sole 1994). In addition, it is likely that animals from smaller nesting colonies are also present on the Nicaragua foraging ground but have remained undetected because they represent a small proportion of the foraging aggregation, possible high tag loss, and lack of tagging studies on many of the other nesting beaches. Carr et al. (1978) suggested that the foraging aggregation in Nicaragua is the largest in the Atlantic, and probably the most extensive for green turtles in the world (Carr et al.

1982). Numerous other smaller foraging areas occur throughout the region, such as in the southeastern United States, Dominican Republic, Bahamas, Jamaica (Carr et al. 1982), and probably Cuba.

Summary. The largest rookery for green turtles in the Atlantic occurs at Tortuguero, Costa Rica, and the most important foraging ground for adult females from this population occurs in the extensive seagrass habitat off the Caribbean coast of Nicaragua, which is also probably the largest foraging habitat for green turtles in the Atlantic. Foraging habitat of small juveniles tends to be separate from large juvenile and adult habitat. Foraging habitats contain mixed stocks of either small juveniles or large juveniles and adults. Adults from one population may use different resident foraging habitats.

Human Use of Green Turtles in the Western Caribbean

The use and overuse of green turtles for food and other products has occurred for many years in the Caribbean. The extent of this use for local consumption and for commercial gain is described below for the purpose of providing a context with which to view the current status of green turtle populations in the region.

Green Turtles as a Resource

Green turtles are herbivorous, which is said to be the reason their meat is so highly palatable (Parsons 1962) and is usually preferred over the meat of other sea turtle species. Among the sea turtles, green turtles are second only to leatherback turtles in size, weighing a minimum of a few hundred pounds as adults, providing a large quantity of meat per animal. Green turtles were also once very abundant in most tropical waters and on nesting beaches, making them a reliable food source in many areas. Almost every part of a green turtle, except the skeleton and a few glands, is consumed by many indigenous

and ethnic groups. Oil and leather products have also been widely produced and used. For many years, the cartilaginous parts of the shell, known as calipee and calipash, were in great demand in European and North American markets for making turtle soup. In addition to the harvest of green turtles for meat, oil, and leather, the eggs are also harvested and used as a source of protein, for baking, and as an aphrodisiac.

Historical Use

Exploitation of green turtles spans more than 400 years in the Caribbean (Thorbjarnarson et al. 2000). In addition to harvest by indigenous people for local consumption, green turtles were harvested from throughout the Caribbean to feed crews on ships exploring the region, and quickly became an important export item (Rebel 1974). Green turtles are said to be the single most important food source that supported the opening up of the Caribbean to explorers and the colonization of the region (Carr 1954). In the western Caribbean, the Cayman Islands, historically, probably the largest rookery for green turtles in the Atlantic, were visited by ships from many nations for almost 200 years to harvest green turtles (Parsons 1962). The Cayman people are well known for their pursuit of green turtles throughout the Caribbean to supply markets in the Caribbean, Europe, and North America with sea turtles. After depleting green turtle stocks from their own beaches and waters, they pursued turtles in the waters off Cuba, Honduras, and then Nicaragua, where they developed good relations with the Miskitu Indians, who were known as exceptional turtle fishers (Parsons 1962).

Indigenous (Miskitu and Rama Indians) and ethnic (Creole and Garifuno) groups of Caribbean Nicaragua have harvested marine turtles for hundreds of years (Carr 1954, Parsons 1962), and like many other coastal inhabitants have come to depend on turtles for protein. Prior to the 1960s, harvest by local coastal people of Nicaragua was primarily

for local consumption. Harvest rates by these coastal people prior to European arrival are unknown, however, in the early 1900s, in addition to the harvest for local consumption, 2,000 to 3,000 turtles were taken each year from the Miskito Cays by Cayman vessels (Parsons 1962). In the 1940s, from 1,600 to 3,600 turtles were exported annually from Nicaragua (Rebel 1974). In the late 1960s, the Nicaragua government closed its waters to Cayman vessels and began processing and exporting turtle meat to the international market. The demand for green turtles during this time resulted in an estimated harvest of 5,000 to 10,000 turtles annually (Nietschmann 1973, 1979; Groombridge and Luxmoore 1989). International pressure on the Nicaragua government resulted in the closing of Nicaragua's canneries by 1976. However, some harvest for local consumption and export still occurred into the 1980s (Groombridge and Luxmoore 1989, Montenegro-Jiménez 1992).

During the civil war in Nicaragua (1981-1990), Montenegro Jiménez (1992) reported a take of 16,700 green turtles from 1985 to 1990, averaging approximately 2,780 turtles annually. These turtles were brought to market in Puerto Cabezas, Nicaragua, reportedly the only location along the coast where any harvest was permitted during the war.

When heavy exploitation of green turtles occurred in Nicaragua in the late 1960s and 1970s, the rookery at Tortuguero, Costa Rica, was also being heavily exploited. Carr (1969) estimated that 4,000 to 5,000 turtles were taken annually from the Tortuguero rookery from 1966 to 1968, and up to 4,000 per year just prior to 1976 (Carr et al. 1978). Since 1977, there has been almost no legal international trade in green turtles or their products from Costa Rica, however, illegal trade was believed to take place

(Groombridge and Luxmoore 1989). Starting in 1983, the Costa Rica government allowed a legal domestic trade in green turtles (Government of Costa Rica 1983 cited in Troëng et al. unpubl. manu.). The Costa Rica quota system, which allowed the legal take of 1,800 turtles per season, was terminated in 1999 (Silman et al. 2002). Enforcement of the quota, however, was difficult and inadequate, resulting in a take of adult turtles beyond the quota (Campbell and Lagueux 1995).

Current Use

Since the early 1990s, Lagueux (1998) has been collecting data on the Nicaragua marine turtle fishery from seven Miskitu Indian communities and three commercial centers along Nicaragua's Caribbean coast. In her summaries of exploitation rates, harvest levels ranged from a minimum of approximately 9,400 to just over 11,000 green turtles/yr from 1994 to 1999 (Lagueux 1998, Lagueux unpubl. data). These are minimum numbers because not every community that harvests turtles is collecting harvest data, only the principal turtle fishing communities. The Nicaragua turtle harvest focuses on large juvenile and adult green turtles and essentially all turtles captured are taken regardless of size or sex. Currently, the majority of green turtles captured are females, presumably because there is an overall female bias in the population being harvested, and most of these females are immature (Lagueux 1998). This suggests that the population on the foraging ground is largely immature animals and to some extent this is true. However, Nicaragua has both shallow and deep seagrass beds. Apparently the larger turtles are in the deeper areas and there are some smaller turtles that can be found in the shallower areas, such as around Miskito Cay and some of the Pearl Cays. Turtle fishers focus on capturing the larger turtles in the deeper waters, although smaller green turtles

are sometimes captured around reefs by lobster divers and turtle fishers, but regardless of size, all green turtles are consumed.

Although a legal harvest for local commercial use of approximately 1,800 turtles/yr (taken at sea) was allowed by the government of Costa Rica prior to 1999, in fact an estimated 1,720 females were illegally taken on the nesting beach in 1997 (Troëng and Rankin González 2000). Thus a minimum total of 3,520 turtles were probably taken (if the illegal take is combined with the permitted take). The legal harvest was banned in 1999 after being declared unconstitutional by a Costa Rica Constitutional Court because it had no scientific basis (Troëng pers. comm.). Since the ban in 1999 a smaller number of turtles were illegally poached on the Tortuguero beach in 2000 (7 turtles, Mangel and Troëng 2001) and 2001 (8 turtles, Reyes and Troëng 2002).

Green turtles are still harvested in many other countries in the western Caribbean. For example, in Panama at least several hundred adults are taken each year (A. Meylan pers. comm.) by Cuna, Guaymí, and Ngobe Indians. In Honduras, an unknown number are taken, including at least 150 harvested in 1999 by the Garifuno (C. Molinero pers. comm.). In Belize, several hundred are taken each year (Smith et al. 1992). Thus, the combined harvest of green turtles in the western Caribbean probably exceeds 13,000 turtles/yr, with the majority of turtles taken from the large juvenile and adult life stages of the Tortuguero population.

CHAPTER 4
SURVIVAL PROBABILITIES FOR LARGE JUVENILE AND ADULT GREEN
TURTLES

Introduction

Estimates of stage- or age-specific survival probabilities of wildlife populations are necessary to understand life cycles and to evaluate population dynamics, threats, and potential management strategies for the conservation of the target species (Lebreton et al. 1992, Williams et al. 2002). Most populations of marine turtles are declining and in need of strong conservation actions (Limpus 1995). Unfortunately, their life cycles are poorly understood and, consequently, the effects of management practices are unclear.

Estimates of current demographic parameters, primary threats to populations, and the implications of those threats to turtle populations are needed to develop conservation strategies for these endangered species.

Among the most serious threats to green turtle populations in the Caribbean are artisanal turtle fisheries, in particular a large, legal turtle fishery on the Caribbean coast of Nicaragua. An unknown number of green turtles are also captured in shrimp trawlers working along the east coast of Nicaragua, and some of these turtles are brought to commercial centers and consumed along with turtles from the artisanal turtle fishery (Lagueux unpubl. data). The Nicaraguan turtle fishery occurs in one of the most important developmental and foraging habitats for green turtles in the Caribbean. The expansive seagrass pastures in this region attract juvenile and adult green turtles of both sexes. Green turtles from multiple rookeries use the Nicaragua foraging grounds (Bass et

al. 1998). Conversely, Nicaragua comprises the most important foraging ground for the green turtle rookery at Tortuguero, Costa Rica (Carr et al. 1978), which is the largest remaining green turtle rookery in the Atlantic.

The Tortuguero population has been subjected to intense, but variable, harvest pressure on adult females at Tortuguero and on large juveniles and adults in Nicaragua, and elsewhere. After many years of harvest, numbers of nesting females showed signs of decline in the 1960s (Carr 1969). But by the mid 1970s, this population was afforded some protection on the nesting beach in Costa Rica, and harvesting also decreased in Nicaragua due to the closing of three turtle canneries and because of civil unrest, which interfered with fishing activities. A recent evaluation of the nesting population at Tortuguero showed an increasing trend in nesting activity from 1971 to 1996 (Bjorndal et al. 1999). However, intensive harvest pressure in Nicaragua began again in the early to mid-1990s, where now a minimum of 11,000 green turtles are harvested annually (Lagueux 1998). To better understand how this recent increase in harvesting may affect the Tortuguero population as a whole and help identify management needs, an examination of current life history parameters and population status is needed.

The only estimates available on survival rates for any life stage of the Tortuguero population are for nesting females (Bjorndal 1980) and for eggs and emergence success (Fowler 1979, Horikoshi 1992). From Bjorndal's (1980) data, annual survival of nesting females was estimated at 0.61 using an enumeration method on cohorts of animals from 1959 to 1972, which includes a period of heavy exploitation. However, these data are more than 20 years old and current harvest pressure is probably different. In addition, more appropriate methods for parameter estimation (such as mark-recapture and band

recovery models) are now widely used. No information is currently available on survival rates of juvenile turtles in this population, including small, large or subadult stages.

Thus, estimates of current life history parameters are needed.

The primary goals of this chapter are two-fold, 1) estimate current annual survival rates of nesting females at Tortuguero, and 2) estimate current annual survival rates of large juvenile and adult turtles targeted in the turtle fishery in Nicaragua. These data will be used in subsequent chapters for modeling population dynamics and assessing management strategies.

Methods

I analyzed tag recovery data from green turtles tagged at two study areas: (a) foraging grounds off the central Caribbean coast of Nicaragua which are important foraging habitat for large juvenile and adult green turtles of both sexes, and (b) nesting beach at Tortuguero, Costa Rica. Some animals were tagged on the Nicaragua foraging ground and others at the nesting beach at Tortuguero, but the tag recoveries of dead animals from both data sets came primarily from the Nicaragua foraging ground.

Capture-Release and Recovery Methods

Nicaragua – foraging grounds

I conducted the Nicaragua field study from March 1999 to May 2002 in conjunction with the Wildlife Conservation Society's sea turtle conservation program on Nicaragua's Caribbean coast. Field assistance was provided by William McCoy, a local artisanal fisher from Pearl Lagoon, with extensive experience capturing turtles in the region. Mr. McCoy provided advice regarding where and when to capture turtles, and assisted in coordinating other assistants in the field. I trained him to also assist in tagging

and measuring turtles. Cynthia Lagueux, Program Director for the Wildlife Conservation Society Sea Turtle Conservation Program in Nicaragua, also assisted with data collection.

Capture methods were modeled after the most common technique (large-mesh entanglement nets) used by the turtle fishers of the Caribbean coast of Nicaragua (Lagueux 1998). Numerous multi-filament, large-mesh entanglement nets are set over banks or shoals in the late afternoon (Figure 4.1). One end of each net is anchored, using a large piece of dead coral, by wedging it into a large coral out-cropping (Figure 4.2). The coral out-cropping is hoped to be a turtle “sleeping rock” because turtles are known to use the area during the night. The other end of the net is allowed to move freely with the current. The nets are left overnight and then checked at sunrise. Turtles become entangled in the nets when they come up to breathe during the night.

Dimensions of the nets used in this study were approximately 14.7 m long x 5.9 m deep and 40.6 cm bar mesh. Twenty nets per night were used on a single bank. The specific capture locations included Crow Cam, Crowning Spot, Cynthia’s Bank, Little Middle Set, Seal Cay, and South Compass (Figure 4.3).

Turtles were examined, measured, weighed, and marked, and then released near the original capture location on the same day of capture (with few exceptions). Sex was identified whenever possible by external characteristics. When male green turtles are approaching maturity, they develop secondary external sexual characteristics associated with tail length and nail morphology that differ from females. The tail of a mature or maturing male becomes large, muscular and prehensile, whereas the tail of a mature female is short and may project only slightly beyond the marginal scutes (Wibbels 1999). In addition, the nail on the front flippers of mature or maturing males becomes elongated,

thick and decurved. In this study, turtles smaller than approximately 86 cm minimum curved carapace length without observable external male characteristics were deemed of “unknown” sex, while turtles above this size without observable male characteristics were deemed female, with a few exceptions. Four turtles below 86 cm without external male characteristics were deemed females because their tail length, body mass, and carapace length fit into the characteristics distinguished as female by Lagueux (1998) based on external and internal examination of animals. Turtles were double-tagged with either monel or inconel metal cow-ear tags (style 1005-681, National Band and Tag Company, Freeport, Kentucky). A tag (bearing a unique number) was placed proximal to the first scale on the trailing edge of each front flipper.

When local fishers captured marked turtles they returned tags either to me or to one of the other turtle project personnel. For each tag, information was recorded on how, when, and where the turtle was captured. The fishers then received a specially designed t-shirt or hat for their cooperation. On occasion, project personnel sought out fishers who were known to have turtle tags to insure the most accurate recovery data were obtained.

Costa Rica – nesting beach

The Caribbean Conservation Corporation (CCC) conducts a green turtle research and tagging program annually at Tortuguero, Costa Rica. Research on the green turtle population at Tortuguero was initiated by Dr. Archer Carr in 1955 (Carr et al. 1978) and has continued for more than 40 years. For my study, I used data from the 1995 to 2000 nesting seasons provided by the CCC to estimate survival rates of the Tortuguero nesting population.

Prior to 1998, the green turtle tagging program was conducted from early-July to mid-September. Since 1998, however, the program has expanded and is now conducted

from early-June to late-October. For logistical and historical reasons, the tagging program focuses on turtles that nest primarily on the northern eight km of the 35 km-long nesting beach. This eight km section is patrolled nightly by teams of people who tag the turtles subsequent to egg deposition. Nesting turtles are marked in both front flippers (in the same location as described in the Nicaragua study), however there has been some experimental tagging in various combinations of front and rear flippers. Primarily inconel metal tags (style #1005-681, National Band and Tag Company) were used to mark green turtles, however, in some seasons monel metal tags were also used (style #1005-49, National Band and Tag Company).

Fishers and others from throughout the Caribbean have returned turtle tags from the CCC's tagging program primarily to either C. Lagueux, Sea Turtle Conservation Program in Nicaragua, Wildlife Conservation Society, or the Archie Carr Center for Sea Turtle Research, University of Florida. A small monetary reward (\$5.00 USD) is provided by the CCC for each tag recovery.

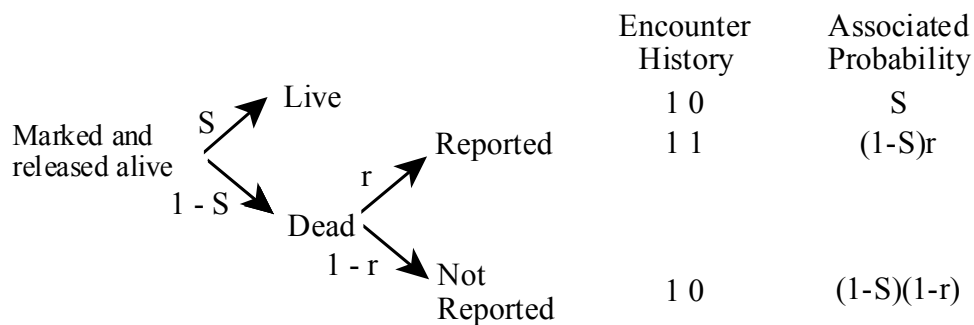
Model Structure, Model Selection, and Parameter Estimation

To generate the band (tag) recovery histories necessary for analysis, I assigned each tagged animal to a marking period and each tagged animal that was reported dead to a recovery period. A marking period (MP) is the period in which a group of animals were captured, marked, and released. I assigned a mid-point (a single date) to each MP in order to establish the recovery periods (RP, the time interval between MPs when tags from dead marked animals are recovered) and assign each tag recovery accordingly.

The mark and recovery histories of green turtles tagged in Nicaragua (representing a mixed group of large juveniles and adults of both sexes) and Costa Rica (representing only adult females) were analyzed using band recovery models implemented using

Program MARK (White and Burnham 1999) to estimate survival rates for each group.

The modeling used for dead recoveries follows the following scenario for one marking and one recovery period:



where a marked animal either i) survives (with probability S and an encounter history of 1 followed by 0 for it being alive at release and not encountered later), ii) dies and is recovered and reported (with probability $(1-S)r$ and an encounter history of 1 1 for being alive at release and being reported when recovered), or iii) dies and is not reported (with probability of $(1-S)(1-r)$ and an encounter history of 1 0 for being alive at release and not being reported when recovered) (Cooch and White 2001). The parameters estimated in this band recovery model include a survival probability, S , and a recovery probability, r (the probability that dead marked animals are reported). These probabilities are calculated through an iterative process in Program MARK from the recovery data, the numbers of tagged animals and subsequent recoveries by time period.

Assumptions of modeling band recoveries include: i) the sample is representative of the population under investigation, ii) there is no tag loss, iii) the date of recovery is correctly tabulated, iv) survival rates are not affected by banding, v) rate parameters for all individuals within a group are homogeneous, and vi) fates of banded individuals are independent of each other (Brownie et al. 1985).

A set of four candidate models for the adult female data set and five candidate models for the mixed large juvenile/adult data set were developed. The global model (model with the most parameters), is a fully time-dependent (t) model, $S_t r_t$, that allows for both S and r to differ between release periods. The other three models used for both data sets are reduced parameter models that allow for other combinations of time-dependence or constant rates for S and r , i.e., $S_t r$ (where S is time-dependent and r is constant), $S r_t$ (where S is constant and r is time-dependent), and $S r$ (where both S and r are constant). The additional model, $S r(d)$, for the mixed large juvenile/adult data is a model in which S is assumed constant (per unit time) and r is a function of the duration of the interval until the next release period. This model was not used for the adult female data because the RPs did not vary in duration. From these sets of models, the “best approximating model” for each set was identified by Program MARK (White and Burnham 1999) using Akaike’s Information Criterion, AIC (Akaike 1985). This type of model selection identifies the most parsimonious model, and using a small sample size correction term yields AIC_c (Hurvich and Tsai 1989). A Bootstrap goodness-of-fit (GOF, Program MARK, White and Burnham 1999) was conducted on each global model to ensure that the data did not drastically violate the assumptions of the model, then each group of models was adjusted for over-dispersion using a quasi-likelihood parameter, \hat{c} , (thus a quasi-likelihood AIC_c (QAIC_c), see Lebreton et al. 1992). There were insufficient data to use other means to evaluate model fit and estimate \hat{c} . The estimate of \hat{c} was based on the observed deviance (of the global model)/mean expected deviance (generated from the Bootstrap GOF test in Program MARK).

For the mixed large juvenile/adult group tagged on the Nicaragua foraging ground, releases of marked animals (MP) from March 1999 to May 2002 were included in the analysis. MPs were not restricted to a particular time of year because animals can be found on the foraging grounds in Nicaragua year around, but rather were limited primarily by weather conditions. All capture-mark-release locations were assumed to have the same recovery probabilities and therefore data from all locations were combined. Some MPs were combined into a single MP because of their temporal proximity, e.g., if the number of releases for a MP was low because of poor weather conditions, we conducted another MP as soon as possible and combined the MPs into one. The RPs (the time interval between MPs when tags from dead marked animals were recovered) were variable in duration and were based on the time interval between the midpoints of each MP.

For adult females tagged on the nesting beach in Costa Rica, releases of newly marked individuals from 1995 to 2000 were used in the analysis. The majority of marking occurs between July and September of each year. The mid-point chosen for all MPs was 15 August, therefore all tag recoveries could be assigned to an appropriate RP, and the duration of each RP was 1 year. Tag recovery dates were sometimes not specific, often either because the fisher did not remember when the turtle with the tags was caught or because the fisher was unavailable to provide the information at the time the tag was obtained. There were 4 types of recovery dates reported: 1) the exact date, which included day, month and year, 2) a partial date which included only the month and year, 3) a year only date, and 4) a cut-off date, where the recovery date was not known, and thus the turtle had been recovered no later than the date the tags were received.

Recoveries with a cut-off date that was greater than a year after the turtle was marked were excluded from the analysis to avoid potential bias in estimates as a result of delayed band reporting (Anderson and Burnham 1980). In addition, criteria were established to assign tag recoveries that lacked the exact recovery dates to a RP. For recoveries where the year and only the month of August was known, I assigned the tag recovery to the RP after 15 August for that year to be conservative (i.e., to avoid underestimating the time to band recovery), all other months could be assigned to a RP either before or after the month of August. For tag recoveries when only the year of recovery was known (this type of recovery date occurred only six times), I assigned the RP depending on whether or not the turtle was tagged in the same year. If the turtle was tagged in the same year, then the RP following the RP when the turtle was tagged was used, however, if the turtle was recovered more than a year after being tagged then I assumed it was captured before 15 August of that year. The reason for this was because there are more months available for fishing prior to 15 August than after and more fishing does occur in those first 7.5 months of the year (Lagueux 1998), thus the probability that the turtle was captured prior to 15 August of that year would be greater.

Comparison of Survival Estimates Between Sites

To determine if the survival estimates for the two groups were homogeneous, a comparison was made using a chi-square test. The chi-square test was implemented using Program CONTRAST (Hines and Sauer 1989).

Results

Mixed Large Juvenile/Adult Group (tagged on Nicaragua foraging ground)

Mark-Release and Recovery Periods – Between March 1999 and May 2002, we marked and released turtles on 16 occasions, or marking periods (MP). MPs 1-16 ranged

from 2 to 24 days in duration and RPs ranged from 0.4 to 7.9 months (Table 4.1).

Although MPs occurred throughout the year, poor weather conditions prohibited marking during the months of July, November and December, and only a few animals were marked during the months of August and October.

Through May 2002, 250 green turtles were captured, marked, and released (Table 4.1). Turtles ranged in size from 67.4 to 102.0 cm straight carapace length (SCL, from the nuchal notch to the longest posterior marginal tip) with a mean of 84.8 cm (SE = 0.43, $n = 250$) (Figure 4.4). Turtles captured in the study area included large juveniles and adults, and both males and females. The sex ratio for turtles where sex could be determined using external secondary characteristics was strongly male biased with a male to female ratio of 3.4:1, which differs significantly from a 1:1 ratio (One-sample Proportion Test, $Z = 7.9$, $p < 0.0001$). Sex was undetermined for 39 animals. If all 39 turtles of undetermined sex were females the sex ratio would be 1.9M:1F, still significantly male biased (One-sample Proportion Test, $Z = 4.8$, $p < 0.0001$).

Turtle fishers reported the harvest of 46 tagged green turtles (18.4% of released animals) through September 2002. For those animals recovered, the average duration between marking and recovery was 303 days and ranged from 13 to 1,003 days (SE = 37.5, $n = 45$, includes approximate capture dates). Most recoveries occurred on the “bank” where the turtle was released ($n = 21$) or at a bank nearby (up to a distance of approximately 14 km from the release site, $n = 18$); when combined these recoveries represent 85% of all recoveries. Six recoveries in Nicaragua occurred away from the original release site, but on the Nicaragua foraging grounds. The straight-line distances between these release and recovery sites varied from 32 to 230 km. Only one recovery

Table 4.1. Mark-release and recovery histories for the mixed large juvenile/adult group of green turtles marked in Nicaragua between March 1999 and May 2002 and recovered through 14 September 2002. Marking period (MP) is a period when animals are captured, marked, and released. Recovery Period is the interval between releases of newly marked animals when recoveries occur.

Marking Period (duration in days)	MP Mid-point	No. Marked/ Released	Number of band recoveries (tag returns of dead marked turtles) in each Recovery Period (duration in months)															
			1 (1.6)	2 (1.8)	3 (3)	4 (0.4)	5 (4.1)	6 (2.1)	7 (1.1)	8 (4.2)	9 (6)	10 (1)	11 (1.3)	12 (7.9)	13 (0.6)	14 (1.5)	15 (1.9)	16 (3.9)
1 (5)	5 Mar 99	14	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 (17)	22 Apr 99	24	-	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0
3 (11)	16 Jun 99	12	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0
4 (2)	15 Sep 99	9	-	-	-	0	2	0	0	0	0	0	0	0	0	0	0	0
5 (11)	27 Sep 99	13	-	-	-	-	1	0	1	0	1	0	2	0	0	1	0	0
6 (3)	31 Jan 00	9	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0
7 (11)	3 Apr 00	20	-	-	-	-	-	-	1	1	4	0	1	3	0	0	1	0
8 (20)	5 May 00	25	-	-	-	-	-	-	-	1	3	0	1	1	0	0	1	0
9 (24)	11 Sep 00	14	-	-	-	-	-	-	-	-	1	0	0	1	0	1	0	0
10 (4)	12 Mar 01	15	-	-	-	-	-	-	-	-	-	0	1	1	0	0	0	0
11 (5)	10 Apr 01	13	-	-	-	-	-	-	-	-	-	-	0	2	0	0	0	0
12 (14)	20 May 01	21	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	2
13 (4)	17 Jan 02	11	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0
14 (12)	4 Feb 02	19	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0
15 (6)	23 Mar 02	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
16 (3)	19 May 02	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

was obtained outside the Nicaragua foraging grounds, a male turtle was recovered in Panama in June 2000 (A. Meylan pers. comm.), two to three months after being tagged in Nicaragua. The straight-line distance from the release site to the recovery site was approximately 380 km.

The mean annual survival probability estimate based on the most parsimonious model (S_r) is 0.5537, 95% Confidence Interval (CI) = 0.332-0.756, SE = 0.115. The reporting rate (r) based on this model was 0.284, CI = 0.180-0.418, SE = 0.062. Model S_r is more than 2.5 times better supported by the data than the next “best” model, $S_r(d)$, using the QAIC_c Weights (Table 4.2). Results from the second “best” model $S_r(d)$ are nearly identical to model S_r , $S = 0.5585$ and 95% CI = 0.334-0.762, SE = 0.117.

These results indicate that there is an estimated 55% probability that a turtle marked at turtle fishing sites in Nicaragua will be alive and available for sampling each year. Thus, there is an estimated 45% probability that marked turtles will have died or are unavailable for sampling each year. It is not possible to separate the mortality (hunting and natural) from permanent emigration out of the sampling area.

Adult Female Group (tagged on nesting beach at Tortuguero, Costa Rica)

From the 1995 through 2000 nesting seasons, 8,025 green turtles were marked and released by the CCC field staff (Table 4.3). Of these turtles, tags from 556 turtles have been recovered (7%) up to 15 August of the 2001 nesting season. Only 493 of these recoveries, however, were included in the analyses due to imprecise recovery dates associated with the data. Those tags for which the recovery date was unknown and the tag was retrieved after the first RP following marking were not used in the analysis.

Table 4.2. Model comparisons from band recovery data for green turtles marked and released on the foraging grounds in central Nicaragua, from March 1999 to May 2002. S = survival probability, r = recovery probability, t = time dependence, and d indicates that r is a function of the duration of the interval until the next release period. Adjusted $\hat{c} = 1.063$, QAICc = corrected quasi-likelihood Akaike's Information Criterion value, Delta QAICc = the difference in the current model QAICc and the model with the lowest QAICc value, QAICc Weight = the likelihood of the current model relative to the other models considered, # Parameters = the number of estimable parameters, QDeviance = difference between the $-2\log(\text{Likelihood})$ for the current model and the $-2\log(\text{Likelihood})$ of the saturated model (the model with the number of parameters equal to the sample size) (White and Burnham 1999, Cooch and White 2001).

Model*	QAIC _c	DeltaQAIC _c	QAIC _c Weight	# Parameters	QDeviance
Sr	373.62	0.00	0.684	2	96.63
Sr(d)	375.53	1.92	0.262	3	96.50
S _t r _t	378.80	5.19	0.051	19	64.56
S _t r	386.62	13.00	0.001	17	77.04
Sr _t	386.95	13.34	0.0009	17	77.37

* Sr = survival and recovery rates are assumed constant (per time unit), Sr(d) = constant survival and recovery rate is a function of the duration of the interval until the next release period, S_tr_t = a fully time-dependent model, S_tr = survival is time-dependent and recovery rate is constant, and Sr_t = survival is constant and recovery rate is time-dependent.

Table 4.3. Number of adult female green turtles marked on the Tortuguero, Costa Rica, nesting beach from 1995 to 2000 and their recovery histories up to 15 August of the 2001 nesting season. Mid-point for all MPs was 15 August.

MP	# Released	Number of band recoveries (tag returns of dead marked turtles) in each RP					
		1	2	3	4	5	6
1995	1156	18	5	26	11	17	17
1996	1395	-	10	34	18	12	11
1997	1922	-	-	72	56	19	30
1998	1225	-	-	-	41	18	14
1999	1041	-	-	-	-	16	17
2000	1286	-	-	-	-	-	31

The average annual survival probability for the adult female group is an estimated 0.8207, 95% CI = 0.7271-0.8871, SE = 0.041. This estimate is based on the model Sr_t , constant survival and time-dependent recovery probabilities (Table 4.4). The average of the six reporting rates (r) from this model was 0.1174. Based on this model there is about an 82% chance that females marked for the first time at Tortuguero will be alive and available for sampling each year, and conversely, there is about an 18% probability that they will have died or are permanently unavailable for sampling.

Table 4.4. Model comparisons from band recovery data for green turtles marked on the Tortuguero, Costa Rica, nesting beach between 1995 and 2000. Adjusted $\hat{c} = 1.7$. $QAIC_c$ = corrected quasi-likelihood Akaike's Information Criterion value, $\Delta QAIC_c$ = the difference in the current model $QAIC_c$ and the model with the lowest $QAIC_c$ value, $QAIC_c$ Weight = the likelihood of the current model relative to the other models considered, # Parameters = the number of estimable parameters, QDeviance = difference in the $-2\log(\text{Likelihood})$ for the current model and the saturated model (White and Burnham 1999, Cooch and White 2001).

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ Weight	# Parameters	QDeviance
Sr_t	2867.1	0.00	0.7959	7	15.74
$S_t r_t$	2870.9	3.80	0.1192	11	11.51
$S_t r$	2871.6	4.47	0.085	7	20.21
Sr	2900.9	33.79	0.0000	2	59.54

Comparison Between Tagging Sites

The hypothesis of homogeneous survival probabilities (i.e., mixed juvenile/adult group = adult females) was rejected at the $\alpha = 0.05$ level (Chi-SQ = 4.793, df = 1, P = 0.029). The survival estimate for the mixed group is more than 30% lower than the estimate for adult females.

Discussion

My results suggest that survival rates of turtles exposed to the fishery in Nicaragua are low for large juvenile and adult green turtles from the Tortuguero population. Below

I discuss the precision and potential bias of my survival estimates, the comparison between estimates, and implications for the conservation of the Tortuguero green turtle population.

Precision and Potential Bias of Survival Estimates

Precision and potential bias of the survival estimates in this study should be examined to determine the reliability of the estimates. Delayed reporting of tag recoveries, when the recovery date reported is later than the actual recovery date, can cause a positive bias in survival estimates (Anderson and Burnham 1980). For the mixed group tagged on the foraging ground in Nicaragua, delayed reporting is not likely to be a problem because of the presence of a turtle conservation program in the area where most of the tags are recovered and frequent reminders to fishers to turn in any tags they have. Delayed reporting is more likely to occur with tag recoveries for the adult female group tagged in Costa Rica since many of the animals are not captured for several years after being tagged. However, it has been shown that band recovery models are generally robust to this problem and thus, this problem would have a negligible effect on survival rate estimates (Anderson and Burnham 1980).

Contrary to delayed reporting, tag loss could cause a negative bias in survival rate estimates (Nelson et al. 1980). Tag loss is probably minimal at the Nicaragua site because tag loss on foraging grounds (using similar tagging methods) over short periods is shown to be low (Limpus 1992), and thus is not a source of bias for this estimate. Tag loss for the adult female group is probably higher because nesting females use their flippers extensively on land during the nesting process, and the duration of the study is longer. Mean tag loss within a nesting season at Tortuguero was 0.031 in 2000 (Mangel and Troëng 2001) and 0.033 in 2001 (Reyes and Troëng 2002). Because turtles are

double tagged, the probability of losing both tags is even lower. In addition, tag loss would have to be severe or mortality rates low to significantly bias the survival rate estimates (Nelson et al. 1980).

Another possible source of bias is permanent emigration (or dispersal). Permanent emigration is thought to be minimal in the mixed group tagged on the foraging ground because the large number of marked animals that have been captured in or near the banks where they were released and some after a few years, suggests at least some turtles are resident in the area, although there may be some temporary emigration.

Precision in the survival estimates for the two sites is much higher for adult females tagged in Costa Rica than foraging animals tagged in Nicaragua; this difference is reflected in the confidence intervals for each mean (CI = 0.73-0.89 for the adult female group, and CI = 0.33-0.76 for the mixed large juvenile/adult group). The CI for the adult female estimate is comparable to those of other studies using similar methods (e.g., Chaloupka and Limpus 2002, In press). The wide CI for the mixed group estimate is at least in part due to the relatively small sample size ($n = 250$ turtles marked-released and 46 dead recoveries). Despite the low precision of the estimate for the mixed group marked on the foraging grounds, at least 18% of the animals tagged over a three-year period were recovered by turtle fishers in just over three years. Additional years of marking and releasing animals on the foraging ground should reduce the confidence intervals for this estimate considerably.

Comparison of Survival Estimates Between Sites

The large difference in survival estimates between the adult female group and the mixed group (Nicaragua estimate is > 30% lower than the Costa Rica estimate) may seem somewhat surprising given that animals nesting at the Costa Rica rookery use the

Nicaragua foraging grounds, and that large juveniles (the life stage most often captured on the Nicaragua foraging ground) may have only slightly lower natural survival rates than adults (< 10% lower for studies of greens and loggerheads in Australia, Chaloupka and Limpus 2002, In press). However, for the estimates in this study to be more similar the following would need to be true: 1) adult females would have to be equally susceptible to turtle fishing as those turtles that were marked and released at fishing sites in Nicaragua, and/or 2) adult females that use foraging areas other than Nicaragua are subjected to similar threats as those using Nicaragua foraging sites. For the first to be true, there would likely be no segregation between adult females and either large juveniles or adult males, so that large juveniles and adult males and females would be using the same habitats and thus would have relatively the same chance of being captured by turtle fishers. However, there is some evidence to suggest that sexual segregation on the Nicaragua foraging ground does occur.

Lagueux (1998) reported that the overall sex ratio for turtles captured in the turtle fishery in the northern region of Nicaragua was 1M:1.7F, while in the southern region the ratio was 1M:1.1F, suggesting a shift from more females in the north to more equal proportions in the south. In this study, which was located at the very southern end of the foraging ground, the sex ratio was strongly male biased at 3.4M:1F. In addition, adult females (n = 9) tracked by satellite from the Tortuguero nesting beach all migrated to foraging areas either in the northern part of the Nicaragua foraging ground or farther north to other foraging areas (Caribbean Conservation Corporation unpubl. data). These patterns provide strong evidence that there is some degree of sexual segregation on the Nicaragua foraging ground, with an apparent preference by adult females for the northern

foraging areas. This apparent preference, however, does not alone explain the difference between the survival estimates in this study since harvest levels in both the northern and southern parts of the foraging ground are very similar (Lagueux 1998). A few striking differences between the north and the south foraging areas provides some insight. First, the distance from the mainland to the foraging grounds in the north is much greater, which likely affects the distribution of turtle fishing activities, and second, the foraging habitat in the north is much more extensive (based on 20 m bathymetric lines, where some species of sea grasses are still able to grow), which probably affects the distribution of turtles on the foraging grounds. The increase in distance from the mainland forces fishers to seek habitation in safe harbors and offshore cays, which in turn probably increases the fishing pressure around those same areas, leaving a number of areas further away from the cays and mainland for turtles to reside with less threat from the fishery. In fact, many of the adult females tracked by satellite to the northern region (Caribbean Conservation Corporation unpubl. data) were using areas that have little or no fishing. This evidence, combined with the fact that more juveniles are captured in the turtle fishery (Lagueux 1998), suggests that adult females have a reduced chance of being captured compared to large juveniles, and possibly adult males, in Nicaragua. In addition, not all adult females from the Tortuguero rookery use the Nicaragua foraging grounds (Carr et al. 1978), and because the fishery in Nicaragua is the largest in the Caribbean, the animals foraging outside of Nicaragua might have a higher survival probability resulting in a higher overall survival rate for adult females than for animals foraging on the Nicaragua foraging ground. So, although adult females are captured in the turtle fishery in Nicaragua, it seems that some degree of segregation and habitat

preference on the foraging grounds consequently reduces their chance of capture and helps explain at least some of the difference between the survival rate estimates of adult females and the mixed large juveniles/adults.

Further evidence that adult females may be less affected by the turtle fishery in Nicaragua is found in inferences about fishing mortality and its relative importance in the two groups of turtles. These inferences emerge from consideration of the survival rate and reporting rate estimates from the two data sets and are based on the assumption that the probability of a marked animal being reported if captured in the fishery is similar for the two groups. An assessment of the relative fishing mortality (RFM), calculated as

$$\text{RFM} = \frac{(1-S)r \text{ for mixed group}}{(1-S)r \text{ for adult group}} = 6.06,$$

suggests that a turtle from the mixed large juvenile/adult group is about 6 times more likely to die in the turtle fishery than a turtle from the adult female group. Further, the relative fraction of total mortality attributed to fishing, estimated as 0.284 (r for mixed group)/ 0.117 (mean r for adult female group) = 2.43 , suggests that about two and one half times more of the total mortality of the mixed group, relative to the adult female group, is attributed to fishing.

Conservation Implications

The use of capture-mark-recapture (CMR) and band recovery (a special case of CMR) models has increased considerably in recent years as a tool to estimate survival rates of many species (Lebreton et al. 1992). These methods are considered more robust than others such as enumeration, life tables, and catch curves, in part, because of the ability to estimate sampling fractions, such as capture, recapture, and band recovery probabilities (Nichols 1994). Limitations of these earlier methods for estimation of

survival probabilities are reported in Anderson et al. (1981), Seber (1982), Nichols and Pollock (1983), and Martin et al. (1995). Only recently have the more robust CMR models been applied to estimating survival rates of marine turtle species (e.g., Heppell et al. 1996*b*; Chaloupka and Limpus 2002, In press; Kendall and Bjorkland 2001).

Survival probability estimates for marine turtles based on the more robust CMR methods indicate that large juvenile and adult marine turtles have naturally high survival rates, and attests to the natural longevity of marine turtles shown in studies on growth (Limpus and Chaloupka 1997, Bjorndal et al. 2000). Survival rate estimates for adult green turtles in Australia are very high (0.9482) and lower for subadults and juveniles, 0.8474 and 0.8804, respectively (Chaloupka and Limpus In press). Survival rate estimates for loggerhead turtles in Australia are lower but similar, 0.875 for adults and 0.859 for immatures (Chaloupka and Limpus 2002). Another study of loggerheads in Australia estimated annual survival rate at 0.91 for adults and 0.83 to 0.88 for immatures in a stable population (Heppell et al. 1996*b*). Kendall and Bjorkland (2001) estimate the annual survival rate of adult female hawksbills nesting at Jumby Bay, Antigua, to be 0.95. Natural survival rates for most of these populations would likely be even higher because at least some of them are subjected to varying degrees of human induced mortality, particularly the Australia loggerheads that are taken incidentally in various fisheries (Slater et al. 1998). Thus, the mean estimates of survival probabilities generated in this study (0.55 for the mixed group and 0.82 for adult females) are extremely low for marine turtles in the large juvenile and adult life stages and have serious conservation implications for green turtles in the western Caribbean.

The survival probability estimates derived in this study are not too surprising when one considers the magnitude of the marine turtle fishery on the primary foraging ground for this population. A minimum of 11,000 adult and large juvenile green turtles are harvested each year on the foraging grounds off the Caribbean coast of Nicaragua (Lagueux 1998). As evidenced from tag recoveries (Carr et al. 1978, Caribbean Conservation Corporation unpubl. data), other direct and indirect mortality from fisheries in other parts of the Caribbean take an additional unknown number of green turtles (e.g., Costa Rica, Cuba, Honduras, Panama), adding to the total annual mortality of animals from the Tortuguero population.

Two parameters, mean life span and half-life, calculated from the Tortuguero survival rate estimate provide a better understanding of the implications of the low survival probabilities for adult females. The mean life span (described in Seber 1982 and Brownie et al. 1985) for nesting green turtles with an annual survival rate of 0.8207 is only 5.1 years and the “half-life,” the time period from banding until half the animals are expected to be dead (Brownie et al. 1985), is 3.5 years. Thus, about half of the adult females are able to produce young during only two nesting seasons, since three years is the mean inter-nesting interval for green turtles at Tortuguero (Carr et al. 1978).

The survival rate estimate for green turtles exposed to the turtle fishery on the Nicaragua foraging ground (0.55), including both males and females, is extremely low for a “long-lived” species. It is widely accepted that marine turtles exhibit life history characteristics that are consistent with other long-lived organisms, such as slow to mature and low mortality of adults. Iverson (1991) suggested that in general turtle species exhibit a Type III survivorship curve (high initial mortality and low mortality in later

stages), and Shine and Iverson (1995) found that age at maturation is positively linked to adult survival in turtles (i.e., high adult survival is correlated with delayed sexual maturity). In light of this relationship, Congdon et al. (1993, 1994) suggested that the life-history traits that co-evolve with longevity result in a limited ability of those species to withstand chronic increases in mortality, especially of the later life stages.

It is likely that the Tortuguero green turtle population as a whole, and possibly other green turtle populations that share the Nicaragua foraging ground, are declining based on the relatively low survival probability estimates of green turtles derived in this study. Population modeling can be used as a tool to better understand the implications of these survival rate estimates, such as population growth rate. The estimated survival rate of adult females in the Tortuguero population is believed to be unbiased and precise enough to be used in a population model. However, the estimate for animals marked on the Nicaragua foraging ground probably applies more directly to large juveniles and possibly males, and represents the expected survival probability of only those animals that use the turtle fishing areas. Assuming this is true, a more accurate estimate of large juvenile survival for this population could be made by estimating the proportion of animals on the foraging ground that are subjected to the turtle fishery in Nicaragua. For example, if about 50% of the large juvenile foraging population is exposed to the fishery and survival probabilities of animals not subjected to the fishery is approximately 0.90, the overall survival rate for large juveniles, using a weighted mean, would be approximately 0.725. A modified estimate could then be used to approximate the average survival rate for large juvenile green turtles in the Tortuguero population.

The primary purpose for generating these survival rate estimates is to use them to help assess the status of the Tortuguero population. In subsequent chapters matrix population modeling will be used to better understand the implication of these survival rate estimates and to evaluate strategies to manage the marine turtle fishery in Nicaragua.

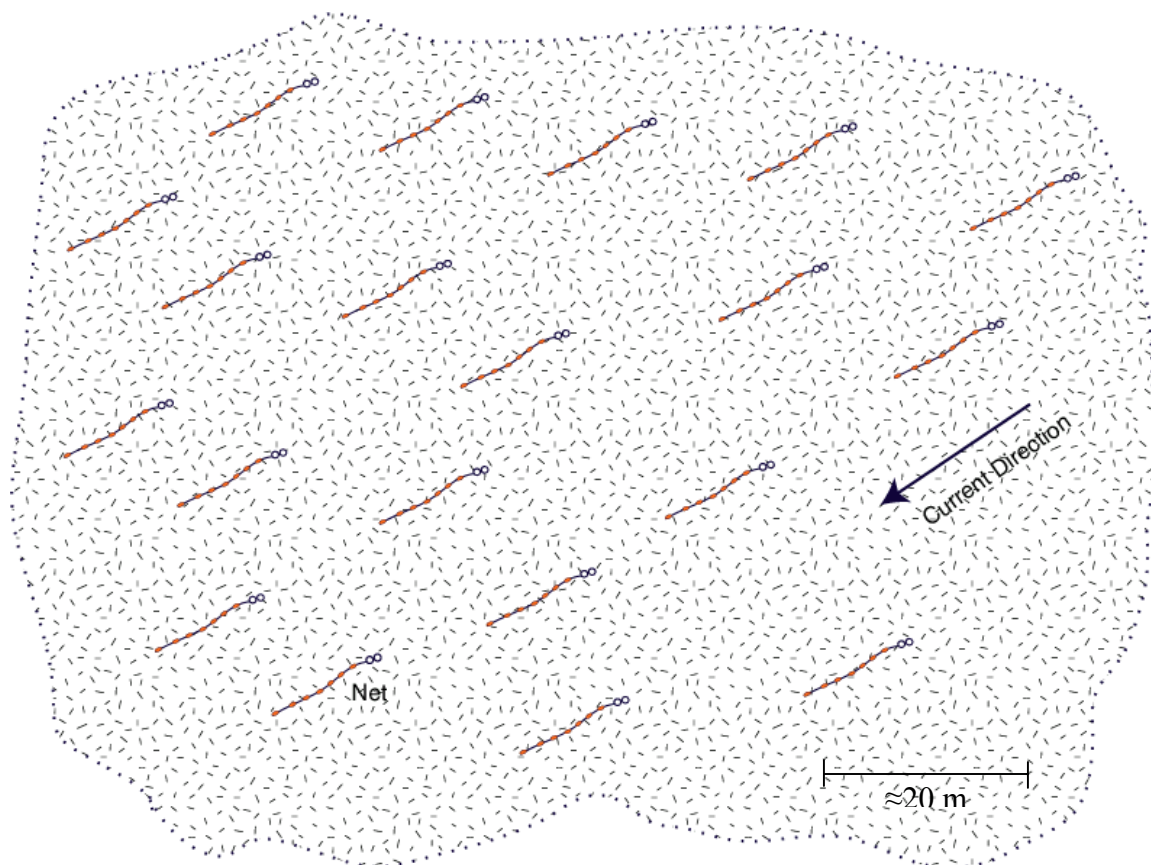


Figure 4.1. Aerial view of hypothetical set of turtle nets on turtle fishing bank.

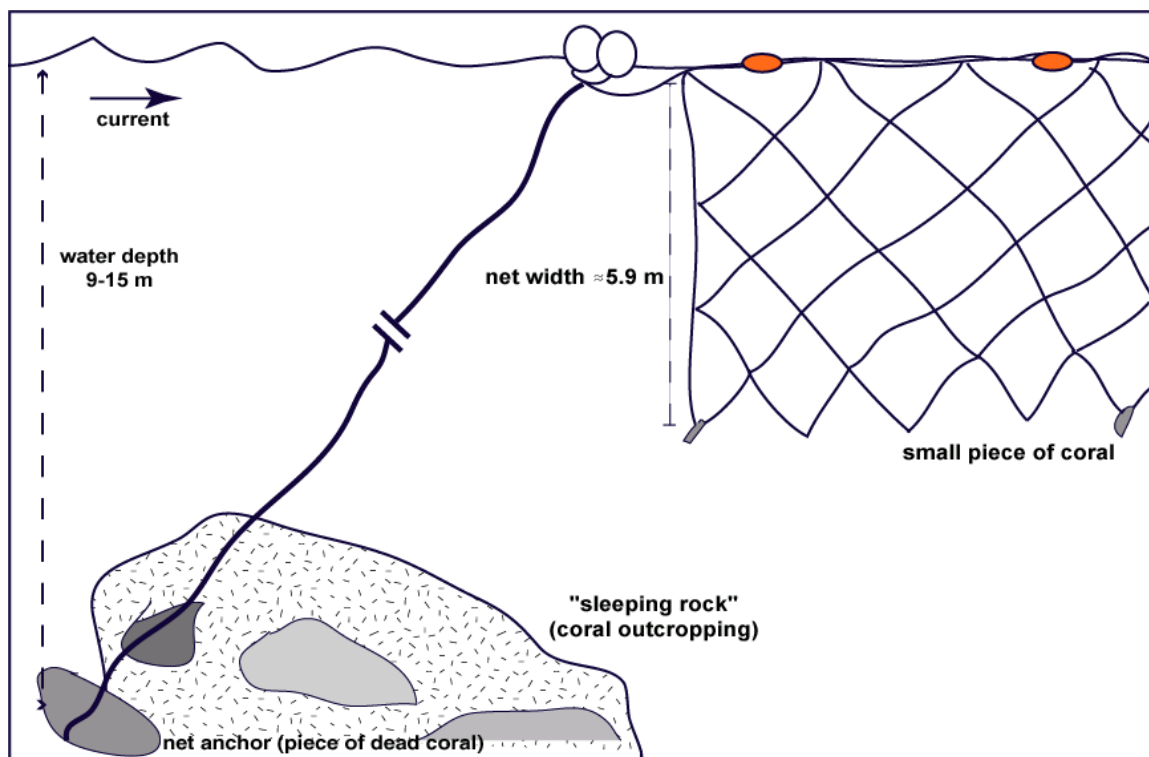


Figure 4.2. Schematic of net set method used to capture green turtles on the Caribbean coast of Nicaragua. Diagram not to scale.

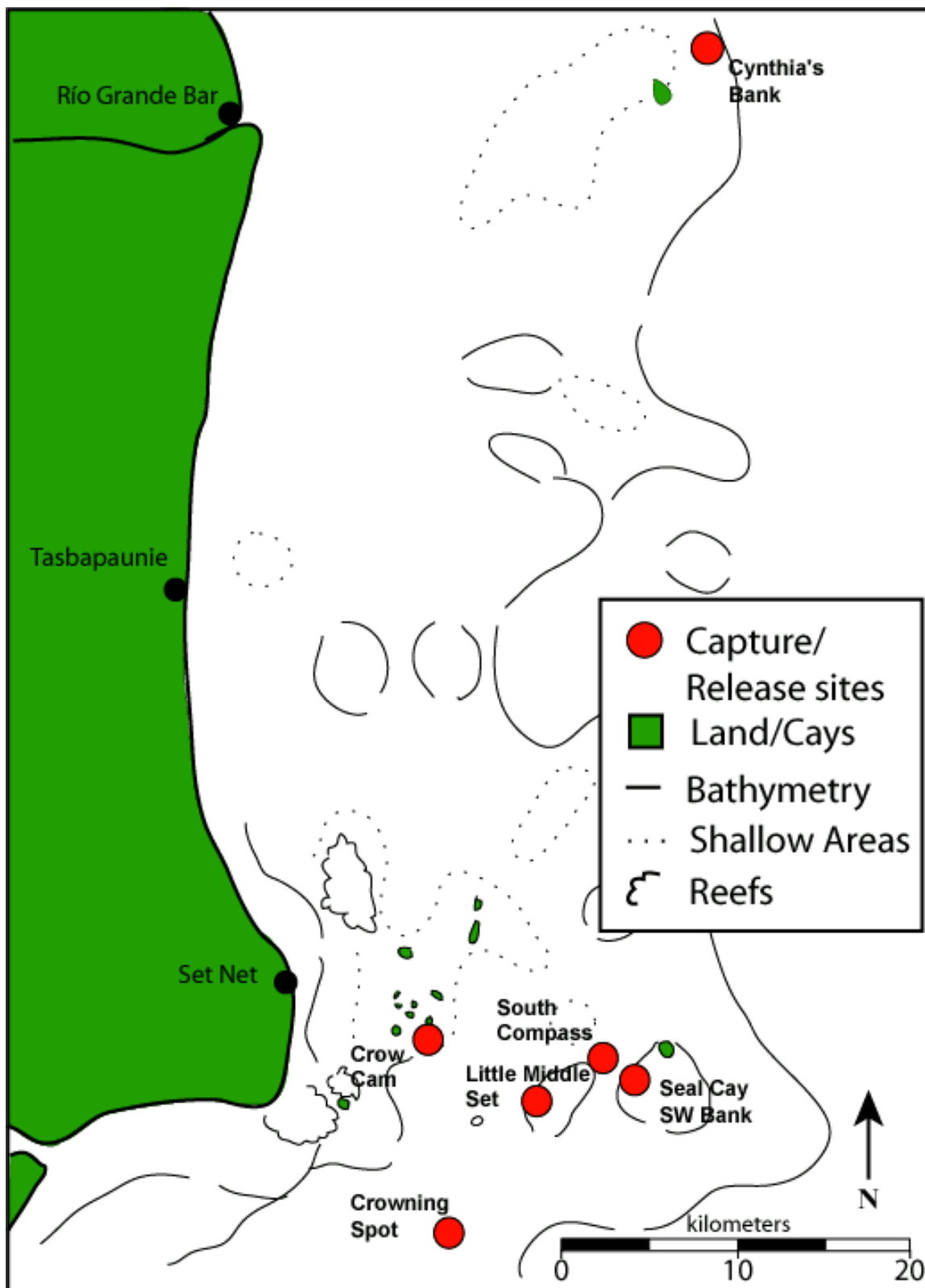


Figure 4.3. Capture/release locations on the southern foraging ground in Nicaragua.

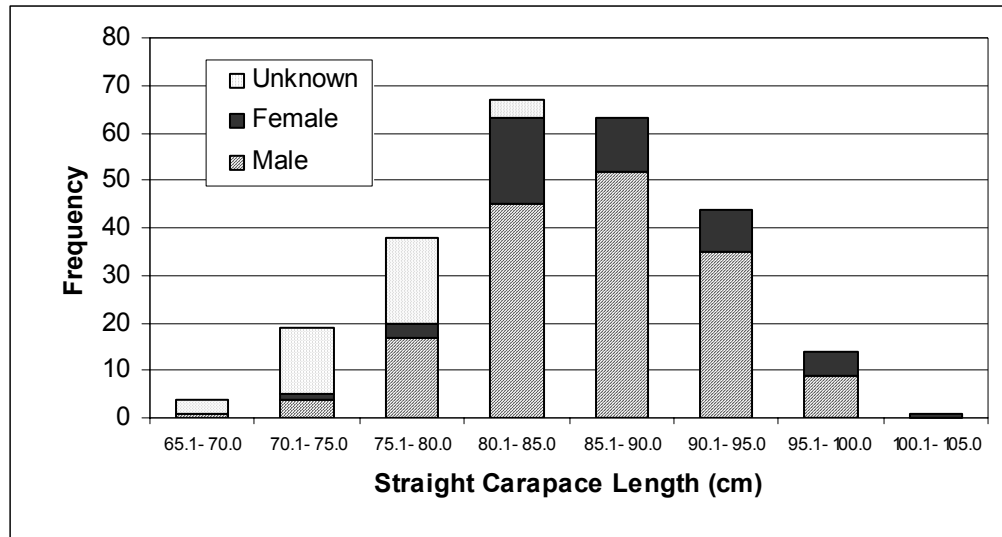


Figure 4.4. Size distribution according to sex of green turtles captured and marked on the foraging ground in Nicaragua between March 1999 and May 2002. Straight carapace length was measured along the mid-line from the nuchal notch to the longest posterior marginal tip.

CHAPTER 5
ANALYSIS OF A WESTERN CARIBBEAN GREEN TURTLE POPULATION
USING DETERMINISTIC MATRIX MODELS

Introduction

The mark-recapture results from Chapter 4 suggest that the Tortuguero, Costa Rica, green turtle population may be threatened by the commercial green turtle fishery in Nicaragua and elsewhere in the Caribbean. This evidence consists of low survival rates for the large juvenile ($O = 0.5537$, $SE = 0.115$) and adult ($O = 0.8207$, $SE = 0.041$) life stages. However, survival rates for some life history stages alone are not sufficient to understand the overall dynamics of any population. Reproductive rates, age-at-maturity, and survival rates of all life stages contribute to the dynamics and persistence of a population. The estimation of population size over time would be one way to determine whether a population is increasing, decreasing, or stable. However, population size is often difficult to estimate, particularly for species such as green turtles that have numerous life history stages that use multiple, widely dispersed developmental habitats. Trends in levels of nesting activity have been used as an index of sea turtle population status (Bjorndal et al. 1999). However, trends in nesting emergences, while valuable, provide little indication, in the short-term, of increased mortality to other segments of the population such as juveniles and males, particularly for long-lived species such as sea turtles.

Another method for evaluating the status of a population involves modeling the hypothetical consequences of present conditions using a matrix population model

(Caswell 2001). Matrix population models have been used frequently in recent years to model sea turtle population dynamics for various purposes, in particular to evaluate the impact of turtle excluder devices (Crouse et al. 1987, Crowder et al. 1994), head-starting (Heppell et al. 1996a), and harvesting (Heppell et al. 1996b, Siddeek and Baldwin 1996). A few studies have also used matrix population models to evaluate population status (Heppell et al. 1996b, Turtle Expert Working Group 2000). Matrix population models can also be used to evaluate age- or stage-class contributions to population growth (elasticity analysis) to improve understanding of population dynamics and direct management efforts (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996a, b), although the cost of management actions should also be considered (Nichols and Hines 2002).

In this study, I used matrix population models to evaluate heuristically the status of the Tortuguero, Costa Rica, population of green turtles and potential for future changes in numbers of females on the nesting beach. In addition, I conducted elasticity analysis to determine the proportional sensitivity of population growth or lambda (λ) to changes in vital rates. Because there is uncertainty in some demographic parameters (quantified and unquantified), I simulated several hypothetical scenarios of population status.

Methods

Model Structure

I used an age-structured deterministic matrix model to estimate the long-term growth rate of the Tortuguero, Costa Rica, green turtle population. An age-structured population projection matrix (also known as a Leslie matrix) is a general matrix \mathbf{A} such that $x_{t+1} = \mathbf{A} x_t$, where x_t is the abundance of animals in an age-class at time t . Using age-specific vital rates, the matrix takes the form:

$$A = \begin{bmatrix} 0 & 0 & \cdots & F_{\alpha-1} & F_{\alpha} \\ S_1 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & S_{\alpha-1} & S_{\alpha} \end{bmatrix}$$

where S_i is age specific survival probability (noted as S_{fy} , S_{sj} , S_{lj} , and S_a in the actual projection matrix in Appendix A and Figure 5.1), F_i is age specific fertility, and α is age-at-maturity. The simulated population can be projected by post-multiplying the matrix by the population vector. After several iterations of multiplying the matrix by the population vector, the population converges to the stable age distribution so that the proportion of individuals in each age-class remains constant over time and the population grows at a constant rate. The population growth rate, lambda (λ), is estimated as the dominant eigenvalue (or largest real root) of the matrix. Lambda represents projected population growth per projection interval, such that $\lambda = e^r$, where r is the intrinsic rate of increase of the population. If $\lambda = 1$, then $r = 0$ and the population remains stable. Likewise, if $r > 0$ ($\lambda > 1$) the population is increasing and if $r < 0$ ($\lambda < 1$) the population is declining.

Demographic Parameters and Model Development

I developed an age-structured matrix model for the Tortuguero green turtle population, with a projection interval of one year, based on the life cycle graph shown in Figure 5.1 and the corresponding projection matrix in Appendix A. To estimate parameters for the projection matrix, I first divided the life cycle of female green turtles into stages: 1) 1st year post hatching, from hatchling emergence to completion of the first year, including a portion of the pelagic, oceanic phase; 2) small juvenile, from the second year of the pelagic, oceanic phase to completion of the shallow benthic feeding phase,

estimated at a total of 14 years based on 12 years in the benthic phase (Bjorndal et al. 2000) and two years in the pelagic phase; 3) large juveniles, when they enter deeper benthic feeding habitat until the year before they reach sexual maturity, since the duration of this stage is unknown I used two rates 12 years and 16 years; however, because I used a post-breeding census, the last year of the large juvenile stage (maturing juveniles) was separated from the other large juveniles to include a contribution to reproduction, and 4) reproductive females. I then estimated vital rates for each of these stages.

The matrix parameter for reproduction, fertility (F), defined as the number of female hatchlings produced per female per projection interval, was based on a birth-pulse, postbreeding census (Caswell 2001). Mean fertility (\bar{F}) was derived as follows:

$$\bar{F} = S \times m,$$

$$m = \frac{CS \times CF \times ES \times PF}{RI},$$

where CS is average clutch size, CF is average clutch frequency for a season, ES is average emergence success, PF is the proportion of females produced (assumed to be 0.50), and RI is the re-migration interval (the interval between reproductive migrations from foraging habitat to the nesting beach, usually greater than one year). Bjorndal and Carr (1989) reported mean CS of 112 eggs \pm 24 ($n = 2,544$ clutches). CF was 2.8 clutches per season (Carr et al. 1978), ES was 0.56 using the average over three years reported by Horikoshi (1992), and RI was three years (Carr et al. 1978). Only maturing juveniles and adults have a fertility term greater than zero.

Annual survival rates (S) for each stage were estimated using different methods. For Stage 1, survival probabilities are unknown, thus I assumed that survival from post-hatching through the first year was similar to the following stage and used a survival rate

of $S_{fy} = 0.80$, which is within the range of estimates of “true” survival reported for small juveniles in the Bahamas (Bjorndal et al. In press). Two survival rate estimates were used for Stage 2, small juveniles (S_{sj}), 0.80 and 0.90, since only one study has empirical survival rate estimates of wild small juvenile green turtles in the Caribbean (Bjorndal et al. In press). In addition, there is likely much variation across the widely dispersed developmental habitats used by green turtles in this stage from the same population. These small juvenile survival rates are similar to mean estimates of “true” survival rates reported for small juveniles in the Bahamas (Bjorndal et al. In press), of which the majority have been identified as originating from the Tortuguero population (Lahanas et al. 1998). The size range of turtles in the Bahamas study was from 25 to 84 cm carapace length (Bjorndal et al. In press), which does not include the smaller sized, open ocean, pelagic turtles that are included in Stage 2 in this study, thus, the 0.90 survival rate is considered a very optimistic estimate of S_{sj} .

For Stage 3, large juvenile survival (S_{lj}), I used the estimate presented in Chapter 4 for the mixed large juvenile/adult group marked on the Nicaragua foraging ground, $S_{lj} = 0.5537$ (standard error, SE, = 0.117, 95% confidence interval, CI, = 0.33-0.76). Although the mixed group survival estimate included both large juveniles and adults, the majority of turtles captured in the turtle fishery are large juveniles (78 % of females captured and 57 % of males captured, Lagueux 1998). An additional consideration when I used this survival rate estimate was that both males and females were included in the sample. The sample size for turtles marked on the foraging ground was too small to estimate survival rates by sex, however, Chaloupka and Limpus (In press) reported that survival rates of green turtles in Australia did not differ between males and females for

either juveniles, subadults, or adults. Thus, it seems reasonable to use the survival rate estimate from the mixed large juvenile/adult group marked on the foraging ground as an estimate of S_{ij} in the population models. The survival rate estimate presented in Chapter 4 for adult females tagged on the nesting beach in Costa Rica was used as an estimate of adult female survival in the projection matrix, $S_a = 0.8207$ (SE = 0.041, CI = 0.727-0.887).

To have a better idea of the range of possible values for λ , I incorporated the error associated with the large juvenile and the adult female survival rate estimates into the modeling by allowing the survival rates for each group to be randomly selected based on a normal distribution, and the SE of the estimates, within the 95% CI. In addition, because the proportion of large juveniles subjected to the turtle fishery is unknown, I incorporated a survival rate without harvesting of 0.90 for large juveniles into a separate model set. The survival rate of 0.90 is based on the assumption that large juvenile green turtles in the Caribbean can attain survival rates as high as green turtles in Australia (CI = 0.79-0.908) (Chaloupka and Limpus In press). The upper end of the 95% confidence limit reported by Chaloupka and Limpus (In press) was used based on their belief that the survival rate was underestimated due to permanent emigration out of their study area. I used a weighted mean (Zar 1996) to obtain an overall survival rate for large juveniles that includes a proportion of large juveniles with a 0.90 survival rate and a proportion that was allowed to range from a survival rate of 0.33 to 0.76 based on the mixed group of animals tagged in Nicaragua. I used a weighted mean as an ad hoc approximation of the large juvenile survival rate, a more detailed approximation is used in Chapter 6. Stage-specific demographic parameters for each model are summarized in Table 5.1.

Table 5.1. Demographic parameters used in six projection matrices to evaluate the hypothetical consequences of present conditions on the Tortuguero, Costa Rica, population. A description of each stage is provided in the text, and justification for stage durations is provided below the table. A change in large juvenile stage duration results in two estimates of age-at-maturity, 28 and 32 years, which are within the range of previous estimates (27-33 yr, Frazer and Ladner 1986; 25-30 yr, Mendonça 1981; and 26-34 yr, Zug and Glor 1998).

Set A Assumes 100% of large juvenile stage is subjected to Nicaragua fishery					Set B Explores what proportion of large juveniles could be subjected to fishery and maintain a stable population				
Model	Stage	Stage Duration (yr)	Annual Survival	Annual Fertility	Model	Stage	Stage Duration (yr)	Annual Survival	Annual Fertility
1a	first year	1	.80	0	1b	first year	1	.80	0
	small juvenile	14 ^a	.80	0		small juvenile	14	.80	0
	large juvenile	15 ^b	.33-.76	0		large juvenile	15	.90	0
	maturing juvenile	1	.33-.76	9.7-22.3		maturing juvenile	1	.90	26.4
	adult	-	.73-.89	21.4-26.1		adult	-	.73-.89	21.4-26.1
2a	first year	1	.80	0	2b	first year	1	.80	0
	small juvenile	14	.80	0		small juvenile	14	.80	0
	large juvenile	11 ^c	.33-.76	0		large juvenile	11	.85-.887	0
	maturing juvenile	1	.33-.76	9.7-22.3		maturing juvenile	1	.85-.887	24.9-26
	adult	-	.73-.89	21.4-26.1		adult	-	.73-.89	21.4-26.1
3a	first year	1	.80	0	3b	first year	1	.80	0
	small juvenile	14	.90	0		small juvenile	14	.90	0
	large juvenile	11	.33-.76	0		large juvenile	11	.67-.84	0
	maturing juvenile	1	.33-.76	9.7-22.3		maturing juvenile	1	.67-.84	19.6-24.6
	adult	-	.73-.89	21.4-26.1		adult	-	.73-.89	21.4-26.1

^a Based on average growth rates, Bjorndal et al. (2000) estimates 12 yr for the benthic juvenile segment of this stage, 2 additional years were added for the open ocean, pelagic phase, which combined with the first year represents 3 years in total for the open ocean, pelagic phase and is within the estimate of 3-6 yr presented by Zug and Glor (1998) and 1-3 yr presented by Ehrhart and Witherington (1992).

^b Based on 1.7 cm/yr growth from 70-80 cm (average of estimated growth rates reported by Bjorndal and Bolten 1988 and Mendonça 1981), and 1.0 cm/yr growth from 80-90 cm (because no data are available for Atlantic greens for this size range, this rate is based on the assumption that the decreasing trend in growth rates as turtles increase in size (Bjorndal et al. 2000) continues beyond 80 cm).

^c Due to uncertainty in the duration of the large juvenile stage, a 12 year duration was also modeled and is based on a hypothetical growth rate of approximately 1.7 cm/yr from 70-90 cm.

Model Implementation

I expanded the demographic parameters of each stage into age-classes for modeling purposes based on the duration of each stage (Table 5.1); for example, a stage duration of 15 years for small juveniles would result in 15 age-classes for that group. I projected 5,000 iterations of two sets of three models each with distinct demographic parameters to incorporate parameter uncertainty due to variability associated with some vital rate estimates. Model Set A assumes that all large juveniles in the population are subjected to the turtle fishery in Nicaragua (Models 1a-3a, Table 5.1). The uncertainty of vital rates addressed in these models includes random selection of survival rates within the 95% CI for both large juveniles ($O = 0.55$, $CI = 0.33-0.76$) and adults ($O = 0.82$, $CI = 0.73-0.89$) (see Chapter 4 for survival rate estimate analysis). The uncertainty of two relatively unknown parameters, large juvenile stage duration and small juvenile survival rate, was also incorporated into the models as previously stated by using a 12 and 16 year stage duration for large juveniles, and survival rate estimates of 0.80 and 0.90 for small juveniles. Set A goes from a “worst-case scenario” in Model 1a to a more optimistic scenario in Model 3a (Table 5.1).

Although the proportion of large juveniles subjected to the turtle fishery in Nicaragua is unknown, it is likely $> 50\%$ based on evidence presented in Chapter 4. Thus, with the goal of achieving a $\lambda = 1.0$ in the simulated population, the second set of models (Set B, Table 5.1) was designed to explore what proportion of the large juveniles could be exposed to the turtle fishery in Nicaragua while the remaining proportion of large juveniles had a “natural” survival rate of 0.90. In model Set B, I used the same demographic parameters that were used in Set A, with the exception of the survival rate for large juveniles. Survival rates for the proportion of large juveniles exposed to the

Nicaragua fishery were selected in the same manner as for Set A, i.e., they were randomly selected for each iteration from a normal distribution of parameter values. The final large juvenile survival rate for each iteration was determined using a weighted mean. For example, if 9% of large juveniles were exposed to the fishery and 0.55 was the survival rate randomly chosen for the iteration, the final large juvenile survival rate used to estimate λ was $(0.55 \times 0.09) + (0.90 \times 0.91) = 0.8685$. Through trial and error I determined for each model the proportion of large juveniles that could be exposed to the turtle fishery and achieve a mean λ of 1.0.

The proportional sensitivity (i.e., elasticity) of λ to changes in survival and fertility rates was determined for each model (Caswell 2001). Elasticities (e_{ij}) were estimated as follows:

$$e_{ij} = \frac{a_{ij} v_i w_i}{\lambda \langle \mathbf{v}, \mathbf{w} \rangle}$$

where a_{ij} is the matrix element, v_i and w_i represent the i th entry of reproductive value (\mathbf{v}) and stable age distribution (\mathbf{w}) vectors of the matrix, respectively, and $\langle \mathbf{v}, \mathbf{w} \rangle$ is the inner product of the two vectors. The age-class elasticities that correspond to the stages described previously were summed to estimate the proportional contribution of each stage to λ (Heppell et al. 1999).

Results

Distribution of projected population growth rates (λ) for each model are presented in Figure 5.2. In Set A, which assumes that all large juveniles are exposed to the turtle fishery in Nicaragua, nearly all λ were less than 1.0. In Model 1a, the “worst-case scenario,” λ ranged from 0.729 to 0.943 ($O = 0.841$, $SE = 0.0006$), indicating a projected population decline of between 5.9 and 31.6% per year. There was only a slight increase

in λ in Model 2a ($O = 0.863$, $SE = 0.0006$, $range = 0.734-0.965$), resulting from a decrease in the duration of the large juvenile stage to 12 years (which in turn decreased the mean age-at-maturity to 28 years). Results from Model 2a indicate a population decline of between 3.6 and 30.9%. In model 3a, λ increased to a mean of 0.896 ($SE = 0.0007$, $range = 0.746-1.012$), with less than 1% of the λ s between 1.0 and 1.012 (stable or marginal population growth) while the remaining λ s indicate a rate of population decrease of between 0.03 and 29.3%. Thus, projections from Set A indicate that the Tortuguero population is very likely to decline, and possibly rapidly.

In Set B (Models 1b-3b), the proportion of large juveniles that could be subjected to the fishery ranged from 0 to 41%, using a mean λ of 1.0 (Figure 5.2). In Model 1b (where large juvenile stage duration is 16 yr and $S_{sj} = 0.80$), 0% of the large juveniles can be exposed to the turtle fishery to achieve a mean λ of 1.0 (stationary growth), although higher growth rates were achieved when randomly drawn adult survival rates were high. In Model 2b (where large juvenile stage duration is reduced to 12 yr while holding other parameters constant) only 9% of the large juveniles can be exposed to the turtle fishery to achieve a mean λ of 1.0, although again, higher growth rates were achieved when randomly drawn adult survival rates were high. The most dramatic change occurs in Model 3b (where S_{sj} is increased to 0.90 while holding other parameters constant), which indicates that approximately 40% of the large juveniles can be exposed to the turtle fishery.

To show the relationship between the proportion of large juveniles that can be subjected to the turtle fishery in Nicaragua and possible combinations of large juvenile and adult survival rates I used a surface plot (Figure 5.3). Using the same parameters in

three model types described earlier and a target λ of 1.0, I determined the proportion of large juveniles that could be subjected to the turtle fishery with various combinations of large juvenile and adult survival rates within the 95% CI of the estimates, while holding all other parameters constant. In plots 1 and 2, many combinations of adult and large juvenile survival rates allow only a small proportion of large juveniles to be exposed to the turtle fishery in Nicaragua and still achieve stable population growth ($\lambda = 1.0$), and most combinations in plot 1 show that no large juveniles can be subjected to the fishery without causing an eventual decline in the population. A much greater range of possibilities (20-100%) can be observed in plot 3.

Elasticities of λ to changes in vital rates were summed according to the stages described previously and are presented in Figure 5.4. Overall, mean elasticities of λ to adult survival exhibited the largest range (0.101-0.565) and the highest value (0.565). Mean elasticities of λ to small and large juvenile survival were similar within each model, with differences ranging from 0.026 to 0.07. Mean elasticities of λ to survival in Stage 1 and fertilities were very low compared to the other three stages, ranging from 0.001 to 0.032.

In Models 1a and 2a, mean survival elasticities were much higher for Stage 4 (adults) than in other models, whereas, survival elasticities in Stages 2 and 3 were the highest in Models 3b and 1b, respectively. Survival elasticities for Stages 2 and 3 both increased somewhat in Models 1b -3b, when the overall survival rate of large juveniles increased.

Discussion

Population Growth Rates

The Tortuguero, Costa Rica, green turtle population is facing renewed threats from uncontrolled harvesting. The most serious threat is the uncontrolled harvest of large juvenile and adult green turtles on the feeding grounds in Nicaragua. Assuming that the vital rates used in the preceding models reasonably approximate those of the Tortuguero green turtle population, the results presented here allow us to better understand the potential severity of this threat. Based on the worst-case scenario, Set A, where 100% of large juveniles were subjected to the Nicaragua turtle fishery (Figure 5.2), the distribution of growth rates indicates that the Tortuguero population will decline if current harvest pressure persists.

Based on model Set B, where only a proportion of large juveniles were exposed to the turtle fishery, two models (1b and 2b) show that possibly zero or only a small proportion of large juveniles (Figure 5.2) can be exposed to the turtle fishery in Nicaragua to achieve a mean $\lambda = 1.0$, although λ s ranged from 0.989 to 1.014 and 0.979 to 1.022, respectively. Furthermore, Figure 5.3 indicates that 95% of the large juvenile and adult survival rate combinations allow only 0-20% of large juveniles to be exposed to the turtle fishery in Nicaragua while maintaining a stable population. In model 3b (Figure 5.2), approximately 40% of the large juveniles in the Tortuguero population can be exposed to the turtle fishery in Nicaragua and still achieve a mean $\lambda = 1.0$, although λ s ranged from 0.942-1.054.

Unfortunately the proportion of large juveniles subjected to the Nicaragua fishery is unknown, however, no other major developmental habitats for large juvenile green turtles have been identified in the Caribbean. In other studies of green turtle developmental

habitats in the wider Caribbean, such as Florida, Panama, Puerto Rico, and the Bahamas, the vast majority of green turtles are small juveniles and only a very small proportion are in the size range of large juveniles (Bjorndal and Bolten 1988, 1995; Collazo et al. 1992; Bagley pers. comm.; Meylan and Meylan pers. comm.), and are likely animals that will soon transition to deeper benthic feeding habitats typically used by large juveniles and adults. In contrast, thousands of large juveniles are captured in Nicaragua each year on its vast seagrass pastures (Lagueux 1998), although small juvenile green turtles do occur in the region (Campbell and Lagueux unpubl. data). Furthermore, several small juveniles that were tagged in shallow developmental habitats, such as Bahamas, Bermuda, and Florida, were later captured in the turtle fishery in Nicaragua (Bjorndal et al. In press, Bagley pers. comm., Lagueux pers. comm., Meylan and Meylan pers. comm.), presumably as either large juveniles or adults. Results from these and other tagging studies (e.g., Carr et al. 1978) and a genetic stock assessment of green turtles captured on the Nicaragua foraging grounds (Bass et al. 1998) provide strong evidence that Nicaragua is the principal feeding habitat for large juvenile and adult green turtles from the Tortuguero population. Thus, the proportion of large juveniles exposed to the Nicaragua fishery, although not quantified, probably far exceeds most of the proportions that would allow the simulated population to remain stable (Figure 5.3). For example, approximately 85% of all large juvenile and adult survival rate combinations in Figure 5.3 showed that $\leq 40\%$ of the large juveniles could be subjected to the turtle fishery, including the model with the most optimistic demographic parameters. Given these considerations, it seems likely that the Tortuguero population is in jeopardy, and if

current conditions continue, a severe decline in the number of nesting females can be expected.

These conclusions appear to contradict trends in numbers of nesting emergences reported for the Tortuguero nesting beach. Analysis of 26 years of survey data from Tortuguero show an increasing trend in the number of nesting emergences up to 1996 (Bjorndal et al. 1999). In fact, however, our two studies do not necessarily contradict each other. Results from the present study, which assume that vital rates remain constant, are based on an asymptotic growth rate, i.e., once the simulated population reaches a stable age distribution and population growth rate is constant, which might take many years to attain. This does not mean, however, that segments of the population, such as large juveniles, are not already declining. Detection of changes in the size of the nesting population may require many years of trend data given the highly fluctuating annual nesting densities at Tortuguero (Carr et al. 1978, Bjorndal et al. 1999). Another consideration is that the harvest in Nicaragua has been at current levels for about 8-10 years, which is less than the estimated duration of the large juvenile stage (the stage most frequently harvested). This is also the stage prior to sexual maturity, so it may take several more years before the adult female population begins to show a decline on the nesting beach. Such a delay is portrayed in the series of matrix projection models of a hypothetical green turtle population that is subject to varied harvest pressure in the later life stages (Figure 5.5). The time series demonstrates that a lag of several years can be observed prior to the decline of adult females when increased harvest pressure is initiated in 1992 (Figure 5.5). Variation in harvest pressure used in the time series is based on some generalized information about known fluctuations in harvest pressure in Nicaragua

and Costa Rica. The time lag results from a combination of factors, i) delayed sexual maturity, which results in an accumulation of animals in the large juvenile stage and provides a buffer against intensive exploitation (Bjorndal 1985), ii) the life stages subjected to harvesting, and iii) fluctuations in harvest pressure over relatively short time spans relative to the time it might take a green turtle population to stabilize once perturbed. In this case, the simulated green turtle population (Figure 5.5) experienced a period of growth when harvest pressure was reduced for about 14 years (1977-91), subsequently higher harvest pressure resumed, and after several years of simulated harvesting at current estimated levels the adult female population was still intact. This is because fishing mortality is greater for large juveniles (whose stage duration may exceed the 14-year period of population growth) and the reproductive life span of adults is expected to be more than 20 years based on records of re-migrating females at Tortuguero (Hirth 1997, Reyes and Troëng 2002). While the actual number of adults is not accurately reflected in this time series (Figure 5.5), what is shown is that there can be a time lag in a decrease of the adult female population when temporal variation in harvest pressure is considered in combination with life history characteristics. The duration of the lag time needed to detect a decrease in the Tortuguero nesting population cannot be determined without data on population sizes of the various life stages at the time changes in harvest pressure occurred and a better understanding of the high variability in annual nesting density, thus this example illustrates only that a delayed response is possible, and not how long a delay might be. Evaluation of only trends in nesting emergences, while insightful, can be misleading and mask serious threats occurring to other segments of a population (Mortimer 1995).

Admittedly, further studies are needed to more precisely estimate demographic parameters and their variability, and to examine the relationship between survival rates and harvest level. The most notable are i) survival rate estimates for small juveniles since this parameter considerably affects the proportion of large juveniles (model 3b, Figure 5.2) that could be exposed to the fishery and still maintain a stable population, ii) duration of the large juvenile stage because, although reasonable, the durations used in this study were based on sparse scientific data, and iii) an estimate of the actual proportion of large juveniles from the Tortuguero population that are exposed to turtle fisheries in the Caribbean, particularly the Nicaragua fishery. Although additional data are needed, by bracketing some of the most uncertain parameters and incorporating the range of large juvenile and adult survival rate estimates, many of these uncertainties have been accounted for in the various model simulations, providing a range of possible outcomes to assess the status of this population.

Although the range of possible outcomes from model Set A are conclusive and suggest a population decline, the range of possible outcomes from Set B are not. It is conceivable that some proportion of large juveniles could be exposed to the turtle fishery in Nicaragua and still maintain a stable population, depending on the actual duration of the large juvenile stage, the proportion of large juveniles subjected to the fishery in Nicaragua, and survival rate of small juveniles. However, it seems highly unlikely that small juvenile annual survival is as high as 0.90 for all 14 years of this stage (models 3a and 3b, Figure 5.2), particularly when survival rates of larger animals (large juveniles and adults) that presumably have fewer predators are in this range. Thus, the demographic parameters used in models 1 and 2 are likely more realistic, making a stronger case to

conclude that the Tortuguero population as a whole is or will be declining, based on model simulations.

Elasticity Analysis

Elasticity results from other modeling studies of sea turtle populations have frequently shown that survival rates in the later life stages contribute the most to λ (e.g., Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1999). Adult female survival contributes proportionately the most, by a large margin, to population growth in Models 1a and 2a. In Model 3a where small juvenile survival is increased, small juvenile, large juvenile, and adult survival elasticities are generally very similar. From this set of models (Set A) the contribution of small and large juvenile survival rates are similar, while the potential contribution of adult female survival to λ drops considerably in Model 3a (where an increase in small juvenile survival is combined with a decrease in large juvenile stage duration).

In Set B, small and large juvenile survival elasticities, although higher than in Set A, remain similar, while adult survival elasticities dropped considerably from Set A. However, since adult survival in the simulations is also lower than expected natural rates due to harvesting, if harvesting were removed, it is likely that adult survival elasticities would remain high when large and small juvenile survival rates increase. Elasticity results from Set A are similar to those found for other long-lived marine species where elasticities are low for early life stages and much higher for later life stages (Heppell et al. 1999). Modeling results reported by Heppell et al. (1996b) for an Australia loggerhead population also showed that reduced survival in one stage increased the importance of another stage to population growth. This is not surprising since elasticities reflect proportional contributions of changes in vital rates to λ , however, it allows us to

identify which demographic parameters will become more important under certain conditions. Like other studies that modeled sea turtle populations (e.g., Heppell et al. 1996b, Crouse et al. 1987), population growth in this study was affected more by survival rates than by fertility. The demographic parameters that are identified through elasticity analysis to most heavily impact population growth can be the focus of further modeling efforts to identify the most effective management actions.

The primary interest in evaluating elasticities for the models in this study is to aid in subsequent modeling efforts to direct management actions. Unfortunately, the elasticity results are inconclusive and depend primarily on whether or not all large juveniles are subjected to the turtle fishery in Nicaragua or only a small proportion. However, based on the conclusion that the survival rate for small juveniles used in Model 3 (a and b) is too high and that the vast majority of large juveniles in this population are subjected to the fishery in Nicaragua (see previous section), elasticity results from Models 1a and 2a (Figure 5.4) are more relevant to exploring future management options.

Implications for Managing Green Turtle Use

Assuming that the Tortuguero population is facing a decline from overexploitation, conservation and management actions should be put in place before this valuable natural resource is lost or severely depleted. How might conservation and management occur on Nicaragua's Caribbean coast? It is unlikely that the coastal people of Nicaragua will change their harvest patterns and reduce pressure on western Caribbean green turtles unless forced to by severe depletion of the resource or from outside pressure. The Caribbean coast of Nicaragua is poorly developed economically and green turtles have been culturally important for hundreds of years. Today, green turtles not only continue to provide coastal people with an important source of protein, but also provide much needed

income to turtle fishers so that they may purchase other foods and household goods. Loss of this resource on a commercial level would likely be devastating to local turtle fishing communities along Nicaragua's Caribbean coast and thus, outside efforts, such as from the scientific community, local government authorities, and local non-government agencies, must provide the financial means and expertise necessary to aid resource users in a collaborative effort to carefully regulate the green turtle fishery in Nicaragua.

From the scientific community, what remains to be identified are specific recommendations that will allow turtle harvesting but reduce its impact on the Tortuguero green turtle population, and possibly reverse the current projected population decline. Based on the modeling and elasticity results in this chapter, additional model simulations are needed to identify specific harvest strategies for the Nicaragua turtle fishery. In the following chapter I explore various management options and use these results as the basis for management recommendations to the Nicaragua natural resource authorities and local turtle fishing communities.

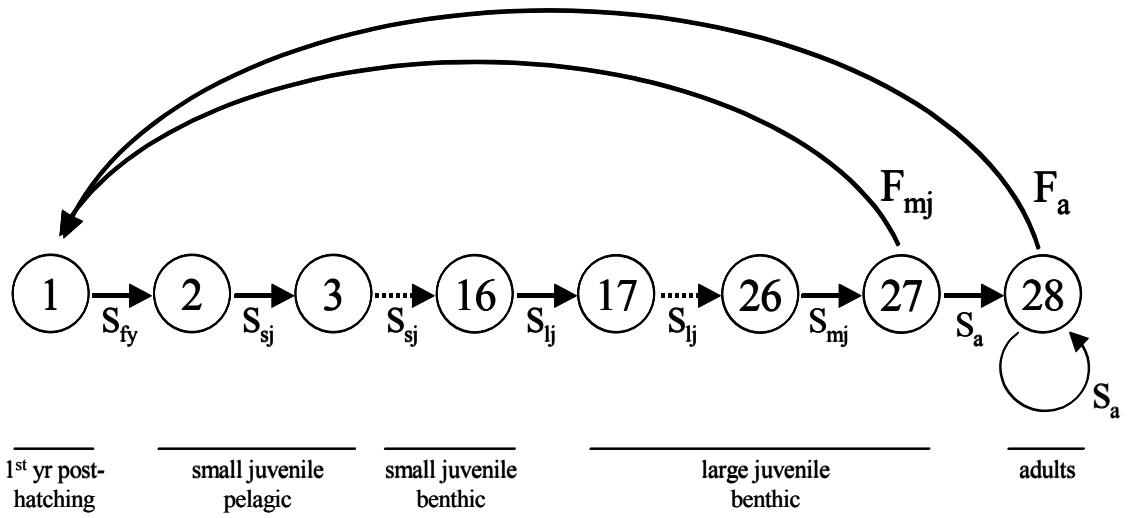


Figure 5.1. Life cycle graph for age-class model of hypothetical Tortuguero, Costa Rica green turtle population. S = survival probability, F = fertility based on a birth pulse, post-breeding census, fy = first year post hatching, sj = small juvenile, lj = large juvenile, mj = maturing juvenile, a = adult. S_a in age-class 28 is on-going.

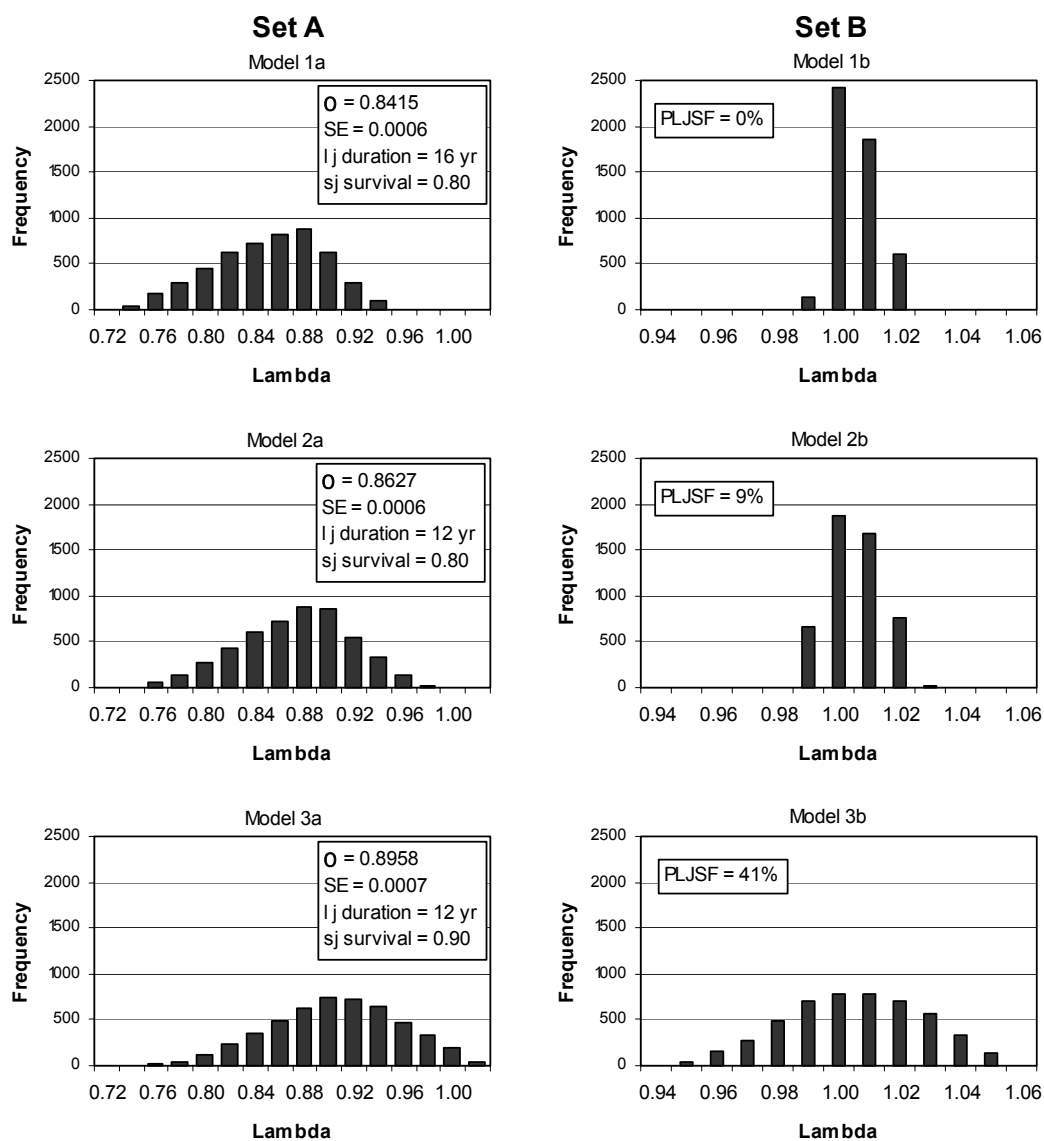


Figure 5.2. Distribution of population growth rates (λ). For models in Set A, 1a-3a, a worst-case scenario is assumed where all large juveniles are exposed to fishing mortality in Nicaragua; and in Set B, 1b-3b, the proportion of large juveniles that can be exposed to the turtle fishery in Nicaragua to maintain a stable population (mean $\lambda = 1.0$) is determined, and the remaining proportion has a survival rate of 0.90. Models 1-3 in both sets have different model parameters to reflect the uncertainty of demographic rates and are progressively more optimistic. In the most optimistic model in Set A, 3a, only a small number of lambdas reach 1.0 or above. In Set B, models 1b and 2b show that few large juveniles can be subjected to the turtle fishery. l j duration = large juvenile stage duration, s j survival = small juvenile annual survival rate, SE = standard error, PLJSF = proportion of large juveniles subjected to fishery to achieve a mean lambda of 1.0. X-axis labels represent the highest value in the range of values included in the bin.

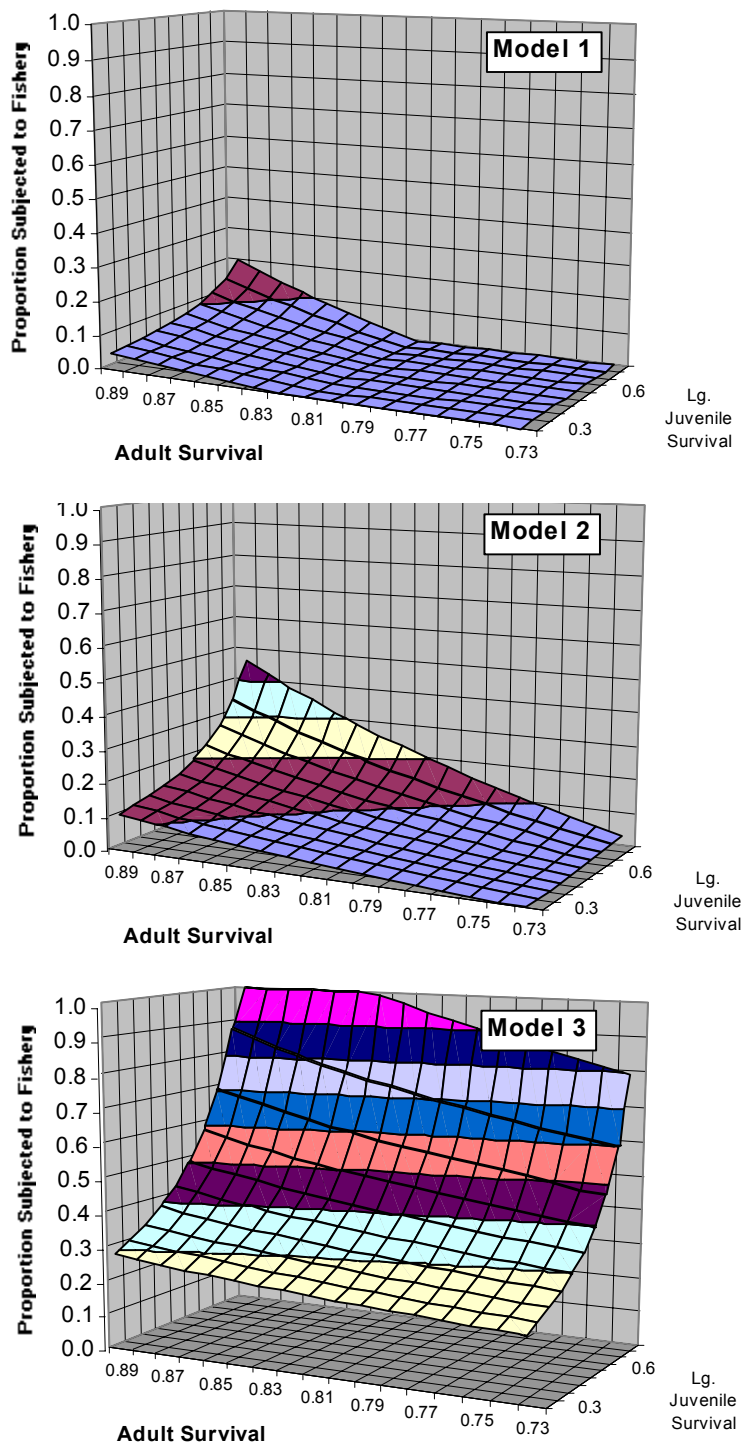


Figure 5.3. The relationship between the range of large juvenile and adult survival rates, within the 95% confidence intervals of the estimates derived in Chapter 4 relative to the proportion of large juveniles that can be exposed to the fishery in Nicaragua and still maintain a stable population ($\lambda = 1.0$). The remaining proportion of large juveniles were assumed to have a survival rate of 0.90.

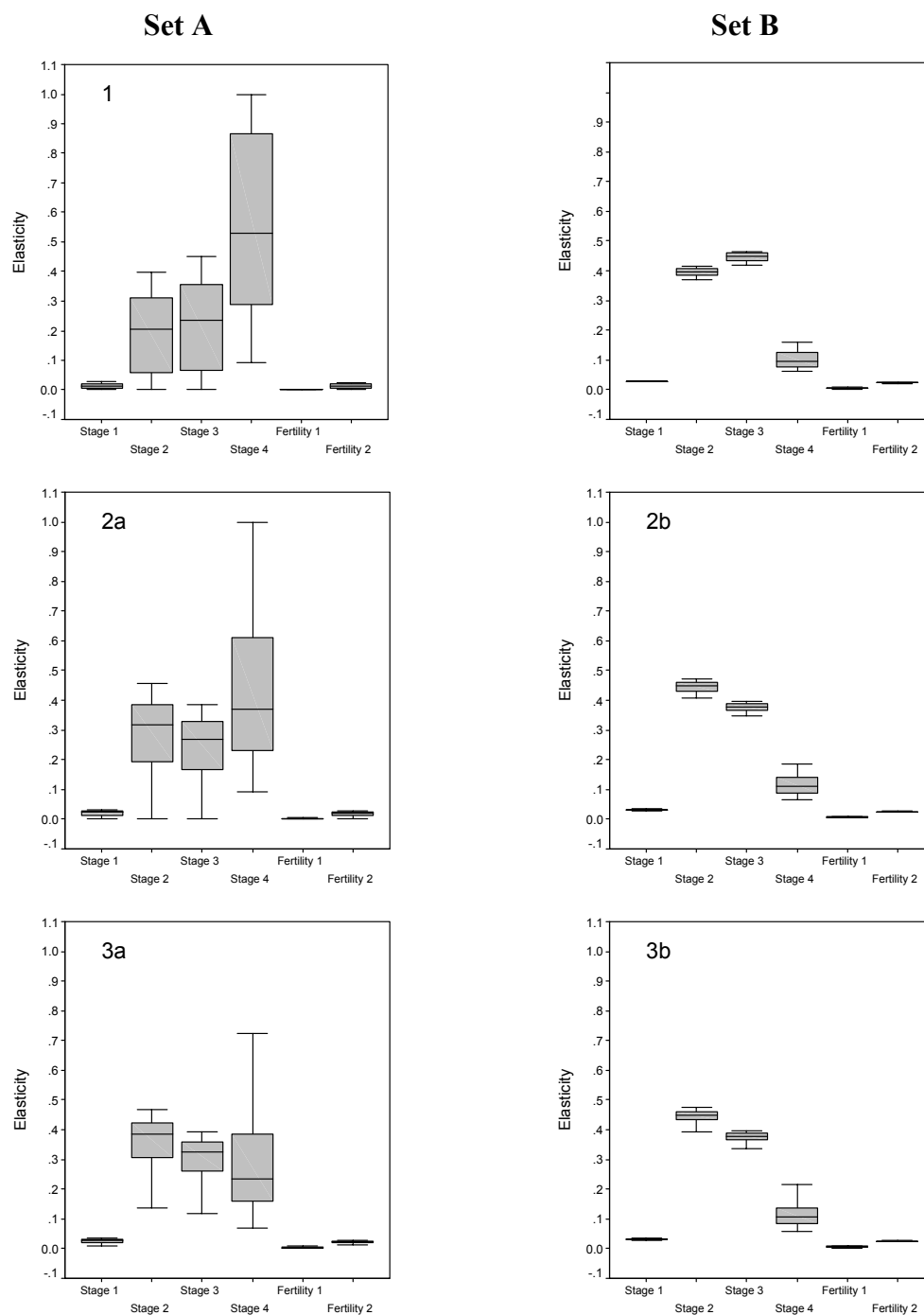


Figure 5.4. Distribution of elasticities of δ for models presented in Figure 5.1.

Elasticities of δ to changes in age-class vital rates are summed into stages as described earlier. In models 1a-3a 100% of large juveniles were subjected to the turtle fishery in Nicaragua. In models 1b-3b the proportion of large juveniles that could be exposed to the turtle fishery and still maintain a stable population (mean $\delta = 1.0$) was determined, the survival rate of the remaining large juveniles was 0.90. Median and quartiles are shown in each boxplot.

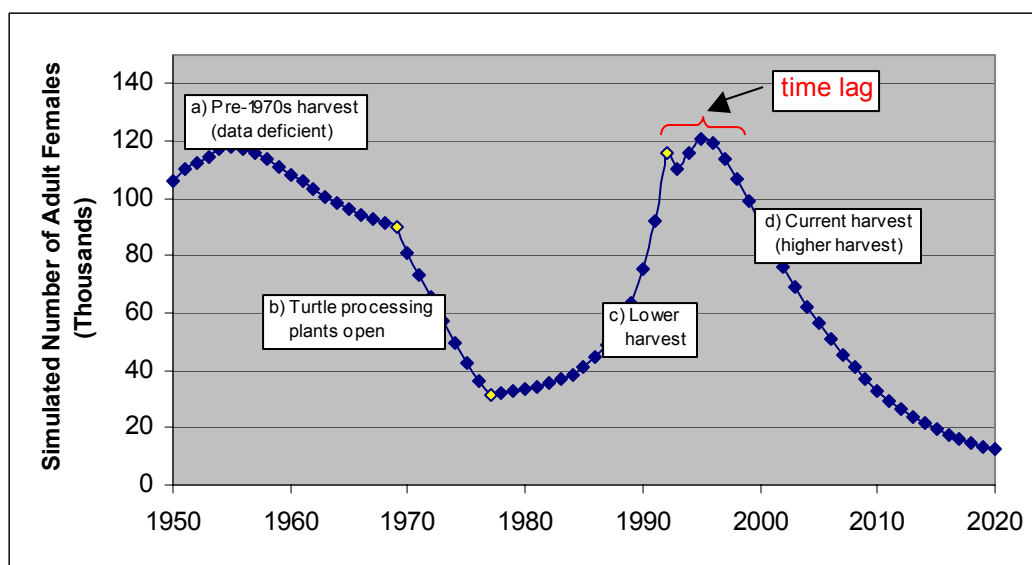


Figure 5.5. Example of variation in population size of adult females and recruits resulting from simulated changes in harvest pressure on large juvenile and adult females. The time series includes: a) low harvest pressure for 49 years starting in 1920 based on sparse and anecdotal information, however, only from 1950 is plotted on the graph; b) eight years of higher harvest pressure from 1969 to 1976, a time during which turtle processing plants were operating in Nicaragua and harvest levels were up to 10,000 turtles/yr (Nietschmann 1973, 1979; Groombridge and Luxmoore 1989); c) 14 years (1977 to 1991) of lower harvest pressure after closure of processing plants and during the civil war in Nicaragua, during which time an average of 2,780 turtles/yr were taken in Nicaragua from 1985-1990 (Montenegro-Jiménez 1992) and starting in 1983 a take of 1,800 turtles/season was permitted in Costa Rica; and d) higher harvest pressure from 1992 to 2020 based on current survival rate estimates. Yellow dots indicate year in which a change in harvest pressure was initiated. Although tenuous, this highly simplistic representation of simulated variation in harvest pressure demonstrates that after 1991 when harvest pressure increases, there is a delay of several years before the simulated adult population begins to decline.

CHAPTER 6 EVALUATING HARVEST STRATEGIES

Introduction

Green turtle populations have suffered severe declines (and in some cases extirpation) from overexploitation for centuries, and are recognized globally as species threatened with extinction (Hilton-Taylor 2000). In the Caribbean, green turtles were heavily exploited for many years and the resulting population declines prompted efforts to protect them. Now, after several years of concerted conservation efforts by various countries around the greater Caribbean (e.g., Costa Rica, Mexico, USA), an intensive harvest has re-commenced. Intensive harvest by indigenous and ethnic coastal people of Caribbean Nicaragua may pose the most serious threat ever faced by the Tortuguero, Costa Rica, green turtle population, the largest remaining green turtle population in the Atlantic Ocean. Although this population nests in Costa Rica, the principal foraging habitat for large juveniles and adults is located in the vast seagrass beds off the Caribbean coast of Nicaragua (Carr et al. 1978), and thus this population is subjected to intense fishing pressure.

Based on results from model simulations presented in Chapter 5 (Figure 5.1), it is likely that the Tortuguero population as a whole is, or will be, severely affected by current harvest levels, causing the population to decline. If so, management authorities ideally should close the Nicaragua green turtle fishery (the principal turtle fishery in the region) until the population attains a predetermined size, and at such time a limited, controlled harvest for local consumption might be permitted. However, turtle fishing

communities of coastal Nicaragua rely heavily on the income provided by the sale of green turtles and their meat, and closing the fishery would inflict undue hardship on an already poverty stricken group of people. Furthermore, given limited economic resources for natural resource agencies in Nicaragua and strained political relations between national and local autonomous governments, enforcement of a ban on turtle fishing for commercial purposes is probably not feasible. Since the Tortuguero nesting population still appears to be intact, with high production of young (based on nesting emergences, Troëng et al. unpubl. manu.), it is timely to evaluate management options to determine if some level of harvest is possible while simultaneously moving the projected population decline towards a stable growth rate.

In this chapter, I will address two principal questions: 1) How much do fishing mortality rates attributed to the Nicaragua turtle fishery need to decrease for a simulated Tortuguero green turtle population to achieve a stable growth rate ($\lambda = 1.0$)?, and 2) What is the range of possible maximum allowable harvest levels for the Nicaragua turtle fishery based on estimated reductions in fishing mortality rates, that might halt the projected population decline of the Tortuguero green turtle population (based on model simulations in Chapter 5)? It is my hope that by not attempting to eliminate green turtle harvesting altogether, but rather regulating it, the resource users will be more cooperative in reducing their harvest to a more sustainable level of take. In addition, I am hopeful that collaborative efforts can be initiated among NGO's, local community leaders, and government authorities to begin the process of developing alternatives to turtle fishing for local income. This approach will reduce pressure on green turtle populations

considerably in the region while facilitating the transition of turtle fishing communities to alternate sustainable means of generating income.

Methods

Model Structure

To evaluate the potential effect of changes in fishing mortality rates on a simulated green turtle population, I used a similar age-based matrix population model as was used in Chapter 5, with one principal exception. I split the large juvenile category into two groups, those that use the foraging grounds in Nicaragua and are exposed to the turtle fishery, and those that forage elsewhere in the greater Caribbean. This approach allowed me to manipulate specifically an estimate of fishing mortality rate for large juvenile green turtles exposed to the Nicaragua turtle fishery, the most intensive turtle fishery in the region. Furthermore, since the fishing grounds in Nicaragua are the principal feeding habitat for the Tortuguero green turtle population, management of this fishery could provide the greatest single relief to this turtle population. An additional change I made to the model structure from Chapter 5 was the addition of two age-classes to the model for a total of three adult age-classes to reflect the average remigration interval for Tortuguero adults (Carr et al. 1978) and acknowledge that maturing juveniles must survive the remigration interval to reproduce again. The life cycle for the simulated population is illustrated in Figure 6.1, and the resulting projection matrix can be found in Appendix B.

Demographic Structure and Model Parameterization

To determine the age-structure for the model I first separated the green turtle life cycle into stages, 1st-year post-hatching, small juveniles, large juveniles, maturing juveniles, and adults. These stages were then expanded into age-classes based on an estimated number of years in each stage (Figure 6.1, Table 6.1). The duration of the 1st-

Table 6.1. Initial parameters of four models used to simulate a green turtle population.

Age-class	Duration	Annual Survival	Fertility	Estimated Fishing Mortality
Model 1 (Proportion of lg juveniles that shift to Nicaragua habitat ($p = 0.70$, $\delta = 0.951$))				
1 st yr	1	0.80	0	-
small juveniles	14	0.85	0	-
large juveniles - Nicaragua	15	0.5537	0	0.486
large juveniles - other	15	0.814	0	0.10
maturing juveniles - Nicaragua	1	0.5537	48.6	0.486
maturing juveniles - other	1	0.814	71.5	0.10
adults	-	0.8207	24.0	0.1444 (95% attributed to Nicaragua)
Model 2 ($p = 0.90$, $\delta = 0.8872$)				
1 st yr	1	0.80	0	-
small juveniles	14	0.80	0	-
large juveniles - Nicaragua	15	0.5537	0	0.486
large juveniles - other	15	0.775	0	0.15
maturing juveniles - Nicaragua	1	0.5537	48.6	0.486
maturing juveniles - other	1	0.775	68.0	0.15
adults	-	0.8207	24.0	0.1444 (95% attributed to Nicaragua)
Model 3 ($p = 0.70$, $\delta = 0.9697$)				
1 st yr	1	0.80	0	-
small juveniles	14	0.85	0	-
large juveniles - Nicaragua	11	0.5537	0	0.486
large juveniles - other	11	0.814	0	0.10
maturing juveniles - Nicaragua	1	0.5537	48.6	0.486
maturing juveniles - other	1	0.814	71.5	0.10
adults	-	0.8207	24.0	0.1444 (95% attributed to Nicaragua)
Model 4 ($p = 0.90$, $\delta = 0.9026$)				
1 st yr	1	0.80	0	-
small juveniles	14	0.85	0	-
large juveniles - Nicaragua	11	0.5537	0	0.486
large juveniles - other	11	0.814	0	0.15
maturing juveniles - Nicaragua	1	0.5537	48.6	0.486
maturing juveniles - other	1	0.775	68.0	0.15
adults	-	0.8207	24.0	0.1444 (95% attributed to Nicaragua)

year post-hatching stage is one year, from the time of emergence to the completion of one year, which includes a portion of the pelagic, oceanic phase. The small juvenile stage includes two years in the pelagic, oceanic phase (for a total of approximately 3 years, Zug and Glor 1998 and Ehrhart and Witherington 1992) and 12 years in the shallow benthic feeding habitat (Bjorndal et al. 2000), comprising a total of 14 years for the small juvenile phase. As small juveniles complete their shallow benthic phase they migrate to other, probably deeper benthic feeding habitats (Bjorndal et al. 2000). The principal benthic feeding ground for large juvenile and mature green turtles from the Tortuguero population is in the offshore waters of Caribbean Nicaragua. As previously stated, I separated the large juvenile stage (including maturing juveniles) into two groups, one group that resides in Nicaragua and another that is dispersed into various other deep benthic feeding habitats. Because I separated large juveniles into two habitats, where they reside until maturity, instead of using a weighted mean approach (Chapter 5), population growth rates will be higher than those in Chapter 5. Because the duration of this stage is unknown, I used two durations in different simulations, 12 and 16 years at both habitats (each includes one year for maturing juveniles). This results in age-at-maturity of 28 and 32 years, respectively. Initial survival and fertility rates used in the simulations are presented in Table 6.1.

An assessment of the effects of changes in mortality attributed to fishing requires estimates of current fishing mortality rates. Total mortality (Z) is the sum of fishing mortality (FM) and natural mortality (NM) rates, and is related to survival probability (N) such that $N = e^{-Z}$, or $e^{-(FM + NM)}$. To estimate the fishing mortality rate of Tortuguero

adult females (FM_a), I estimated natural mortality rate (NM_a) based on the mean survival rate estimate of 0.9482 for an unexploited population of green turtles in Australia (Chaloupka and Limpus In press), thus, $NM_a = -\ln(0.9482)$, or 0.0532. I then estimated FM_a using the relationship between current Tortuguero adult female survival rate (0.8207, Chapter 4) and NM , thus, total current estimated $FM_a = (-\ln(0.8207)) - NM$, or 0.1444. Because Nicaragua is the primary location where green turtle fishing occurs in the western Caribbean, but not the only location, I separated total FM into Nicaragua fishing mortality (FMn_a) and all other (non-Nicaragua) fishing mortality (FMo_a). I used 0.95 as the proportion of FM_a attributed to the Nicaragua turtle fishery based roughly on the percent of tag recoveries of Tortuguero nesting females tagged from 1995 to 2001 that occurred in Nicaragua (500 of 513 recoveries, Caribbean Conservation Corporation unpublished data), thus, $FMn_a = 0.1401$, and $FMo_a = 0.0043$.

For the Nicaragua group of large juveniles, I used the mean survival rate estimate of 0.5537 from Chapter 4 to estimate FM for large juveniles (FM_j) in Nicaragua (FMn_j). I assumed a natural survival rate of 0.90 which results in a NM_j rate of 0.1054, and using the current survival estimate of 0.5537, $FMn_j = 0.486$. For large juveniles outside of Nicaragua, FM_j is unknown, thus I arbitrarily chose two rates, $FMo_j = 0.05$ and 0.10, to use in different simulations, assuming that FMo_j is considerably lower than FMn_j . In addition to estimates of FM_j , it was also necessary to estimate the proportion of large juveniles occurring in Nicaragua as this would affect the proportion of turtles transitioning into the two large juvenile groups and exposed to different mortality rates. As stated earlier (Chapter 5, Discussion), there is evidence that the primary foraging habitat for large juvenile green turtles in the western Caribbean is in the offshore waters

of Nicaragua, but the proportion of large Tortuguero juveniles in this foraging habitat is unknown. I assumed that the proportion (p) of Tortuguero large juveniles in Nicaragua is between 70% and 90%, and incorporated the lower and upper percentages into different simulations.

Fertility rates for the last year of the large juvenile stage (maturing juveniles, F_{mj}) and for adults (F_a) were determined as follows:

$$F_{mj} = S((CS)(CF)(NS)(PF)), \text{ and}$$

$$F_a = S((CS)(CF)(ES)(PF))/RI,$$

where S is annual survival rate for the age-class, CS is average clutch size, CF is average clutch frequency for a breeding season, ES is average emergence success, PF is the proportion of females produced and is assumed to be 0.50, and RI is the remigration interval. Bjorndal and Carr (1989) report mean CS at 112 eggs based on more than 2,500 clutches. CF is 2.8 clutches per season (Carr et al. 1978), ES is 0.56 using the average over three years reported by Horikoshi (1992), and RI is three years (Carr et al. 1978). As previously stated, fertility for adults was assigned to the third adult age-class, thus fertility is greater than zero only for the maturing juvenile age-class and the third adult age-class.

Model Implementation

Four models, each with a different set of initial parameters, were simulated; two were based on a 12-yr large juvenile stage duration and two on a 16-yr large juvenile stage duration (Table 6.1). Each pair was simulated based on a worst and best-case set of initial parameters, the difference in parameters from worst to best being the same for the two pairs. In each of the four models, I conducted simulations to evaluate three strategies: i) the percent reduction in fishing mortality rate attributed to Nicaragua

fisheries necessary for both large juveniles and adults to achieve $\delta = 1.0$ (Strategy 1), ii) the percent reduction in large juvenile fishing mortality rate attributed to Nicaragua fisheries necessary to achieve $\delta = 1.0$ with a 95% reduction in adult fishing mortality rate attributed to Nicaragua fisheries (Strategy 2), and iii) the percent reduction in adult fishing mortality rate attributed to Nicaragua fisheries necessary to achieve $\delta = 1.0$ with a 95% reduction in large juvenile fishing mortality rate attributed to Nicaragua fisheries (Strategy 3). Because size at maturity is variable (Carr and Carr 1970), it would be difficult from a management standpoint to reduce either large juvenile or adult FM by 100%. Thus, I used a fishing mortality reduction of 95% in an effort to be more realistic.

Change in Nicaragua Turtle Harvest

To estimate reduced harvest levels in Nicaragua that would allow a stable population growth rate, I used the proportional reductions in fishing mortality rates from the 12 model simulations (Results) and applied them to estimates of current annual harvest levels. Estimates of reduced harvest levels for females were based on recent harvest rates of 11,000 turtles/yr (Lagueux 1998, unpubl. data) and an extrapolation of size and sex data reported for the Nicaragua turtle fishery from 1994 to 1996 (Lagueux 1998). Reduced total harvest (males and females) was estimated by dividing the maximum take of large juvenile and adult females by the estimated proportion of each in the population based on fishery data. Because sex ratios are different in the northern (Región Autónoma del Atlántico Norte, RAAN) and southern (Región Autónoma del Atlántico Sur, RAAS) regions of the coast (Lagueux 1998), estimates of reduced take are presented separately for each region.

Results

Model Results

For Strategy 1, where Nicaragua fishing mortality rate was reduced equally for large juveniles and adults, the reduction in fishing mortality needed to achieve a population growth rate of 1.0 ranged from 60% to 89% (Table 6.2). For Models 1 and 2, the range in percent reduction of Nicaragua fishing mortality needed was approximately 10% (78.5% and 89%). For Models 3 and 4 where large juvenile stage duration was 12 years the range in percent reduction needed was larger at approximately 20% (60% and 79.5%).

For Strategy 2, where Nicaragua fishing mortality for adults was reduced by 95%, the reduction in large juvenile Nicaragua fishing mortality needed to achieve $R = 1.0$ ranged from 12% to 87% (Table 6.2). For Models 1 and 2 the range in percent reduction of fishing mortality was again fairly similar, 73% and 87%, however for Models 3 and 4 the reduction needed was very different, 12% and 75%.

Table 6.2. Percent reduction in Nicaragua fishing mortality rate (FM) needed to achieve $R = 1.0$ based on three strategies to reduce fishing mortality for each of four models (see Table 6.1). Strategy 1 is based on equal proportional reductions in both large juvenile (LJ) and adult (AD) FM, Strategy 2 is based on a 95% reduction in AD FM and variable reduction in LJ FM, Strategy 3 is based on a 95% reduction in LJ FM and variable reduction in AD FM. () = Reduced estimated fishing mortality rates based on percent reductions.

Model	Strategy 1		Strategy 2		Strategy 3	
	LJ	AD	LJ	AD	LJ	AD
1	78.5 (0.104)	78.5 (0.029)	73 (0.131)	95 (0.007)	95 (0.024)	0 (0.137)
2	89 (0.053)	89 (0.015)	87 (0.063)	95 (0.007)	95 (0.024)	48 (0.071)
3	60 (0.194)	60 (0.055)	12 (0.428)	95 (0.007)	95 (0.024)	0 (0.137)
4	79.5 (0.01)	79.5 (0.028)	75 (0.122)	95 (0.007)	95 (0.024)	0 (0.137)

For Strategy 3, where Nicaragua fishing mortality rate for large juveniles was reduced by 95%, the percent reduction in adult Nicaragua fishing mortality rate needed to achieve $R = 1.0$ was generally much lower (0 to 48%) than for large juveniles in Strategy 2 (12 to 87%). Model 2 gave the only result greater than 0%.

Change in Nicaragua Harvest

I converted the estimated reductions in fishing mortality rates (Table 6.2) based on results from the three strategies into a range of reduced harvest levels of females in the Nicaragua turtle fishery using a current harvest rate of 11,000 turtles/yr. For Strategy 1, reduced harvest levels from the four models ranged from 694 to 2,526 females, Strategy 2 ranged from 676 to 4,053 females, and Strategy 3 ranged from 1,167 to 2,037 females (Table 6.3). Strategy 3 gives the highest harvest level for Models 1, 2, and 4. The estimated total harvest (both males and females) broken down by region and by life stage, are presented in Table 6.4. Results indicate a minimum reduction in the Nicaragua turtle harvest of 5,499 turtles/yr is needed (Model 3, Strategy 2). However, a reduction of more than 9,900 turtles may be necessary (Model 2, Strategy 2).

Table 6.3. Estimates of reduced harvest levels of large juvenile (LJ) and adult (AD) female green turtles in Nicaragua based on four models with different initial parameters (see Table 6.1) and three strategies for reducing fishing mortality rates. For Strategy 1, Nicaragua fishing mortality was reduced equally for LJ and AD. For Strategy 2, Nicaragua fishing mortality was reduced by 95% for AD and varied for LJ. For Strategy 3, Nicaragua fishing mortality was reduced by 95% for LJ and varied for adults. All model results are based on achieving a population growth rate of 1.0.

Strategy	Model 1			Model 2			Model 3			Model 4		
	LJ	AD	Total	LJ	AD	Total	LJ	AD	Total	LJ	AD	Total
1	968	390	1358	495	199	694	1801	725	2526	923	371	1294
2	1215	91	1305	585	91	676	3962	91	4053	1125	91	1216
3	225	1812	2037	225	942	1167	225	1812	2037	225	1812	2037

Table 6.4. Estimates of total maximum allowable harvest based on results of estimated decrease in Nicaragua fishing mortality rates of large juvenile (LJ) and adult (AD) green turtles necessary to achieve $\delta = 1.0$. Four models with different initial model parameters were projected using three approaches (Strategies 1-3) to reducing Nicaragua fishing mortality rates of LJ and AD green turtles. RAAN = Región Autónoma del Atlántico Norte, RAAS = Región Autónoma del Atlántico Sur.

	Model			
	1	2	3	4
<u>Strategy 1</u>				
RAAN	1077	551	2004	1027
RAAS	1287	658	2394	1227
Total Allowable Harvest	2364	1209	4398	2254
<u>Strategy 2</u>				
RAAN LJ	626	301	2040	580
RAAN AD	134	134	134	134
RAAS LJ	985	474	3210	912
RAAS AD	117	117	117	65
Total Allowable Harvest	1862	1027	5501	1691
<u>Strategy 3</u>				
RAAN LJ	116	116	116	116
RAAN AD	2690	1399	2690	2690
RAAS LJ	182	182	182	182
RAAS AD	2337	1215	2337	1293
Total Allowable Harvest	5325	2912	5325	4281

Discussion

This study is the first to estimate levels of maximum harvest of green turtles from the Tortuguero green turtle population in the Nicaragua green turtle fishery. The estimates calculated in this study are maximum levels based on the concept of sustained yield harvesting where the harvest rate is equal to the population's rate of increase in the absence of harvesting, hence, harvesting maintains the population at a stable state (Caughley and Sinclair 1994). However, the modeling approach used in this study does not account for density-dependent effects or any temporal variation in demographic

processes associated with the environment. Variability in demography related to environmental variability for processes such as growth rates and breeding behavior are known to occur in some sea turtle populations (Limpus and Nicholls 1988, Limpus and Chaloupka 1997, Bjorndal et al. 2000, Chaloupka 2001, Solow et al. 2002). However, environmental and demographic data are currently insufficient to incorporate temporal variability into modeling the Tortuguero population. In the absence of such data, the use of a deterministic model where demographic processes are constant to evaluate management options provides a starting place to begin regulating the use of green turtles in Nicaragua to minimize harvest pressure on the Tortuguero green turtle population. As additional demographic data and the effect of environmental influences on Caribbean green turtle populations are better understood, more complex models can be developed.

Based on the results from each simulation and an estimated current harvest rate of 11,000 turtles/yr, the annual harvest of males and females in Nicaragua should be reduced to a maximum allowable harvest of between 1,027 and 5,501 turtles/yr (Table 6.4). If the current annual harvest rate in Nicaragua is lower than 11,000, the estimated maximum allowable harvest will be less since it is based on a proportional reduction of the current harvest. While the range of sustained yield estimates is quite large, it reflects both the effect of applying different strategies to reducing harvest levels and our uncertainty in some model parameters. For example, a change in the duration of the large juvenile stage by four years (16 to 12 years) had a considerable affect on the estimated sustained yield for Models 1 (16 yr duration) and 3 (12 yr duration), where the difference in estimates was as much as 3,639 turtles, and less so for Models 2 (16 yr duration) and 4 (12 yr duration) where the difference was as much as 1,369 turtles (Table 6.4). Thus,

data on the average duration of the large juvenile stage would considerably improve the estimates of sustained yield for the Nicaragua turtle fishery. Additionally, information on the proportion of large juveniles that use the Nicaragua feeding grounds and fishing mortality rates of large juveniles in other foraging areas are needed because these parameters affect the survival rates of the two large juvenile groups.

Results from the three strategies to reducing fishing mortality attributed to the Nicaragua turtle fishery show that the highest estimated sustained yield is achieved by reducing large juvenile Nicaragua fishing mortality rate by 95% and reducing adult fishing mortality between 0 and 48% (Strategy 3), with the exception of Model 3. Assuming that adults are more valuable than immatures to population growth (Chaloupka 2002), the results of Strategy 3 were initially somewhat surprising because Strategy 2 protects more adult females than Strategy 3 by reducing their Nicaragua fishing mortality rate by 95%. However, a 95% reduction in adult female fishing mortality rate (from 0.137 to 0.007) results in a minimum decrease in the harvest of approximately 1,700 turtles (based on a current harvest rate of 11,000 turtles/yr, of which about 16.5% are adult females, Lagueux 1998), whereas a 95% reduction in large juvenile fishing mortality rate (from 0.486 to 0.024) results in a minimum decrease of approximately 4,200 turtles (approximately 41% of 11,000 turtles in the harvest are large juvenile females). Thus, it is logical that the same proportional change for either life stage would have a different impact on the estimated harvest levels. Even so, differences in the estimated total sustained yield between Strategy 2 and 3 are considerable at more than 2,200 turtles among three of the four models (Table 6.4). It is important to consider that

different strategies to reduce fishing mortality rates may affect estimated levels of take so that the impact on resource users affected by reduced harvest levels can be minimized.

Because Nicaragua is one of the poorest countries in the Western Hemisphere (Central Intelligence Agency 2002), many of its people are sorely lacking sufficient income-generating activities. In Strategy 3, estimates of sustained yield range from 3,314 to 5,324, compared to estimates as low as 1,057 in Strategy 2. While the highest sustained yield was estimated in Model 3 of Strategy 2, Strategy 3 more consistently estimates the highest yields across models. Thus, given the uncertainty of some demographic values, the approach used in Strategy 3 to reduce fishing mortality rates in the Nicaragua fishery is more likely to minimize the hardship on resource users while having the same impact as the other strategies on reducing the pressure on the turtle population.

Estimates of sustained yield in this study are somewhat optimistic when compared to other modeling studies that have examined harvesting sea turtle populations. A study evaluating harvest levels of Oman green turtles shows that only a few hundred animals in the later life stages may be harvested without causing the simulated population to decline (Siddeek and Baldwin 1996). Studies of Australia loggerhead (Heppell et al. 1996*b*) and green turtle (Chaloupka 2002) populations show that a harvest of even a small number of large turtles (100 subadult and adult loggerheads, Heppell et al. 1996*b*; 165 adult greens, Chaloupka 2002), may cause population declines. The studies of Australia green and loggerhead turtles were based primarily on data from long-term population studies and thus should reasonably portray the potential effects of harvest on these populations. However, simulations in both cases were based on populations that exhibited stationary

population growth ($\lambda = 1.0$), whereas the Tortuguero nesting population has shown strong evidence of increasing for more than 20 years (Bjorndal et al. 1999). Thus, production in the Tortuguero population may be much higher than in either of the Australia turtle population studies. On the other hand, higher harvest levels estimated in this study could be a result of using survival estimates that may be higher than average rates for 1st year post-hatching and/or a large juvenile stage duration that is too short. Unfortunately, no data are available on survival rates of Caribbean green turtles after emergence and in the pelagic phase, although one study on Australia green turtle hatchlings reports a range of predation rates of between 0 and 81% (Gyuris 1994). Sufficient growth rate data for large juveniles in the Caribbean are not available, thus there are no empirical estimates of mean stage duration. Mean duration of Australia subadult (similar to the large juvenile stage in this study) green turtles is estimated at 19 years (Chaloupka 2001), three years longer than the maximum duration used in simulations of Tortuguero green turtles. However, growth rates of Australia green turtles are slower than for Caribbean green turtles based on comparisons of growth rates of smaller green turtles among the two regions (Limpus and Chaloupka 1997, Bjorndal et al. 2000). Thus, large juvenile stage durations used in this study may be reasonable, although studies of large juvenile growth rates are needed to better understand their life history and more precisely portray population dynamics.

Harvest rates for the green turtle fishery in Nicaragua should not exceed the rate at which the source population is increasing. Unfortunately, the only information we have on the rate at which the Tortuguero population is changing comes from one segment of the population, nesting females (Bjorndal et al. 1999, Troëng et al unpubl. manu.).

With increased harvest pressure from the Nicaragua turtle fishery since the early 1990s aimed at both immatures and adults (Lagueux 1998) and the long age-to-maturity for the species, the true growth rate of this population will remain unknown until the age distribution stabilizes or census data on all life stages are available. In the absence of such information, sustained yield estimates generated in this study, although imprecise, provide a reasonable target for resource users and managers to begin reducing and regulating the green turtle harvest in Nicaragua. A conservative approach should be used to identify maximum harvest levels from the range of estimates provided in this study (Table 6.4). I suggest that the model with the most conservative parameters, Model 2 (Table 6.1), be used as a starting place to develop quotas for the Nicaragua turtle fishery. In addition, I recommend Strategy 3 be used to allow the highest level of sustained yield to minimize the impact of reduced harvest levels on the turtle fishing communities in Nicaragua. Recommendations for specific reductions in harvest levels and how this reduction can be achieved are provided in the following chapter.

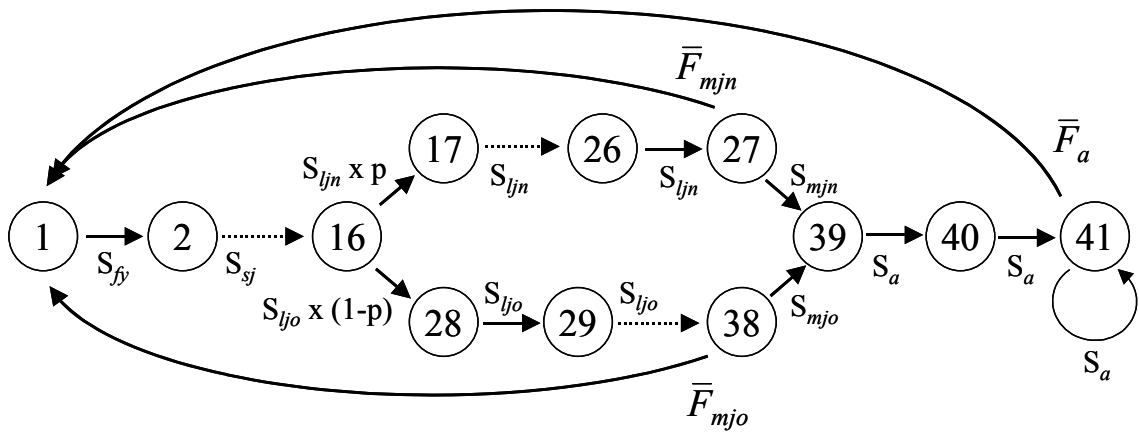


Figure 6.1. An age-structured life cycle graph for the Tortuguero, Costa Rica, green turtle population. S = survival probability, p = proportion of population transitioning to Nicaragua habitat, F_i = fertility based on a birth pulse, post-breeding census, fy = first year post hatching, sj = small juvenile, ljn = large juveniles that use Nicaragua foraging habitat, ljo = large juveniles that use foraging habitats other than Nicaragua, mjn = maturing juveniles that use Nicaragua foraging habitat, mjo = maturing juveniles that use foraging habitats other than Nicaragua, a = adult.

CHAPTER 7 RECOMMENDATIONS

Introduction

Green turtles (*Chelonia mydas*) have provided a valuable source of protein and much needed income for human inhabitants of many tropical countries for hundreds of years. In many cases, harvest levels for export and local use have exceeded sustainable levels and resulted in severe declines or extirpation of populations on a global scale (for a review of their current status see Seminoff In press). Green turtles are classified by the World Conservation Union (IUCN) as endangered species, and are listed on Appendix I of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). In addition, they are recognized by other international treaties (e.g., SPAW Protocol, Protocol to the Cartagena Convention Concerning Specially Protected Areas and Wildlife; and IAC, Inter-American Convention for the Protection and Conservation of Sea Turtles) and national laws to provide them with some protection. Despite recognition of their depleted status, Caribbean green turtles continue to be harvested commercially and for subsistence in many nations throughout the Caribbean (Fleming 2001).

In recent decades, exploitation of marine turtles appears to have declined throughout the northern Caribbean (Fleming 2001). In Nicaragua, however, commercial harvest levels have increased over the past decade to levels not seen since the 1970s (Nietschmann 1973, Lagueux 1998). The resurgence of this marine turtle fishery prompted concern for the future outlook of the Tortuguero, Costa Rica, green turtle

population because the fishery in Nicaragua occurs in what is believed to be the principal foraging habitat for large juvenile and adult green turtles from this population. Although reduced harvest pressure on this green turtle population from 1977 to the early 1990s (resulting from the closure of turtle processing plants and a civil war in Nicaragua, and increased protection of reproductive animals at the nesting beach in Costa Rica) enabled the population to increase, the current level of harvest of approximately 11,000 turtles/yr has been considered a serious threat (Lagueux 1998). In addition, this intensive harvest is unregulated and no attempt has been made by resource management authorities in Nicaragua to evaluate its impact on green turtles. In this study, I collected mark-recapture data and constructed matrix population models to evaluate the current status of the Tortuguero green turtle population. I further explored the potential for changes in harvest levels in the Nicaragua turtle fishery.

My conclusion is that the population of green turtles that originates at the Tortuguero rookery is probably in decline. Although this appears to contradict the increasing trend in nesting emergences reported by Bjorndal et al. (1999) for the Tortuguero nesting population, in fact it does not. There is no doubt that nesting activity has increased over the past 20 years or more, however, this does not necessarily reflect either the status of the population overall, or certain segments of the population not visible on the nesting beach. Green turtles are long-lived, so perturbations to some segments of the population on the foraging grounds may not manifest themselves in the short-term on the nesting beach. Moreover, emergences on the nesting beach fluctuate widely from one year to another due to changes in reproductive periodicity of individual females. Thus, the effect of the renewed intensive harvest in Nicaragua may not become

visible on the nesting beach for many years. For this reason, the use of nesting beaches as index sites to determine the status of sea turtle populations should be done with caution. Currently, the Marine Turtle Specialist Group of the IUCN is using nesting beaches as index sites to assess sea turtle populations, and current threats to other segments of the populations are not quantitatively considered.

Results from my study indicate that major reductions in the harvest in Nicaragua are needed. To do so, however, is likely to cause hardships to the turtle fishing communities in Nicaragua unless turtle fishers are able to diversify their income-generating activities. Numerous meetings were held in turtle fishing communities to discuss sea turtle conservation issues. During these meetings, community members identified the need to develop alternatives to harvesting turtles for income. Alternative income generating activities suggested by community members include development of other fisheries, agriculture, and animal husbandry. These and other suggestions have been outlined in the recently developed "Draft Management Strategy for Sea Turtle Conservation on the Caribbean Coast of Nicaragua" (Lagueux et al. 2002). This is the first phase of a larger project to develop and implement a management plan aimed at the conservation of sea turtles foraging or nesting along Nicaragua's Caribbean coast. Additional research and identification of funding sources will be needed to assess the feasibility of these income generating activities and provide the seed money necessary to develop those activities deemed most feasible. Regulating and controlling the use of green turtles in Nicaragua is a multifaceted issue. It requires not only the restricted use of this resource so that healthy turtle populations can be maintained, but also aiding resource users in the development of a diverse base of income-generating activities. How

reductions in harvest levels will be implemented will have to be determined by community members and resource management authorities. However, consideration for communities most heavily dependent on turtles and those that receive assistance to develop alternatives should be weighed in the decision making process.

Recommendations

Based on the results of this study, I make the following recommendations.

1. Reduce the harvest of green turtles in the Nicaragua turtle fishery. Ideally, annual harvest levels should not exceed 298 large juvenile turtles/yr and 2,614 adults/yr based on Strategy 3, Model 2 (Chapter 6). Harvest limits should be adjusted if declines in capture per unit effort or nesting emergences become apparent. Harvest limits also should be updated when more precise demographic information is available and can be incorporated into future model simulations. To allow an increase in the green turtle population, further reductions in harvest levels will be needed. A size cut-off of approximately 95 cm curved carapace length can be used as an approximate size to distinguish between most large juvenile and adult green turtles. The size cut-off is based on measurements of adult females at Tortuguero, Costa Rica (Mangel and Troëng 2001), and results presented by Lagueux (1998) on size and reproductive condition of green turtles captured in Nicaragua. Potential approaches to regulate the use of green turtles in Nicaragua are reviewed in the following section.
2. Develop a management plan to regulate the use of green turtles in cooperation with the efforts of other nations (such as Costa Rica and Panama) to conserve the Tortuguero green turtle population, and possibly other green turtle populations in the region. A sea turtle management plan should be developed as part of a collaboration among all sea turtle stakeholders in Nicaragua, including turtle fishing communities, local government authorities, non-government organizations, and scientific advisors.
3. Alternative income-generating activities for turtle fishers in Nicaragua need to be developed. Members of the turtle fishing communities need to play a central role in the development of alternatives. A feasibility assessment of recommended alternative income-generating activities is needed and should take into account acceptability of alternatives to the turtle fishing communities, economic benefits, environmental impacts, and sustainability.
4. Additional research is needed to better understand green turtle population dynamics and improve the precision of model simulation results. More data are particularly needed to: a) determine growth rates of large juveniles in order to estimate stage duration and obtain better estimates of age-at-maturity; b) estimate survival rates for small juveniles in other developmental habitats used by the Tortuguero

population in order to incorporate the range of estimates into model simulations; c) estimate fishing mortality rates in areas used by large juveniles outside of Nicaragua in order to improve estimates of sustained yield within Nicaragua; and d) estimate temporary and/or permanent emigration rates from the Nicaragua foraging ground in order to improve survival rate estimates, which will also improve estimates of sustained yield.

5. Updated information on harvest levels from 2000 to 2002 is needed. Sustained yield estimates are based on a proportional reduction in harvest rates, which may have increased or decreased since the late 1990s.
6. Mark-recapture studies should be expanded to include the central and northern turtle fishing areas in Nicaragua so that additional survival rate estimates can be derived and used in future model simulations.
7. Other possible indicators of the status of the Tortuguero green turtle population should be monitored. These include: a) Capture per unit effort which could provide some evidence of increases or decreases in the target species. (As previously stated, however, this indicator can be misleading due to hyperstability.) b) Trends in number of emergences on the nesting beach, which will be useful over the long-term. c) Changes in the mean size of adult females, which may indicate changes in the average life span of adults (since green turtles continue to grow, although minimally, after they reach maturity). d) The proportion of neophyte nesters to remigrating nesters, which can indicate changes in the reproductive population. None of these potential indicators, however, is completely reliable on its own to determine the status of the Tortuguero green turtle population. Taken within the context of other indicators they may provide supporting evidence for the status of the population. Thus, monitoring changes in all of these potential indicators should allow changes to be made to resource use before severe depletion occurs.

Potential Management Options To Regulate The Harvest In Nicaragua

There are a number of approaches that might be used to manage the harvest of green turtles in Nicaragua, such as the use of closed seasons or size and/or sex restrictions. The advantages and disadvantages of different approaches are discussed here within the context of how effective they might be at mitigating impacts to the turtle populations, the feasibility to enforce regulations in Nicaragua, and the likelihood of acceptance by the turtle fishing communities. The approaches summarized here are described by Lagueux and Campbell (2002).

Closed season. *Closed seasons* can be used to restrict the time when harvesting can occur. Currently, Nicaragua has a closed season from 1 March to 30 June. By law this temporary closed season restricts the harvest, consumption, or sale of green turtles on the Caribbean coast during the designated time period (Resolución Ministerial 007-99). The closed season, however, is unenforced and only restricts the sale of turtles in the major port towns of Bilwi (Puerto Cabezas), Bluefields, and Corn Island. Currently the closed season has no impact on the number of turtles harvested or sold in the local communities. Closed seasons have the potential to be highly effective because the overall harvest can be reduced by limiting the time available to fishers to extract turtles. Also, enforcement of closed seasons could be relatively simple because the transportation and butchering of turtles is not easily done clandestinely. For closed seasons to be effective, better enforcement is needed. Currently, regulating agencies in Nicaragua often allow continued take and sale of turtles during the closed season, rendering it an ineffective means of regulating the turtle fishery at the present time.

Community leaders appear willing to accept the enforcement of a closed season. Community members have suggested that large fines be imposed on violators and that strict enforcement by the Navy, Police, and the ministry of natural resources (Ministerio del Ambiente y Recursos Naturales, MARENA) are needed. For a closed season to be effective, police and military personnel should be involved in enforcing the closed season, and trained inspectors should be assigned to each of the principal turtle fishing communities (Awastara, Dakura, Río Grande Bar, Sandy Bay Sirpi, Sandy Bay, and Tasba Pauni). The appropriateness of the time and duration of the current closed season

should be investigated to determine its effectiveness for protecting reproductive animals, particularly females, and reducing harvest levels.

Restrict catch according to size and/or sex. *Size and/or sex restrictions* can be an effective means of reducing harvest pressure on foraging aggregations. They have the potential to provide better protection for segments of populations critical to population growth, such as subadults and adults. Community members have indicated that they would accept restrictions on size and/or sex of harvested green turtles. Size restrictions could be relatively easily enforced by inspectors in the principal turtle fishing communities. As with *closed seasons*, however, enforcement will be critical to its effectiveness.

Quotas. *Quotas* to restrict the harvest of turtles by each community have the potential to be highly effective at reducing the overall harvest. Enforcement of quotas is relatively simple with the use of inspectors and involvement of MARENA and police. Establishment of quotas for each community may be more problematic because comments by community members thus far indicated they may be overly optimistic about the number of green turtles they would be allowed to harvest. They are in agreement, however, to use a quota system.

Zoning. *Spatial restrictions* would involve zoning fishing grounds as areas of either no use, limited use, or restricted use. This approach is not likely to effectively reduce harvest levels because green turtles are highly migratory and move long distances between nesting and foraging areas. They may also use multiple resting and feeding sites, exposing them to different levels of vulnerability within a short period of time. Enforcement of zoning would be difficult because it would require patrolling large areas

of open sea by boat. Nevertheless, community members have expressed a willingness to establish spatial restrictions on turtle fishing.

Permitting system. *Permits* to harvest green turtles might restrict the number of boats or fishers involved in turtle fishing. On its own, however, it would probably not regulate the number of turtles harvested since the same boat could be used year around to capture turtles. Enforcement would be difficult without inspectors at sea and in the communities to identify violators. In general, community members were not in favor of a permit system, but some indicated that whatever was necessary would be accepted.

Monetary incentives. Monetary-based incentives have been suggested from outside Nicaragua as possible mechanisms to close or regulate the turtle fishery. A buy-out would compensate turtle fishers in exchange for their agreement to stop harvesting turtles. Based on the results of this study, however, I do not believe it is necessary to close the fishery in order to achieve stable population growth, rather, the harvest needs to be reduced and regulated. A less stringent monetary incentive to reduce harvest levels could be employed. In general, I do not believe that monetary incentives represent a viable strategy for this system because they create dependency and do not encourage development of responsible and sustainable natural resource use by local stakeholders. Indeed, economic incentives could even discourage resource users from developing long-term solutions to socioeconomic issues. Lack of regulatory authorities and enforcement agencies on the Caribbean coast of Nicaragua would also make compensation programs ineffective and unlikely to reduce the harvest of green turtles; and possibly result in additional social conflict, such as animosities between and among communities and their members that do or do not participate in an incentive program.

The use of any single approach is likely to be less effective than a combination of approaches. For example, the use of permits to allow individual fishers to harvest might be combined with a quota system so that the harvest would be limited to a specified number of turtles per boat or captain. Quotas might also be used in conjunction with size and/or sex restrictions so that the harvest has the least impact on the most valuable animals in the population. A closed season can also be combined with a quota and/or permit system. The primary concerns when establishing the mechanisms to regulate the green turtle harvest in Nicaragua are that resource users are involved in managing resource use, the harvest is not detrimental to the turtle population, and enforcement is feasible.

APPENDIX B
PROJECTION MATRIX FOR CHAPTER 6 MODELS (BASED ON MODELS 3 & 4)


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Each row and column represents a single year. The parameters for the first large juvenile age-class (column 16) are calculated as $S_{ljn} \times p$ (row 17) and $S_{ljo} \times 1 - p$ (row 28), respectively, where p is the proportion of large juveniles that use the Nicaragua foraging habitat. S = survival, F = fertility, fy = first year post-hatchings, sj = small juveniles, ljn = large juveniles in Nicaragua, ljo = large juveniles in other habitats, mjn = maturing juveniles in Nicaragua, mjo = maturing juveniles in other habitats, a = adults.

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BIOGRAPHICAL SKETCH

Cathi Campbell was born 10 August 1959 in Dunedin, Florida. She grew up with five siblings in Southern Pines, North Carolina. She graduated from Pinecrest High School in 1978 and graduated from the University of North Carolina at Greensboro with a B.S. degree in physical education. She supervised high school work groups for five summers for the Student Conservation Association which kept her close to her interest in wildlife. After receiving her teacher's certification she began teaching in the North Carolina public school system in 1986. Her interest in working with endangered species prompted her to volunteer for a sea turtle research project in Costa Rica in the summer of 1988. The following year she enrolled in the wildlife ecology program at the University of Florida. She received her master's degree from the University of Florida in 1994.