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**DEMOGRAPHIC AND CONSERVATION IMPLICATIONS OF ALTERNATIVE FORAGING
STRATEGIES IN JUVENILE LOGGERHEAD TURTLES (*CARETTA CARETTA*)
OF THE NORTH PACIFIC OCEAN**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

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ABSTRACT

DEMOGRAPHIC AND CONSERVATION IMPLICATIONS OF ALTERNATIVE FORAGING STRATEGIES IN JUVENILE LOGGERHEAD TURTLES (*CARETTA CARETTA*) OF THE NORTH PACIFIC OCEAN

S. HOYT PECKHAM

This research investigated key aspects of juvenile loggerhead ecology using a combination of satellite telemetry, fisheries observations, strandings surveys, and diet studies. Though linked both theoretically and thematically, this research was divided into three discrete chapters.

In the first chapter, I used a combination of satellite telemetry and fisheries observations to identify loggerhead high-use areas off the coast of Baja California Sur, Mexico. I used fisheries observations to assess levels of bycatch mortality in local small-scale fisheries. I found that loggerheads frequented a very small area in the Bight of Ulloa at very high densities. I also found that bycatch rates were problematically high in local small-scale fisheries and that they rivaled those reported for industrial scale fisheries spanning the entire North Pacific basin.

In my second chapter, I assessed anthropogenic mortality of endangered North Pacific loggerhead turtles in the coastal waters of Baja California Sur (BCS) through the synthesis of three sources: 1) intensive surveys of an index shoreline from 2003-2007, 2) bimonthly surveys of additional shorelines and towns for stranded and consumed carcasses from 2006-7, and 3) bycatch observations of two small-scale fishing fleets. Through five years of daily surveys of an index shoreline I found that loggerhead carcasses are beachcast along that coast at the highest rates reported worldwide. Through fisheries observations I found that bycatch and mortality rates of loggerheads in both local gillnet and longline fisheries are 1-2 orders of magnitude higher than anywhere else reported worldwide and concluded that conservation action is urgently needed.

In my third chapter, I compared habitat selection, movement, size frequency, and diet between juveniles at the coast of Baja California Sur, Mexico (neritic) with those observed in the Central North Pacific (oceanic). Oceanic juveniles traveled significantly further, faster and straighter and experienced lower SST and surface chlorophyll-a concentrations. These findings plus results published elsewhere suggest that neritic juveniles realize higher growth and eventual fecundity rates. Demographic modeling that I conducted suggests however that small advantages in survivorship for oceanic juveniles may balance the large disadvantages in growth and fecundity that result from the oceanic strategy.

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Small-Scale Fisheries Bycatch Jeopardizes Endangered Pacific Loggerhead Turtles

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High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003-7

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Demographic implications of alternative foraging strategies

in juvenile loggerhead turtles (Caretta caretta) of the North Pacific Ocean

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INTRODUCTION

Non-random habitat use and its relationship with individuals' performance and the dynamics of populations are fundamental to our understanding of ecology. For example, the fitness consequences of habitat selection have been key to the development of core ecological theory including the niche concept (Hutchinson 1957; Vandermeer 1972), optimal foraging (MacArthur and Pianka 1966; Fretwell and Lucas 1970; Charnov 1976; Orians and Pearson 1979) and source–sink dynamics (Pulliam 1988). Nearly all of these theories are built on the assumption that individuals within a species or population are ecologically equivalent, using population averages of factors such as habitat selection to identify niches and optima. There are obvious reasons for this - pioneering ecologists were balancing limited empirical data and limited analytical techniques with a quest for theoretical generality.

But more recent work has revealed that there is broad intraspecific variation in characteristics such as habitat choice between individuals within populations. Specialization and individuality are increasingly recognized to play important roles in determining the fitness of individuals and dynamics of populations (Bolnick et al. 2003; Estes et al. 2003; Tinker et al. 2007). Another body of work focuses on resource polymorphisms, defined as the occurrence of discrete morphs within a population (Skulason and Smith 1995; Smith and Skulason 1996). Differences in the

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behavior or morphology of these morphs within populations can produce differential niche use and foraging biology. Smith & Skulason's 1995 review of the subject showed such polymorphisms to be common in fish and avian taxa. Both literatures show that intraspecifc variation is widespread and can affect individuals' perfomance and drive whole populations' dynamics.

Behavioral examples of intraspecific variation concerning habitat selection include populations of both red deer and western gulls which show individual variation in habitat and diet selection (Clutton-Brock et al. 1982; Annett and Pierotti 1999). These differences between individuals produce corresponding differences in individual performance and are thought to affect population dynamics.

Studies such as these show the potential importance of intraspecific variation for understanding the ecology of the individuals and populations we study. This is especially true in the case of marine megafauna. Their large geographic ranges and long lives present great potential for the development of intraspecific variation. Elucidating this variation could prove especially important for understanding their ecology, population dynamics, and for informing their conservation. Since marine megafauna are long-lived, slow-growing, and late to reproduce, their population growth is particularly sensitive to changes in growth and mortality of older juveniles and adults, and they are predisposed to demographic vulnerability (Crowder et al. 1994; Crouse 1999; Heppell et al. 1999). The demographic vulnerability resulting

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from their slow-life histories has lead to the decline of most of the migratory marine megafauna populations for which abundance indices are available, including predatory fish and sharks (Baum et al. 2003; Myers and Worm 2003), tuna (Block et al. 2005), seabirds (Weimerskirch et al. 1997), cetaceans (Caswell et al. 1999; Estes 2007) and sea turtles (Spotila et al. 2000). Despite the demographic importance of large juveniles, the ecology and life history of juvenile megafauna remain poorly understood for large marine vertebrates.

Delayed maturity, high mobility, and freedom from having to return to a central location to reproduce enable juvenile migratory megafauna to choose among ocean-wide habitats and foraging strategies. Because prey availability, predation risk, and other factors often vary among habitats, differential habitat use and corresponding foraging strategies may result in differential growth, survival and ultimately fecundity among individuals of the same species or population (Skulason and Smith 1995; Bolnick et al. 2003). Sustained variation in the foraging strategies of juveniles and their resulting vital rates could have profound implications for the demography and conservation of migratory megafauna.

Loggerhead sea turtles exhibit several life history patterns that make them useful subjects for examining the effects of alternative foraging strategies. During their extremely long juvenile life stage that lasts upwards of three decades (Snover 2002; Heppell et al. 2003), the animals are opportunistically omnivorous and capable of

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transoceanic movements: they have no parental care or social structure; and they are not tied to a central location for reproduction, enabling them to choose from an ocean wide range of habitats (Bolten 2003). As juveniles, loggerheads use both oceanic and neritic habitats (Pitman 1990; Polovina et al. 2000; Bolten 2003; McClellan and Read 2007). I investigated alternative foraging strategies in juvenile loggerhead turtles in order to evaluate potential effects on individual perfomance and resulting population dynamics as well as to evaluate their bearing on conservation opportunities.

On another front, based on the success of MPAs for coastal populations (Halpern and Warner 2002), place-based conservation has been proposed to protect pelagic predators (Norse et al. 2005). Though pelagic species have great ecological, cultural, and economic importance, they have been even more poorly managed and have experienced more severe declines than many coastal fisheries. Unfortunately, establishing MPAs for pelagic predators is inherently difficult because of their vast ranges and complex life histories; long-lived and highly mobile, pelagic predators can utilize a variety of habitats that span ocean basins during their long lives, precluding comprehensive population-level protection.

As an alternative, MPAs focused on regions where pelagic predators concentrate at vulnerable life history stages (i.e. breeding and nursery habitats, etc.) have been advocated (Norse et al. 2005). This approach requires an understanding of the

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physical and biological processes that concentrate key species to select temporal/spatial closures that will reduce overharvest and minimize bycatch of large pelagic predators (e.g. sharks, billfish, tuna, sea turtles, seabirds, and marine mammals; reviewed in Gerber et al. 2005). While protected areas focused on vulnerable life history stages have the promise to yield conservation benefits, there is no theoretical framework for the selection, design, and efficacy of MPAs for pelagic predators (Hooker and Gerber 2004), beyond "drawing lines around the features" Norse et al. (2005). To develop life-history based MPA models that can be realistically used by managers, advances in biologging technology that provide detailed information on the long-term movement patterns of pelagic predators at various life history stages over large spatial scales must be used (Block et al. 2001; Etnoyer et al. 2006). In addition to evaluating the potential importance of alternative juvenile strategies I used satellite telemetry and a combination of bycatch and stranding assessments to identify turtle high-use areas and high conservation leverage opportunities where MPAs could result in important protection.

My dissertation research focuses on information that is needed to conserve North Pacific loggerhead turtles specifically and marine megafauna in general. I have attempted to link these applied data to key elements of ecological theory through three chapters. In my first chapter, I used a combination of satellite telemetry and fisheries observations to identify loggerhead high-use areas off the coast of Baja California Sur, Mexico and assess levels of bycatch mortality in local small-scale

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fisheries. In my second chapter, I assessed anthropogenic mortality of endangered North Pacific loggerhead turtles in the coastal waters of Baja California Sur (BCS) through the synthesis of three sources: 1) intensive surveys of an index shoreline from 2003-2007, 2) bimonthly surveys of additional shorelines and towns for stranded and consumed carcasses from 2006-7, and 3) bycatch observations of two small-scale fishing fleets. In my third chapter, I compared habitat selection, movement, size frequency, and diet between juveniles at the coast of BCS Mexico (neritic) with those observed in the Central North Pacific (oceanic).

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PLoS one

Small-Scale Fisheries Bycatch Jeopardizes Endangered Pacific Loggerhead Turtles

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Background. Although bycatch of industrial-scale fisheries can cause declines in migratory megafauna including seabirds, marine mammals, and sea turtles, the impacts of small-scale fisheries have been largely overlooked. Small-scale fisheries occur in coastal waters worldwide, employing over 99% of the world's 51 million fishers. New telemetry data reveal that migratory megafauna frequent coastal habitats well within the range of small-scale fisheries, potentially producing high bycatch. These fisheries occur primarily in developing nations, and their documentation and management are limited or non-existent, precluding evaluation of their impacts on non-target megafauna. *Principal Findings/Methodology.* 30 North Pacific loggerhead turtles that we satellite-tracked from 1996–2005 ranged oceanwide, but juveniles spent 70% of their time at a high use area coincident with small-scale fisheries in Baja California Sur, Mexico (BCS). We assessed loggerhead bycatch mortality in this area by partnering with local fishers to 1) observe two small-scale fleets that operated closest to the high use area and 2) through shoreline surveys for discarded carcasses. Minimum annual bycatch mortality in just these two fleets at the high use area exceeded 1000 loggerheads year^{-1}, rivaling that of oceanwide industrial-scale fisheries, and threatening the persistence of this critically endangered population. As a result of fisher participation in this study and a bycatch awareness campaign, a consortium of local fishers and other citizens are working to eliminate their bycatch and to establish a national loggerhead refuge. *Conclusions/Significance.* Because of the overlap of ubiquitous small-scale fisheries with newly documented high-use areas in coastal waters worldwide, our case study suggests that small-scale fisheries may be among the greatest current threats to non-target megafauna. Future research is urgently needed to quantify small-scale fisheries bycatch worldwide. Localizing coastal high use areas and mitigating bycatch in partnership with small-scale fishers may provide a crucial solution toward ensuring the persistence of vulnerable megafauna.

INTRODUCTION

Though the unintended catch *(bycatch)* of industrial-scale fisheries can cause declines in migratory megafauna including seabirds, marine mammals, and sea turtles [1–7], the bycatch of small-scale fisheries has been overlooked. Small-scale fisheries, including artisanal, traditional and subsistence fisheries, occur in coastal waters worldwide, employing over 99% of the world's 51 million fishers [8]. But bycatch assessment and mitigation has focused on industrial rather than small-scale fisheries because the magnitude of industrial operations can yield high total bycatch, and data have not been available for small-scale fisheries [9].

Small-scale fisheries occur primarily in developing nations, and their documentation and management are limited or non-existent [10,11], precluding evaluation of their impacts on non-target megafauna in coastal waters. New telemetry data reveal that migratory megafauna frequent coastal high use areas well within the range of small-scale fisheries, potentially producing high bycatch mortality with grave conservation consequences for vulnerable populations [12,13].

Because many migratory megafauna are declining yet have ecological, economic, and cultural importance [5,14,15], assessing and mitigating bycatch that threatens them is a global conservation priority [4,6]. Many species of migratory megafauna have delayed reproduction and low fecundity, making their populations vulnerable to bycatch of reproductively-valuable, late juvenile and adult stages [16], especially where they overlap with intense fisheries.

As a case study, we quantified the impacts of small-scale fisheries bycatch on the North Pacific loggerhead turtle population. North

Pacific loggerheads nest exclusively in Japan, and annual censuses indicate as much as a 90% decrease in nesting females within the past three generations to fewer than 1000 yr^{-1}, qualifying the population for critically endangered status [17]. Their juvenile stage lasts several decades during which turtles can migrate across the North Pacific [18,19]. Extensive telemetry studies have recently revealed important foraging habitat for juvenile loggerheads in the central North Pacific [20,21], and high levels of

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bycatch have been documented where industrial-scale fisheries overlap with this habitat both historically in drift gillnets [22] and more recently in longline fisheries [7].

Although the impact of small-scale fisheries on this population has not been quantified, reports indicated that juvenile loggerheads aggregate off of Baja California Sur, Mexico (BCS) exposing them to mortality in coastal fisheries operating from small (6–8 m) skiffs up to 55 km offshore [18,23]. Small-scale fishing generates important income in BCS, but due to overfishing, landings and profits are dwindling [24]. Local fishers reported unintentionally catching dozens of loggerheads day^{-1} skiff^{-1}, particularly while fishing bottom-set gear. Entangled and hooked turtles are generally drowned, and carcasses are discarded at sea [18]. We identified high use areas and quantified bycatch mortality of North Pacific loggerheads (*Caretta caretta*) in the small-scale fisheries of BCS and compared it with their bycatch in industrial-scale pelagic fisheries.

RESULTS

In partnership with local fishers, we used satellite telemetry to identify loggerhead high-use areas (or *hotpots*) and compared these with small-scale fishing grounds. We satellite-tracked 30 loggerhead turtles (curved carapace length (CCL); 72±9 cm, mean±SD; Table S1) from the Pacific coast of BCS from 1996–2005 to document loggerhead movement (mean track duration = 205± 176 days and length = 5,041±4,460 km; Table S2). Though the observed range of tracked loggerheads spanned an area of ~10^6 km^2 across the North Pacific, turtles generally used a relatively small region during the 5,594 turtle days observed (Fig. 1). Only the four largest loggerheads (CCL = 88±7 cm) migrated from BCS waters towards Japanese nesting grounds; the other 26 turtles (CCL = 69±5 cm) spent 70.3%±25.8% (mean±SD between individuals) of their 4,059 observed days within the maximum range (55 km) of a dozen or more small-scale fishing fleets (Fig. 1 *inset*, Table S2).

Figure 1. Kernel Density of Loggerhead Turtle Habitat Use in the North Pacific. *Inset:* Positions of tracked loggerheads (yellow) spanned the North Pacific Basin. The 50% utilization distribution for observed loggerheads consisted of an area of 4,115 km^2 centered ~32 km from the BCS coast, well within the 55 km range of small-scale fisheries (white line).
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We assessed loggerhead bycatch mortality by partnering with local fishers to observe two small-scale fleets that operated closest to the high use area. One fleet fished bottom-set gillnets (Puerto López Mateos) and the other bottom-set longlines (Santa Rosa; Fig. 1). In June-July 2005, we observed 11 loggerheads in 73 gillnet day-trips, or 0.16±0.7 loggerheads day⁻¹. Eight of the 11 loggerheads were landed dead, resulting in an observed mortality rate of 73% in bottom-set gillnets. All loggerhead bycatch in bottom-set gillnets occurred during the 17 trips at the fleet's deepest of three fishing areas (32–45 m), where an average 0.65±1.3 loggerheads were caught per deep fishing trip.

In September 2005, we observed 26 loggerheads in seven longline day-trips (total 1,400 hooks) (Table S1). Loggerheads were caught on all observed longline trips (3.7±2.4 loggerheads day⁻¹). Twenty-four loggerheads were landed dead or died shortly thereafter, resulting in an observed bycatch mortality rate of 92% during longline.

We estimated *minimum* annual loggerhead bycatch in each small-scale fishing fleet as the product of the observed mean of turtles killed per boat per day, the minimum number of boats fishing per day, and the minimum number of days fished per year. We estimated that in the 2005 season *at least* 299 and 680 loggerhead turtles died in the observed bottom-set gillnet and longline fleets, respectively. Our *minimum* estimate of total loggerhead mortality during 2005 in just two small-scale fishing fleets thus approached 1000 turtles. Although the estimates of *minimum* annual bycatch for the fleets we sampled are based on a limited number of fishing trips, actual loggerhead mortality for the region is likely to be much higher because 1) we used minimum values for all factors except bycatch rates, for which we used observed point estimates and 2) we estimated annual bycatch for two among twelve or more fleets which fish in or near the loggerhead high use area.

We also conducted daily (May-September) and weekly (October-April) shoreline surveys from 2003–2005 along the 43 km Playa San Lázaro, BCS, which is adjacent to the observed fishing grounds. Nearly 80% (N = 781) of the 982 loggerhead carcasses encountered were observed from May-September, corresponding to seasonal operation of local small-scale fisheries (Fig. 2). Carcasses were comprised of large juveniles or subadults (71±10 cm CCL; Table S1). In the Northwest Atlantic, only ~15–30% of loggerhead carcasses discarded at sea strand, and the probability of stranding declines with distance from shore [25,26]. Thus the 299 loggerhead carcasses that stranded during the months the fisheries operated in 2005 (May-September) likely represent a small fraction of discarded bycatch and corroborate our estimate of minimum bycatch mortality in 2005.

DISCUSSION

The long-term tracks of loggerhead turtles presented here plus the observed mortality confirm preliminary identification of a high use area for juvenile loggerhead turtles in the coastal waters of Baja California Sur, Mexico [18,27]. The extended time periods over which juvenile loggerheads were tracked using this region suggests that it represents important developmental habitat for the population.

The US National Marine Fisheries Service noted that 37-92 large juvenile North Pacific loggerheads killed per year would "appreciably increase their extinction risk" [28]. Given that *minimum* annual loggerhead mortality due to bycatch in just two local BCS fleets is more than an order of magnitude greater, we conclude that these two fleets alone may threaten the persistence of the North Pacific loggerhead population.

Our minimum bycatch estimate (~1000 loggerheads yr⁻¹) for the two small-scale fleets rivals that of North Pacific industrial-scale fisheries. For example, the international pelagic driftnet
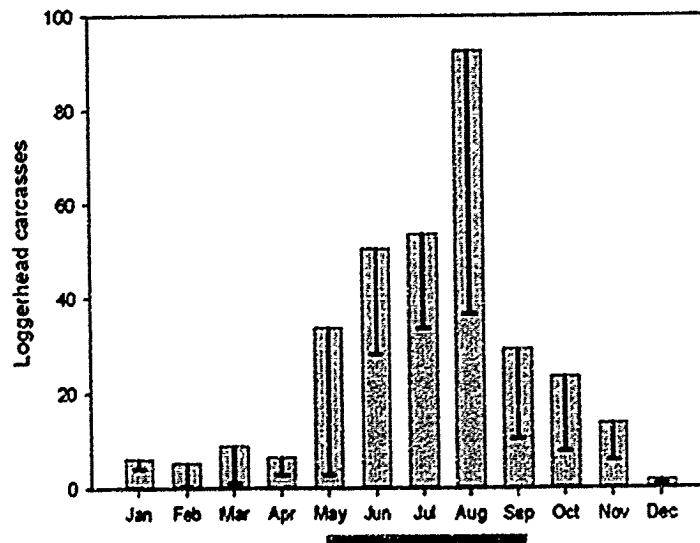

Figure 2. Loggerhead Carcasses Stranded at Playa San Lázaro 2003-5. 985 loggerhead carcasses stranded along the 43 km Playa San Lázaro from 2003–5. Nearly 80% (N = 781) of carcasses stranded from May-September, corresponding to seasonal operation of local small-scale fisheries (red line). Bars represent SD within months.
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fishery killed an estimated ~800 loggerheads yr^{-1} until it was banned by international accord in 1992 [28]. The pelagic longline fishery was estimated to kill a minimum of 2690 loggerheads yr^{-1} across the entire Pacific Basin, roughly half of which (1300 loggerheads yr^{-1}) may be killed in the North Pacific [7].

Bycatch per unit effort (BPUE) was at least an order of magnitude higher in the small-scale longline fleet (19.3 turtles per thousand hooks) than in Mexican and US pelagic longline fleets (0.00–1.40 loggerheads per thousand hooks) [9]. BPUE in the observed gillnet fishery (0.85 turtles gillnet km^{-1}) was also more than an order of magnitude higher than that recorded for industrial-scale fisheries (0.01 turtles gillnet km^{-1}) [22]. Furthermore, mortality of bycaught turtles was much higher in small- vs. industrial-scale fisheries (73–92% vs. 4–27%) [9,22]. The disproportionately large impact of the two small-scale fisheries in this study is striking because of their spatially restricted, limited effort relative to the ocean basin-wide, massive effort of industrial-scale fisheries.

Because small-scale fisheries are conducted primarily in developing nations where management and enforcement are limited, assessing and mitigating their bycatch presents an international conservation challenge. Command-and-control approaches such as fisheries closures are often impractical and inadvisable, particularly in developing nations [8,29,30]. Because fishers' investment in the conservation process can increase their subsequent adoption of conservation strategies, solutions may depend on fishers' direct involvement and support in developing new social norms and economic alternatives [30,31].

Accordingly, we forged innovative partnerships with local fishers and their families to assess and mitigate their bycatch [32]. From their participation in this research, fishers learned firsthand about the Pacific-wide impacts of their local bycatch and the potential for sustainable fishing and tourism in the newly identified hotspot. Concurrently we ran a bycatch awareness campaign using locally resonant media including murals, comic books, and regional festivals to celebrate loggerheads as a valuable resource and to empower fishers and their families as their stewards. As a result, fishers of Puerto López Mateos declared the core high use area a "Fishers' Turtle Reserve" in 2006. With the support of local, state, and federal governments, a coalition of fishers, managers, scientists, and citizens is now seeking federal legislation to establish and co-manage the reserve.

This case study demonstrates that a co-management strategy that directly engages local fishers and their families holds considerable promise in assessing and mitigating small-scale fisheries bycatch. Mexico is recognized worldwide for its successful protection of gray whales, and it has established numerous marine protected areas along the Baja California peninsula. The establishment of a co-managed loggerhead refuge would greatly reduce the extinction risk of this endangered population.

While bycatch in industrial-scale fisheries has driven declines in marine megafauna, small-scale fisheries can apparently have similarly severe effects where they overlap with megafauna high use areas. New telemetry studies are revealing that a range of migratory megafauna spend considerable time in coastal waters during vulnerable life history stages [12,13,33]. Furthermore, where quantified, small-scale fisheries are known to kill large numbers of non-target seabirds [34], marine mammals [35] and sea turtles [12] and to drive declines in megafauna target species [24].

Small-scale gillnet and longline fisheries are ubiquitous in coastal waters worldwide [8,11] and can be expected to result in similarly high rates of bycatch mortality as exemplified by the two fleets observed in this study. Where small-scale fisheries and megafauna high use areas overlap worldwide, our case study

showing population-level impacts of small-scale fisheries bycatch may be representative; small-scale fisheries may be among the greatest current threats to non-target megafauna. Further research is urgently needed to evaluate the impact of small-scale fisheries on vulnerable megafauna populations worldwide.

Although mitigating small-scale fisheries bycatch presents a daunting conservation challenge, the high BPUE of these fisheries provides an unexpected advantage. For each unit of small-scale fishing effort modified to reduce bycatch, a much higher benefit accrues for the megafauna than might be expected for industrial-scale fisheries. Localizing coastal distributional hotspots of vulnerable megafauna will be important for identifying previously unquantified bycatch mortality. Protecting coastal hotspots in partnership with local fishers may provide unforeseen leverage for ensuring the persistence of endangered marine megafauna.

METHODS

Habitat use

The movements of loggerhead turtles were monitored using platform transmitting terminals (PTT) deployed on loggerhead turtles (n = 30) released along the Pacific coast of Baja California Sur (BCS), Mexico from 1996–2005. Twenty-seven of these turtles were captured by hand from small fishing boats and released within 18 hours and 10 km of capture. Two turtles were retrieved from bottom-set longlines on which they were shallowly hooked, instrumented, and released as above. One turtle was retrieved from gillnet fishers in the Gulf of California and held in captivity for 10 years before release.

We attached PTTs to turtle carapaces using polyester resin and fiberglass cloth [18] and monitored them via the Argos satellite system. We included all Argos-derived positions classified as 1, 2 or 3 in the spatial analysis. We filtered all other Argos positions (location classes A, B and O) based on a maximum rate of travel of 5 km h^{-1}. Positions of location quality Z and those that clearly fell outside each turtle's track were omitted. In order to preserve the highest spatiotemporal resolution of the data, consecutive ARGOS hits were linearly interpolated to 3 positions per day based on great circle distances, based on the observed mean of 2.7 ± 2.9 hits/day.

Multi-individual hotspots off the BCS coast were determined through an effort-weighted kernel density analysis of 9244 filtered positions to derive an index of turtle residence probability per unit area. From our dataset of filtered and interpolated positions, we derived an index of turtle residence probability per unit area as follows: 1) we extrapolated the number of turtle days spent per $0.01°\times0.01°$ cell using kernel density analysis with a search radius of 0.5° and 2) we weighted the kernel density estimate of turtle days spent in each cell by multiplying it by the number of individual turtles using that cell. In this way we downweighted cells frequented by single or few individuals for extended periods to avoid biasing our identification of multi-individual high-use areas. We present turtle residence probability per cell as utilization distributions (UD) based on polygon coverage using least squares cross validation [36,37] providing probability contours for the 50%, 75% and 95% UDs with the 100% contour reflecting the total range (Fig. 1).

Fisheries observations

From June to July 2005, we made 73 day-long bottom-set gillnet trips with 5 fishing crews of Puerto López Mateos, the fishing community closest to the loggerhead high use areas identified in this study. Each boat fished a total of fifteen days across the fleets' range of gillnetting depths, with five days in each of three depth

ranges that spanned the fleet's fishing grounds (5 to 18 m, 18 to 32 m, and 32 to 45 m) to standardize for boat-specific bycatch rates. Gillnet captains were compensated MN$500 per day, roughly 2/3 of daily gasoline expenditure for bycatch observations to be made.

The gillnet crews of Puerto López Mateos reportedly fish daily from May through August (70 to 110 day trips) in depths ranging from 5 to 45 m, with nets soaked for 20-48 hrs. Fishers worked from 6-8 m outboard-powered skiffs and targeted primarily California halibut (Paralichthys californicus, Ayres) and used 20.3 cm mesh monofilament gillnets of 400 m length and height from 3 m to 6 m. All nets were fished with "suspenders" connecting the float line to the sink line resulting in loose bags of net material. The fleet numbered up to 75 boats in 2005, with 9 to 40 boats fishing the fleet's deep area on a given day (32–45 m depths).

In September 2005, we made 7 daylong bottom-set longline trips with 5 local fishing crews from Santa Rosa. Longlines targeted shark species and were anchored in 60 to 90 m depths and checked each day. Crews checked and baited an average of 200 hooks per day.

The longline crews of Santa Rosa reportedly fished daily from August through September in 2005 (40 to 60 day trips), targeting primarily demersal sharks, with lines soaked 20-48 hours. Fishers used freshly caught mackerel or bycaught tuna or marlin for bait on "Japanese J-hooks" with inflected shanks. The Santa Rosa fleet numbered 5 to 6 boats in 2005.

In both fisheries we recorded the number, species, condition, and measurements of sea turtles captured.

Shoreline mortality surveys

From January 2003 through December 2005, we conducted shoreline surveys on daily (May-September) and weekly (October-April) schedules along the 44 km Playa San Lázaro the shoreline closest to the loggerhead high use area described here. All turtle carcasses encountered were identified, measured, and marked. Data recorded on each stranded carcass included the following: observer name, stranding date, species, turtle number by day, location, curved carapace length and width (CCL and CCW), condition of carcass (decomposition state), tag numbers (if present), sex of carcass (when externally obvious), and observer notes. Curved carapace length was taken from the nuchal notch to the posterior marginal tip. Curved carapace width was taken at the widest part of the shell. All animals were painted and dragged well above the high tide line to avoid recounts.

Estimating annual, local loggerhead bycatch

For the gillnet fishery, because bycatch was highly dependent on fishing depth, we multiplied the observed mean number of turtles caught per boat per day in depths from 32–45 m (0.65), by the reported minimum number of boats working waters deeper than 32 m on a given day (9; range 9 to 40) by the minimum number of days fished per year (70; range 70 to 110 trips) and discounted by the proportion of turtles released alive (27%). Based on this simple calculation we extrapolated a *minimum* annual bycatch mortality to be 299 loggerhead turtles for the 2005 season of the observed gillnet fleet*. For the bottom-set longline fishery, we multiplied the mean observed number of turtles caught per boat per day (3.7) by the minimum number of boats fishing (5; range 5 to 6) by the minimum number of days fished per boat in 2005 (40; range 40 to 55) and discounted by the proportion of turtles released alive (8%). We thus extrapolated a *minimum* annual bycatch mortality rate of 680 loggerhead turtles in the 2005 season for the observed bottom-

set longline fleet*. Our *minimum* estimate of the total loggerhead mortality during 2005 for the two small-scale fishing fleets observed totaled ~1000 loggerhead turtles.

Comparing small- vs industrial-scale fisheries bycatch

The estimates of minimum annual bycatch and observed BPUE for the two fleets we sampled are based on relatively small numbers of fishing trips because of the inherent difficulties of documenting bycatch in small-scale fisheries [9,18]. These difficulties include 1) logistical issues due to lack of space for observers on small-scale vessels, remoteness of fishing camps; 2) political issues due to lack of legal precedent for managing bycatch in small-scale fisheries and wariness of fishers; 3) sampling issues due to variability in gear, techniques, and effort both between and within fleets.

Gillnet bycatch estimates and BPUE for the Japanese pelagic driftnet fleet was published based on 25,500 km of observed gillnet sets [22], while we observed 58.4 km of gillnets (13.2 km of deep sets >32 m). Longline BPUE was reported for the US and Mexico fleets based on 1400×10^3 and 69×10^3 hooks observed respectively [9], whereas we observed 1400 hooks.

Despite our relatively small sample sizes, we are confident that our samples are representative because 1) in semi-structured interviews we conducted in 2003, local fishers reported an average of 4 loggerheads caught per week per boat (roughly 0.65 per day-trip) and 2) in informal interviews made during this study longline fishers reported that the observed bycatch rates were normal. Furthermore, longline observations made both prior to and following this study showed similarly high bycatch rates.

Participatory research

We partnered with fishers, community members, and managers to assess habitat use and bycatch and to design and conduct experiments to reduce turtle bycatch [38]. Complementing this research and drawing from the field of community-based social marketing [39-41], we designed a suite of outreach initiatives to empower fishers and their families to reduce bycatch [32]. Our approach grew from and was facilitated by the *Grupo Tortuguero*, a community conservation network that unites fishers and other conservationists of the Baja California peninsula and beyond [41]. Informative workshops for fishers and curriculum enrichment for schoolchildren conveyed the facts about bycatch. To supplement these experiences across whole communities, we offered a range of locally resonant media and formed local committees to organize public events such as regional festivals, parades, and sports competitions. Moreover, we partnered closely with local fishers and ecotour operators to demonstrate the feasibility of turtle and sportfishing tours as alternatives to depleted, high-bycatch fisheries.

SUPPORTING INFORMATION

Table S1
Found at: doi:10.1371/journal.pone.0001041.s001 (0.03 MB DOC)

Table S2
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DGVS/10358, and SGPA/DGVS/03501/06. Animal handling was in full compliance with CARC/IACUC protocol at UC Santa Cruz.

Author Contributions

Conceived and designed the experiments: SP DM WN. Performed the experiments: SP DM WN. Analyzed the data: LC AW SP GR WN. Contributed reagents/materials/analysis tools: AW SP. Wrote the paper: LC SP GR.

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Contribution to the Theme Section 'Fisheries bycatch: problems and solutions'

High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003 to 2007

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ABSTRACT: Assessing mortality of long-lived organisms is fundamental for understanding population trends and for implementing conservation strategies, but doing so for marine megafauna is challenging. Here we assessed anthropogenic mortality of endangered North Pacific loggerhead turtles in the coastal waters of Baja California Sur, Mexico (BCS), through the synthesis of 3 sources: (1) intensive surveys of an index shoreline from 2003 to 2007; (2) bimonthly surveys of additional shorelines and towns for stranded and consumed carcasses from 2006 to 2007; and (3) observations of bycatch by 2 small-scale fishing fleets. Using Monte Carlo simulations we estimate that 1500 to 2950 loggerhead turtles died per year at BCS from 2005 to 2006 due to bycatch in the 2 observed fleets. Actual mortality may be considerably higher due to bycatch in other fisheries, directed hunting for black market trade, and natural factors including predation and disease. From 2003 to 2007 we encountered 2719 loggerhead carcasses on shorelines and in and around towns of BCS. Along the 43 km Playa San Lázaro, 0.25 loggerheads km^{-1} d^{-1} were stranded during summer fishing months over 5 yr, which is among the highest reported stranding rates worldwide. This stranding rate corroborates similarly high observed bycatch rates for local small-scale longline (29 loggerheads 1000 hooks^{-1}) and gillnet (1.0 loggerhead km^{-1} of net) fisheries. A significant increase in mean length of 2636 carcasses measured at BCS occurred from 1995 to 2007. Given the endangered status of the North Pacific loggerhead population, conservation action to reduce bycatch and poaching at BCS is urgently needed.

KEY WORDS: Loggerhead sea turtle · Bycatch · Small-scale fisheries · Wildmeat · Poaching · Strandings · Mass mortality · Length frequency · Marine conservation

INTRODUCTION

Marine megafauna, including predatory fish, seabirds, marine mammals, and sea turtles, have declined worldwide due to anthropogenic threats such as overfishing, bycatch, infectious disease, and habitat loss (Jackson et al. 2001, Myers & Worm 2003, Aguirre & Tabor 2004, Lewison et al. 2004a). Many of these declines result from reduced survival rates, and determining these rates is important for understanding population trends and for developing and implementing conservation strategies (NRC 1995, Morris & Doak 2002). However, assessing survivorship during the oceanic life stages of marine megafauna populations is notoriously difficult due to their oceanwide distributions, generally low densities, and the resulting challenges of direct observation. The demography of seabirds and sea turtles, for instance, is fairly well

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understood during nesting, but relatively little is known about their oceanic life stages and developmental migrations. Elucidating these life stages is a conservation priority (NRC 1990, NMFS 2007).

Developmental migrations that last decades and take juvenile North Pacific loggerhead turtles from their Japanese rookeries as far as Mexico (Bowen et al. 1995, Nichols 2003) have precluded understanding the dynamics of the population. Censuses of Japanese rookeries showed declines in nesting females as high as 90% within the past 3 generations to fewer than 1000 yr^{-1}, qualifying the population for critically endangered status (Kamezaki et al. 2003). Nesting abundance throughout the Japanese archipelago has fluctuated at historically low levels over the past 2 decades, exhibiting a quasi-cyclic trend that may be environmentally induced (Chaloupka et al. 2008, N. Kamezaki et al. unpubl. data).

Where they aggregate at foraging grounds in the central North Pacific, juvenile loggerheads are exposed to high levels of bycatch mortality in industrial USA and international longlines, and also in illegal, unreported and unregulated (IUU) longline fisheries (Wetherall et al. 1993, Polovina et al. 2003, Lewison et al. 2004b). But many juvenile and subadult loggerhead turtles also aggregate in large numbers off the Pacific coast of Baja California Sur, Mexico (BCS), presumably to forage until they reach maturity and migrate back to Japan to reproduce (Ramirez-Cruz et al. 1991, Nichols 2003). At BCS, small-scale fisheries have been shown to cause high levels of loggerhead mortality (Gardner & Nichols 2001, Koch et al. 2006, Peckham et al. 2007a).

In addition to incidental bycatch and natural factors such as predation and disease, in northwestern Mexico sea turtles are killed for human consumption, despite a federal ban on turtle hunting and trade (Gardner & Nichols 2001, Nichols 2003). As observed in the case of cetacean wildmeat (Millner-Gulland et al. 2003, Clapham & Van Waerebeek 2007), turtle bycatch fuels both local consumption and black market trade in BCS. Sea turtles caught accidentally and retrieved dead are usually discarded; generally only live turtles are retained for personal consumption or black market sale (Nichols 2003). Turtles are also directly hunted for personal consumption or black market sale (Nichols & Safina 2004). Human consumption is an important source of mortality for loggerhead turtles at BCS (Koch et al. 2006), despite associated human health risks (Aguirre et al. 2006).

Large numbers of loggerhead carcasses stranded each summer at BCS have been attributed to bycatch in local fisheries, but it was not possible to directly link strandings to bycatch mortality because turtle carcasses rarely show evidence of fisheries interactions (Gardner & Nichols 2001, Koch et al. 2006). Observations of small-scale fisheries at BCS uncovered a strong correspondence between the seasonality of loggerhead turtle bycatch and strandings from 2003 to 2005, revealing that a large proportion of strandings result from local fisheries bycatch (Peckham et al. 2007a).

Assessing mortality of oceanic species is notoriously difficult. Mortality rates have been inferred from telemetry observations, but these are limited to tracked animals, resulting in generally small sample sizes due to high costs (Hays et al. 2003, Block et al. 2005). Shoreline and town surveys for stranded and consumed carcasses can provide mortality data for species that frequent nearshore waters, but these severely underestimate overall mortality because (1) surveys are usually limited to a small fraction of coastlines and (2) the majority of turtles that die at sea either naturally or due to bycatch do not strand (Epperly et al. 1996, Hart et al. 2006, Leeney et al. 2008, Tomás et al. 2008, this Theme Section).

As with terrestrial wildmeat (or bushmeat) consumption, assessment of turtle consumption and black market trade through carcass surveys severely underestimates this important mortality source because carcasses may be discarded at sea or in unpopulated areas, and live turtles are exported to distant markets (Millner-Gulland et al. 2003, Brashares et al. 2004, Koch et al. 2006, A. Mancini & V. Koch unpubl. data). Observations of fisheries bycatch also provide mortality data, but these are limited to the small proportion of vessels that can be observed.

Here, we integrated 3 different approaches to assess anthropogenic mortality of loggerhead turtles at BCS, Mexico. Following Koch et al. (2006) and extending results reported in Peckham et al. (2007a) by 2 more years we quantified (1) strandings of loggerhead turtles at an index shoreline from 2003 to 2007; (2) strandings of turtles at 12 other shorelines in the BCS region; (3) carcasses from surveys of 21 towns and fish camps plus their dumpsites; and (4) annual mortality rates of turtles taken as bycatch by 2 small-scale fishing fleets observed from 2005 to 2007. Based on these data, we estimated annual loggerhead mortality in regional small-scale fisheries, exclusive of mortality due to bycatch in additional fisheries, hunting, and natural factors including predation and disease.

MATERIALS AND METHODS

Study area. Our study area extended along the Pacific coast of Baja California Sur, Mexico, from the Vizcaíno Peninsula (27° 50' N, 115° 05' W) to Bahía Magdalena (24° 30' N, 112° 00' W; Fig. 1). The Bight of Ulloa (Fig. 1) is an important high-use area for loggerhead turtles
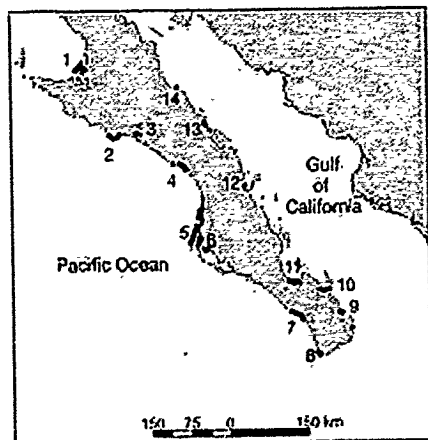
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Fig. 1. Study area, including the shoreline of Playa San Lázaro. Shorelines (S) and/or dumpsites (D) were surveyed at each site: 1, Guerrero Negro (S/D); 2, Punta Abreojos (S/D); 3, Laguna San Ignacio (S/D); 4, San Juanico (S/D), 5, Playa San Lázaro (S); 6, Bahía Magdalena (S/D); 7, Todos Santos (S); 8, Los Cabos (S); 9, Cabo Pulmo (S); 10, Bahía La Ventana (S/D); 11, La Paz (S); 12, Loreto (S/D); 13, Mulegé (S/D); 14, Santa Rosalia (D)

(Ramirez-Cruz et al. 1991, Peckham et al. 2007a) and loggerhead turtles also occur irregularly in the waters of the Sea of Cortez (Nichols 2003, Seminoff et al. 2004).

Sampling. *Bycatch observations:* We accompanied fishing crews of Puerto López Mateos BCS on 21 day-trips using bottom-set gillnets from 23 July to 11 August 2006 and 6 August to 4 September 2007. The observed trips were made opportunistically and resulted in 18 trips observed in deep areas (32 to 45 m depths). Day trips consisted of a single haul of each net each between 06:00 and 14:00 h Pacific Standard time (PST). Fishers worked from 6 to 8 m outboard-powered skiffs and targeted primarily California halibut *Paralichthys californicus*, using 20.3 cm stretched mesh monofilament gillnets of 100 to 200 m length and 3 to 6 m height. We interviewed 2 master fishermen from Puerto Lopez Mateos to assess the effort of the local gillnet fleet in terms of ranges of the number of boats fishing d^{-1} and days fished yr^{-1}.

On 16 August 2006, we made 1 daylong bottom-set longline trip with a fishing crew from Santa Rosa, BCS, during which 236 hooks were checked and baited. Longlines targeted demersal fish and were anchored in 85 to 105 m depths and checked daily. Fishers used freshly caught mackerel or bycaught tuna or marlin for bait on 'Japanese J-hooks' with inflected shanks or 14/0 circle hooks. We interviewed the president of the Santa Rosa fishing cooperative to assess the effort of the longline fleet.

In both fleets we recorded the number, species, condition, and measurements of sea turtles captured. For both fleets, fishing and observations were conducted exactly as in Peckham et al. (2007a) in order to pool and analyze data.

Estimating annual bycatch: To extrapolate the range of annual loggerhead bycatch in the 2 observed fleets we combined observed bycatch and mortality rates with reported fishing effort levels for each fleet, and used Monte Carlo simulations to incorporate all known sources of uncertainty in our data. Specifically, we developed a simple iterative model that allowed for random variation in 4 different parameters: (1) the number of fishing days season^{-1}; (2) the number of boats fishing d^{-1}; (3) the bycatch rate (turtles caught boat^{-1} fishing d^{-1}); and (4) the mortality rate of bycaught turtles. For the first 2 variables we utilized the range of values reported by master fishermen to set upper and lower bounds and assumed that variation could be modeled by uniform random numbers drawn from within these ranges. For the daily bycatch rate, we pooled the bycatch observations reported here with those from the same fleets in 2005 (Peckham et al. 2007a), for gillnet (n = 35) and long-line trips (n = 8) to fit probability distributions, and for each iteration of the model we drew numbers randomly from the appropriate distribution. For this step we first evaluated 5 alternative probability distributions: 2 continuous (normal and log-normal) and 3 discreet (binomial, poisson and negative binomial). Based on a comparison of Akaike's information criterion (AIC) values (Hilborn & Mangel 1997), the negative binomial provided the best fit to bycatch data for both fleets (Fig. 2). For the parameter representing probability that a bycaught turtle would be killed, we fitted binomial distributions to our raw data on bycatch mortality rates and used these fitted distributions to generate random per-day mortality rates. For parameter estimates and distributions used for model simulations see Table 2. We ran the Monte Carlo model for 100 000 iterations for both fleets; every iteration simulated bycatch and mortality of turtles over 1 fishing season. The result was a frequency distribution of seasonal loggerhead bycatch and mortality estimates from which we calculated 95% confidence limits (CL$_{95}$). Finally, we combined the estimates to arrive at the total projected annual loggerhead bycatch mortality for the 2 observed fleets.

Shoreline and town mortality surveys: Continuing the protocol employed from 2003 to 2005 (Peckham et al. 2007a), from January 2006 through December 2007 we conducted shoreline surveys by all-terrain vehicle (ATV) on daily (May to September) and weekly (October to April) schedules along the 44.3 km Playa San Lázaro (Fig. 1). Furthermore, we conducted shoreline
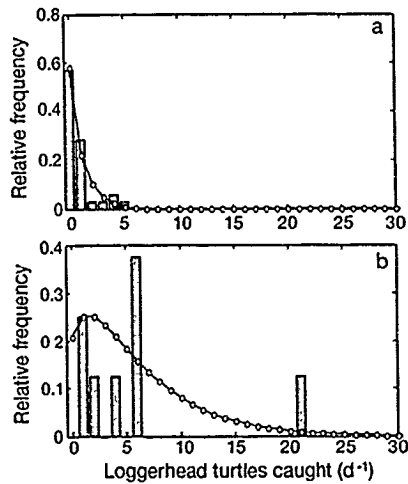
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Fig. 2. *Caretta caretta*. Per-day bycatch rates for (a) bottom-set gillnet and (b) longline fleets. Negative binomial distributions (O) were fit to raw data from observer trips (bars) using maximum likelihood techniques and these distributions were used to generate random values for Monte Carlo simulations (see 'Estimating annual bycatch' in 'Materials and methods' for details)

surveys by ATV once every 2 mo along each of the 12 shorelines on both coasts of BCS, totaling 299.7 km from February 2006 to December 2007. Overall we surveyed 344 km of shoreline, representing 15% of the ~2200 km BCS coast. We also monitored sea turtle mortality in 21 towns and fish camps plus their dump-sites, representing 20 to 25% of all coastal communities in BCS (Fig. 1).

All turtle carcasses encountered were identified, measured, and marked to avoid recounts. Data recorded on each stranded carcass included observer name, stranding date, species, turtle number by day, location, curved carapace length and width (CCL and CCW, respectively), tag numbers (if present), sex of carcass (when externally obvious), condition of carcass (decomposition state), cause of death (if possible) and observer notes. CCL was taken from the nuchal notch to the posterior marginal tip. CCW was taken at the widest part of the shell.

Human consumption of loggerheads. Based on surveys of towns and dumps we determined minimum annual levels of turtle consumption in BCS coastal communities. We assumed that the majority of turtles consumed locally were caught as bycatch and thus did not add observed consumption to bycatch in calculating overall mortality.

Due to the clandestine nature of black market trade for sea turtles and the fact that trafficked turtles are

often exported from the region alive (Nichols 2003, Koch et al. 2006), we could not assess mortality due to hunting. Thus our minimum estimate of anthropogenic mortality for loggerheads in the region was limited to bycatch in the 2 observed fleets and resulting consumption, exclusive of anthropogenic mortality due to hunting and natural mortality due to predation, disease and other natural factors.

Length frequency analysis. We constructed length frequency distributions for loggerhead turtles and estimated the percentage of adults. Length at maturity in females is close to average nesting length in loggerhead sea turtles (Frazer & Ehrhart 1985, Hatase et al. 2004) and we used the average size of Japanese nesters as an approximation of length at maturity: 91 cm (CCL) (Kamezaki et al. 1995, Hatase et al. 2004).

We compared the length distribution of stranded loggerhead turtles during the 5 yr of our study with data from 1995 (Nichols 2003), 1999 (Gardner & Nichols 2001), and 2000 to 2002 (Koch et al. 2006) collected at Playa San Lázaro and the adjacent Playa Santa Maria using the same protocol. Straight carapace lengths (SCL) collected in prior studies were converted to CCL by using the conversion equation

$$SCL = (0.932 \times CCL) + 0.369 \qquad (1)$$

derived from turtles measured locally (N = 163, r^2 = 0.93, p < 0.001). After conversions were completed, all CCL data were rounded to the nearest cm.

The increasing trend in average length of stranded loggerheads from 1995 to 2003 described by Koch et al. (2006) was re-analyzed through 2007 to account for the difference between years in the number of turtles recorded. To ensure that the observed increase in length over time was not a result of differences in sample size or variance, we also analyzed the trend using both mean and median values for each year.

Analyses were conducted using SYSTAT 12 (Systat Software), with the exception of the Monte Carlo simulations, which were coded and run using MATLAB (Mathworks). Unless otherwise stated, results are presented as mean ± SD and intervals represent either absolute ranges or, when denoted as 'CL_{95},' the 95% confidence limits.

RESULTS

Observed bycatch mortality

In the summers of 2006 and 2007, we observed 17 loggerheads caught during 21 gillnet day-trips. Pooling these results with the observations we made of the same fleet in 2005 (Peckham et al. 2007a), we observed 28 loggerheads caught during 94 gillnet day-trips or

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Table 1. *Caretta caretta*. Observed bycatch rates and percent mortality by fishery and depth fished. Gillnets trips were observed from Puerto López Mateos, Baja California Sur, Mexico (BCS), 2005 to 2007 and longline trips from Santa Rosa, BCS, 2005 to 2006

Fishery	No. of day-trips	No. of turtles caught	km of net observed	Turtles km^{-1} net	Turtles d^{-1} (mean ± SE)	Range turtles d^{-1}	Percent mortality
Gillnet (all depths)	94	28	76.0	0.37	0.30 ± 0 09	0–4	68
Gillnet (shallow < 32 m)	59	0	49.1	0.00	0.00		
Gillnet (deep > 32 m)	35	28	26.8	1.04	0.80 ± 0.22	0–4	68
	No. of day trips	No. of turtles caught	Hooks observed	Turtles 1000 hooks^{-1}	Turtles d^{-1} (mean ± SE)	Range turtles d^{-1}	Percent mortality
Longline (85–105 m)	8	48	1636	29	6.00 ± 2.30	1–21	90

0.3 ± 0.1 loggerheads boat^{-1} d^{-1} (mean ± SE) during the summers of 2005 to 2007). Sixty-eight percent of log-gerheads were landed dead. All were caught in bot-tom-set gillnets during the 35 day-trips observed at the fleet's deepest fishing area (32 to 45 m), where 0.8 ± 0.2 loggerheads were caught boat^{-1} d^{-1} (mean ± SE) at deep fishing grounds (Table 1). Across all depths, 0.37 loggerheads were caught km^{-1} gillnet; in waters deeper than 32 m, 1.04 loggerheads were caught km^{-1} gillnet. Loggerheads retrieved from gill-nets were large juveniles (73.3 ± 8.6 cm CCL) and showed no signs of fisheries interaction.

The 2 master fishermen interviewed from Puerto López Mateos reported that the local gillnet fleet numbered up to 75 boats from 2006 to 2007, with 5 to 20 boats fishing the fleet's deep area each day (32 to 45 m depths). Crews reportedly made 70 to 100 day-long trips to fish the fleet's deep area from May to Sep-tember in 2005 through 2007 (J. Lucero & M. Romero pers. comm.).

Twenty-one loggerheads were caught during the single longline day-trip observed in 2006, and fishers reported that this number was not unusual; 4 other boats that fished the same day caught similar num-bers of loggerheads (A. Gaos pers. obs.). Pooling these new data with results from Peckham et al. (2007a), we observed 48 loggerheads during 8 longline day-trips (total 1636 hooks), resulting in a bycatch rate of 29.3 loggerheads 1000 hook^{-1}. Logger-heads were caught on all observed longline day-trips (6.0 ± 2.3 logger-heads boat^{-1} d^{-1} mean ± SE; Table 1). Of these loggerheads, 90% were landed dead or died shortly there-after. Loggerheads caught in bottom-set longlines were large juveniles (77.7 ± 6.2 cm CCL) and showed no morphological evidence of longline interaction.

The president of the Santa Rosa fishing cooperative reported that 5 to 8 boats of his fleet fished bottom-set longlines from 35 to 55 day-trips yr^{-1} in 2005 to 2006 (E. de la Paz pers. comm.). In 2007 the Santa Rosa fleet permanently ceased fishing bottom-set longlines so no further observations were possible.

Estimated loggerhead bycatch.

For the gillnet fleet, because bycatch was highly de-pendent on fishing depth, we limited our analysis to day-trips conducted in depths greater than 32 m. Based on the Monte Carlo simulations, mean estimated by-catch rate in bottom-set gillnets for 2005 to 2007 was 0.8 ± 1.29 turtles caught boat^{-1} d^{-1} (CL$_{95}$ = 0 to 5), or 830 ± 102 turtles season^{-1}. For bycaught turtles, the probability of mortality was 68% (CL$_{95}$ = 48 to 84%; Table 2). The mean estimated seasonal mortality for turtles in the Puerto Lopez Mateos gillnet fleet for 2005 through 2007 was 547 loggerheads yr^{-1} (CL$_{95}$ = 356 to 777; Fig. 3).

For the bottom-set longline fishery, the mean esti-mated bycatch rate for 2005 to 2006 was 5.9 ± 5.35 tur-

Table 2. *Caretta caretta*. Parameter estimates and distributions used for Monte Carlo simulations of bycatch in gillnet and longline fleets. CL$_{95}$: 95% confidence limits

|	Distribution	Parameter values	Predicted mean ± SD	Predicted CL$_{95}$
Gillnet > 32 m				
Day-trips yr^{-1}	Uniform	Min = 70, max = 100	n/a	n/a
Boats d^{-1}	Uniform	Min = 5, max = 20	n/a	n/a
Turtles d^{-1}	Neg. binomial	R = 0.734, p = 0.478	0.8 ± 1.29	0–5
% mortality	Binomial	p = 0.68	68%	48–84%
Longline				
Trips yr^{-1}	Uniform	Min = 35, Max = 55	n/a	n/a
Boats d^{-1}	Uniform	Min = 5, Max = 8	n/a	n/a
Turtles d^{-1}	Neg. binomial	R = 1.516, p = 0.205	5.9 ± 5.35	0–20
% mortality	Binomial	p = 0.89	89%	77–96%

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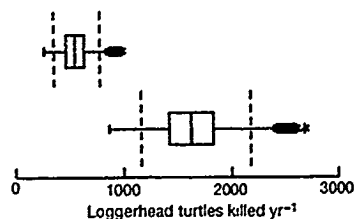
Fig. 3. *Caretta caretta*. Estimated bycatch mortality from 2 fleets of Baja California Sur, Mexico, the bottom-set gillnet (above) and longline fleets (below). Distributions were generated from 100 000 iterations of a Monte Carlo model parameterized from observed bycatch and mortality data and reported fishing effort levels (see Table 2 for parameter values and 'Materials and methods: Estimated annual bycatch' for details). Dashed lines represent 95% confidence limits for each fleet

Table 4. *Caretta caretta*. Mean and SD of curved carapace length (CCL) measured at Bahía Magdalena, Baja California Sur, Mexico, from 1995 to 2007, with percent of individuals with CCL <50 cm. Data from 1995, 1999, and 2000 to 2002 were taken from Nichols (2003), Gardner & Nichols (2001) and Koch et al. (2006), respectively

	Mean CCL	SD	%<50 cm	N of carcasses
1995	57.5	13 5	29	49
1999	62.0	13.0	16	63
2000	67.9	9.8	3	152
2001	68.1	9.2	3	184
2002	69.1	8.6	2	270
2003	70.5	9 4	2	325
2004	69.4	10.5	3	144
2005	72.9	9.4	2	334
2006	72.9	8.5	1	795
2007	70.5	9.2	2	320

tles caught boat^{-1} d^{-1} (CL$_{95}$ = 0 to 20), or 1885 ± 286 turtles season^{-1}. For bycaught turtles, the probability of mortality was 89% (CL$_{95}$ = 77 to 96%; Table 2). The mean estimated seasonal mortality of turtles in the Santa Rosa longline fleet for 2005 and 2006 was 1635 loggerheads yr^{-1} (CL$_{95}$ = 1160 to 2174; Fig. 3). These estimates result in a total projected bycatch mortality of 2182 loggerheads yr^{-1} (CL$_{95}$ = 1516 to 2951) for both fleets combined.

Shoreline and town mortality surveys

From 2003 to 2007 we encountered a total of 2719 loggerhead carcasses on shorelines and in and around towns of BCS. A total of 2385 of the carcasses were found along the 44.3 km Playa San Lázaro from 2003 to 2007, resulting in 476 ± 274 carcasses yr^{-1} at Playa San Lázaro. Of the loggerhead carcasses encountered at Playa San Lázaro, 70% (1674) were observed from May to September, corresponding to seasonal operations of small-scale fisheries primarily working bottom-set gillnets (Table 3). Stranded carcasses at Playa San

Lázaro from 2003 to 2007 were encountered at mean rates of 0.15 loggerheads km^{-1} d^{-1} annually and 0.25 loggerheads km^{-1} d^{-1} from May to September. Most of the stranded turtles (95%) for which data were collected were in moderately to very decomposed condition. Eighty-five turtles (4.2%) stranded in fresh condition, and 9 stranded alive. Fourteen stranded carcasses showed evidence of fisheries interactions, evidenced by hooks or entanglement in fishing gear. Nine of 1918 (0.5%) carcasses measured had a CCL of 91 cm or greater.

Fewer carcasses (277) were encountered during bimonthly surveys of 12 additional shorelines in the region from February 2006 through December 2007, yielding a 2 yr mean of 138.5 loggerhead carcasses yr^{-1}. Combined, the mean 476 loggerhead carcasses that stranded along the 44 km Playa San Lázaro from 2003 to 2007 and the mean 138.5 that stranded at our other regional survey sites from 2006 to 2007 total an average of ~600 carcasses yr^{-1}.

We encountered 57 carcasses during bimonthly surveys of 21 towns, fish camps and surrounding dumpsites in the region from February 2006 through

Table 3. *Caretta caretta*. Number of carcasses encountered along the 44.3 km Playa San Lázaro from 2003 to 2007

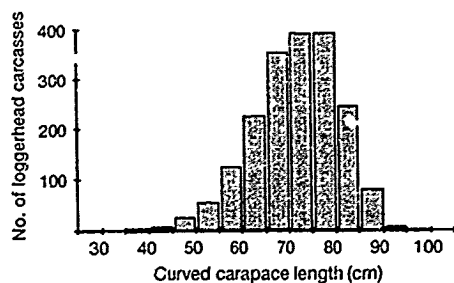|	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	May–Sep total
2003	7	11	5	5	68	75	73	92	36	14	7	1	394	344
2004	4	2	4	4	7	31	55	37	8	42	23	3	220	138
2005	8	3	18	11	27	46	33	149	44	15	12	2	368	299
2006	4	2	1	2	2	19	84	243	145	352	76	11	941	493
2007	6	14	2	4	15	30	134	119	102	16	16	4	462	400
Mean	6	6	6	5	24	40	76	128	67	88	27	4	477	335

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Fig. 4. *Caretta caretta*. Size frequency of stranded carcasses measured at Playa San Lázaro from 2003 to 2007 (N = 1918)

December 2007, yielding a 2 yr mean of 28.5 loggerheads consumed yr^{-1}. All carcasses encountered in towns, fish camps, and surrounding dumps showed signs of human consumption (e.g. cuts, burns, harpoon holes).

An anomalous mass-stranding event occurred from August to November 2006, during which 816 loggerhead carcasses were encountered at Playa San Lázaro (Table 3). During 19 to 21 October 2006, tissues were collected from 56 turtles in various states of decomposition. Full necropsies were conducted on 12 individuals stranded in fresh condition. Several bacteria were isolated from these specimens but no common disease condition could explain the stranding event (A. Aguirre & H. M. Zepeda unpubl. data).
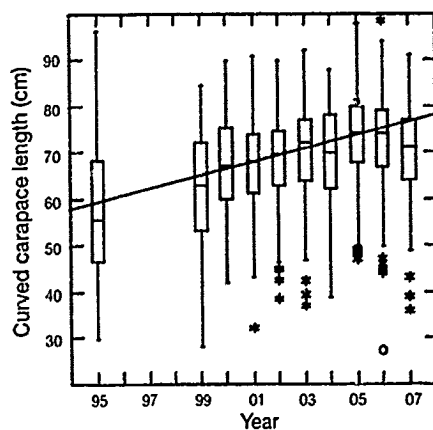

Fig. 5. *Caretta caretta*. Distribution and mean length (solid line) of carcasses measured from the study area 1995 to 2007. Data from 1995, 1999, and 2000 to 2002 were taken from Nichols (2003), Gardner & Nichols (2001) and Koch et al. (2006), respectively

Length distribution of loggerhead carcasses

Length frequency histograms showed that all but 9 stranded loggerhead carcasses were of juvenile size (71.8 ± 9.2 cm CCL, N = 1918; Fig. 4). The length of stranded loggerhead carcasses increased significantly from 1995 to 2007 (N = 2636, r^2 = 0.847, p < 0.0001; Fig. 5). The proportion of juvenile turtles <50 cm CCL decreased precipitously over the same period (Table 4).

DISCUSSION

Many juvenile loggerhead turtles die at BCS each year. Based on (1) our intensive surveys of an index shoreline from 2003 to 2007; (2) bimonthly surveys of shorelines and towns across the region from 2006 to 2007; and (3) observations of bycatch by 2 small-scale fishing fleets, we estimated that 1500 to 2950 loggerhead turtles yr^{-1} died at Baja California Sur from 2005 to 2006. Our assessment represents a conservative estimate of bycatch mortality in small-scale fisheries. Actual anthropogenic mortality due to bycatch in additional small- and industrial-scale fleets and hunting, which we could not assess in this study, is likely to be considerably higher. This human-caused mortality is additive to natural mortality, including disease and predation, the rates of which are currently unknown.

Bycatch mortality

The minimum annual bycatch estimate (1500 loggerheads yr^{-1}) for 2005 to 2006 in the 2 small-scale fleets observed represents an increase from the previously reported estimate (1000 loggerheads yr^{-1}), which was based only on observations conducted in 2005 (Peckham et al. 2007a). New data collected in 2006 and 2007 resulted in more comprehensive observations of bottom-set fisheries, augmenting the confidence of our estimate of annual bycatch mortality for the 2 fleets we evaluated. Furthermore, our modeling approach more rigorously accounts for all sources of uncertainty, including sampling error (or observer error), the estimation error associated with fitting of probability distributions, and the process error inherent in stochastic rates of bycatch and mortality. Thus, the lower 95% confidence limit (1516 loggerheads killed yr^{-1}) represents a very conservative estimate of actual mortality.

The observed bycatch rates of small-scale longlines (29 loggerheads 1000 hooks[-1]) and gillnets (1.04 loggerheads km^{-1} gillnet; Table 2) are orders of magnitude higher than industrial bycatch rates reviewed in Peckham et al. (2007a). We attribute the perennially

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high bycatch and stranding rates described here to the overlap of locally intense small-scale fisheries with the very high local abundance of loggerheads (Seminoff et al. 2006, Peckham et al. 2007a). All bycatch of loggerheads in gillnets occurred in nets set in waters deeper than 32 m, corresponding to the inshore margin of the loggerhead high use area described in Peckham et al. (2007a). Moreover, the high bycatch rates of the Santa Rosa longline fleet were observed in depths greater than 85 m, 10 to 20 km further offshore from the gillnet deep fishing grounds, in the core of the loggerhead high use area (Peckham et al. 2007a). These unusually high bycatch rates are corroborated by what are apparently the highest strandings rates reported worldwide. Our new results emphasize that where high-use areas of small-scale fisheries and megafauna overlap, very high rates of bycatch can ensue that may jeopardize the persistence of vulnerable or endangered megafauna populations.

Loggerhead bycatch mortality for the region is likely to be considerably higher than the range we estimated because our assessment included just 2 of 12 or more fleets that fish at BCS. As is typical worldwide, assessment of bycatch in small-scale fisheries is extremely difficult, because (1) hundreds of boats work along the isolated 700 km coastline that borders the BCS loggerhead high use area; (2) space for observers is limited on small boats; (3) fishers are versatile and switch methods, gear and fishing areas rapidly and frequently to maximize landings; and (4) fishers may fear that bycatch observations are not in their best interests and thus may alter their behavior when observers are aboard.

For these reasons our observations were limited to just 2 fleets, but additional fleets operated from other communities that border the loggerhead high use area described in Peckham et al. (2007a). The fishing location and methods of these fleets suggests that they are also likely to catch considerable numbers of loggerheads. Furthermore, migrant fishers from mainland Mexico based at temporary camps along the same coastline fished bottom-set longlines and gillnets in the loggerhead high-use area, resulting in additional bycatch mortality (A. Gaos pers. obs.). Without direct observation we could not determine the bycatch of these boats due to the high variability of bycatch rates depending on gear and depths fished. However, given the bycatch rates above we estimate that their fishing could not have caused fewer than 75 additional loggerhead mortalities yr^{-1} and could have caused considerably more mortalities.

There are few records of industrial fisheries bycatch in the region. Class 6 tuna purse seiners that fish the region with 100% observer coverage have close to zero loggerhead bycatch (IATTC 2008). Smaller seiners known to work in the region are not observed comprehensively so bycatch rates are unavailable (M. Hall pers. comm.). Industrial shrimp vessels operate well inshore of the loggerhead hotspot (J. Lucero pers. comm.) Industrial longline vessels that fish the region with an order of magnitude more hooks per set may also cause high levels of bycatch.

Shoreline mortality surveys

The 2658 stranded loggerhead carcasses recorded from 2003 to 2007 represent a small fraction of all loggerheads that died naturally or were discarded by fishers in nearby waters because (1) our surveys were limited to just 15% of the BCS coastline and (2) only a small proportion of carcasses discarded are likely to have stranded. In the Northwest Atlantic, an upper limit of ~15 to 20% of loggerhead carcasses discarded at sea washed ashore locally, and the probability of stranding declined sharply with distance from shore (Epperly et al. 1996, Hart et al. 2006). The average of ~600 carcasses that stranded at BCS yr^{-1} corroborate the high bycatch rates observed and overall mortality extrapolated in this study, yet represent only a small proportion of local mortality.

A comparison of stranding rates is problematic because they are extremely sensitive to survey frequency. Nonetheless, the sustained annual stranding rate we directly observed at Playa San Lázaro (0.15 loggerheads km^{-1} d^{-1} over 5 yr) is among the highest reported worldwide. By contrast, an estimated 90 000 olive ridley carcasses stranded along the 480 km coast of Orissa, India, over 10 consecutive summers, yielding an overall mean stranding rate of 0.1 turtles km^{-1} d^{-1} (Pandav 2000, Shanker et al. 2004). In the USA, strandings are most frequent along the Atlantic coast of Florida. Along the 933 km Atlantic coast of Florida, 483 ± 129 loggerheads yr^{-1} stranded from 1998 to 2002, yielding a stranding rate of 0.001 loggerheads km^{-1} d^{-1} (STSSN 2007).

Cause of death of stranded carcasses was undetermined because (1) the majority were very decomposed and (2) unlike other megafauna, such as marine mammals, turtle carcasses discarded from gillnets and longlines in this study showed no signs of fisheries interaction. Peckham et al. (2007a) attributed the majority of seasonally high stranding rates to local small-scale fisheries bycatch, and the 2006 and 2007 strandings and bycatch data reported here add further support to this conclusion.

The cause of the mass-stranding event that occurred from August to October 2006 (Table 3) was not clear. Fishermen reported dead and dying turtles 35 to 55 km from shore (V. de la Toba pers. comm.). Red tides were also reported during the fall of 2006 (I. Romero Aguilar

pers. comm.), but these are not unusual in the region. The small-scale fleets documented here could not have been responsible for the mortality after mid-September because by early September they had switched from bottom-set fishing in the loggerhead high-use area to near-shore fisheries that do not affect loggerheads. Several industrial longline vessels were operating in the loggerhead high-use area during aerial surveys conducted in September 2006 (J. Seminoff pers. comm.). Given the high bycatch per unit of effort (BPUE) of small-scale longlines (29 loggerheads 1000 hooks^{-1}) and gillnets (1.0 loggerheads km^{-1} gillnet) observed in this study, a handful of industrial scale vessels setting thousands of hooks or tens of km of gillnet d^{-1} within the loggerhead high-use area could explain the anomalous stranding event.

Alternatively, anomalous mass-stranding events have been attributed to disease or harmful algal blooms, but none have shown the magnitude of strandings observed at Playa San Lázaro (Jacobson et al. 2006). Necropsies conducted on 12 carcasses stranded in fresh condition during the event revealed no common cause of death, but almost all carcasses stranded during the event were severely decomposed, so the carcasses that arrived fresh may not have died in the area where most of the carcasses came from and may not have died of the same cause. Population-level effects of disease in sea turtles are poorly understood (Herbst & Jacobson 2003) and further research at BCS should focus on biotoxin exposure as a potential cause of death.

Mortality due to human consumption

The annual average of consumed carcasses we encountered in towns, fish camps and dumps was 28.5 and represents a minimum consumption level for the communities surveyed because (1) additional carcasses were undoubtedly discarded at sea or in the desert and (2) live turtles caught locally were exported for black market trade (Nichols 2003, Koch et al. 2006). Residents of BCS prefer black turtles *Chelonia mydas* and olive ridley turtles *Lepidochelys olivaceae* over loggerheads for consumption and trade (Koch et al. 2006). However, loggerhead turtles are consumed more frequently in communities where they are commonly bycaught (e.g. Puerto López Mateos; Koch et al. 2006), a pattern that underscores the important relationship between bycatch and wildmeat consumption and trade worldwide (Clapham & Van Waerebeek 2007). Accordingly, it is reasonable to suggest that the majority of loggerheads consumed locally were caught incidentally in fisheries targeting other species and are therefore represented in our bycatch mortality estimates.

Our results showed a decrease in carcasses found consumed in and around Puerto López Mateos from those reported in Koch et al. (2006). However, increased awareness due to outreach and enforcement programs may also have caused people to conceal a higher proportion of consumed carcasses, contributing to underestimation of human consumption. As with terrestrial wildmeat (or bushmeat) consumption, assessment of turtle consumption and black market trade is particularly difficult and results in underestimation of this important population impact (Millner-Gulland et al. 2003, A. Mancini & V. Koch unpubl. data).

Nichols (2003) reported that hundreds of loggerheads were annually exported from the region for black market trade in the 1990s. During this study, fishers reported informally that dozens of loggerheads are hunted from each of several communities in the region for black market trade each year. Accordingly, we conservatively estimated that no fewer than 50 loggerheads yr^{-1} were poached and exported during the study period on top of the 1500 to 2950 yr^{-1} killed due to local bycatch observations. Because poached turtles are invariably exported for sale, the carcasses of these 50 loggerheads yr^{-1} would not have been counted in the community surveys described above.

The fact that there were only dozens of loggerheads poached per year from each of several communities suggests that poaching levels have decreased since those reported by Nichols (2003). Preliminary survey data also suggested decreases in poaching and sale of loggerheads in the region (S. Delgado unpubl. data). Though poaching for trade appears to have decreased and pales in comparison to bycatch mortality, at a minimum of 50 loggerheads yr^{-1}, it remains an important source of mortality for the endangered North Pacific population.

Our observations of turtle mortality due to human consumption are extremely conservative, and further research is essential for understanding its effects on the North Pacific loggerhead population. Molecular classification of wildmeat (Baker et al. 1996) and capture-recapture methods to estimate the number of individual animals taken (Baker et al. 2007) could be useful in the future.

Size distribution

The length distribution of stranded loggerhead carcasses increased significantly from 1995 to 2007 (Fig. 5). Because all samples were collected on adjacent Pacific beaches of Bahía Magdalena using the same protocol, differences found between years suggest trends in the local loggerhead population rather than sampling bias. Due to the decades-long matura-

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tion time of loggerheads, this increasing trend in turtle size may reflect both long-term declines in nesting described from Japan (Kamezaki et al. 2003) and also historically high bycatch of juvenile loggerheads in both high-seas driftnet (Wetherall et al. 1993) and longline fisheries (Lewison et al. 2004b). The decreasing proportion of smaller juveniles at BCS, especially from 2000 to 2007 (Table 3), could be related to sharp declines in nesting observed across all Japanese rookeries in the 1990s (Kamezaki et al. 2003, Chaloupka et al. 2008, N. Kamezaki et al. unpubl. data).

It is of great concern that almost all of the several thousand carcasses encountered from 2003 to 2007 were large juveniles because numerous studies have demonstrated the importance of the large juvenile size class to population growth in loggerhead turtles (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2005). The large size of bycaught and stranded loggerheads exacerbates concern over the high mortality observed at BCS because of the resulting severe loss of reproductive potential for the population.

Survivorship

There is not sufficient information about the demography and distribution of North Pacific loggerheads to allow for a formal assessment of survivorship for juvenile loggerheads at BCS. However, we can derive a rough understanding of relative mortality rates and their population-level impacts by synthesizing available North Pacific loggerhead data with demographic schedules from other loggerhead populations (Heppell et al. 2003, Lewison et al. 2004a). Aerial surveys conducted over Pacific BCS waters resulted in estimates of from ~5000 to 15000 sightable loggerheads in the region (Seminoff et al. 2006).

Sightability of sea turtles during aerial surveys depends on the percent of time they spend at the surface. For loggerheads, published estimates of time spent at the surface range from 6 to 25% (Byles 1988, Houghton et al. 2002, Mansfield 2006) and surface time has been shown to vary significantly with water temperature, location and season (Mansfield 2006). Preliminary dive data suggest that loggerheads at BCS spent 50 to 80% of their time at the surface during daylight hours (S. H. Peckham unpubl. data), a finding that is consistent with the observation that loggerheads bask at the surface in BCS waters for considerable periods of the day (Pitman 1990, Ramirez-Cruz et al. 1991, Nichols 2003). These preliminary dive data from BCS thus suggest that the Seminoff et al. (2006) abundance estimate should be multiplied by a factor of 1.4 to 2. Accordingly, if we assume that ~7000 to 30000 loggerhead turtles are in Pacific BCS waters, the

annual mortality estimate (1500 to 2950 loggerheads yr^{-1}) suggests that 5 to 42% of loggerheads in BCS waters may die annually due to bycatch in the observed fleets, exclusive of all other sources of mortality (i.e. mortality due to bycatch in other small-scale and industrial fleets, poaching for black market trade, and natural mortality including disease and predation).

The proportion of juvenile loggerheads in the North Pacific population represented by those exposed to mortality in BCS waters remains unknown. Assuming a stable stage distribution in the population based on annual nesting numbers of ~1500 females and a proportion of nesting-aged females of 1.8%, Lewison et al. (2004b) estimated a population size of ~335000 loggerheads, ~67000 of which would be larger juveniles. However, it is unlikely that the North Pacific loggerhead population meets the criteria of a stable age or stage distribution (Morris & Doak 2002). Given the decrease in nesting numbers in recent decades (Kamezaki et al. 2003), the historical depletion of larger juvenile loggerheads in high-sea driftnets (Wetherall et al. 1993), the ongoing depletion in high-sea longlines (Lewison et al. 2004b) and other fisheries (Lewison & Crowder 2007), plus the small-scale fisheries bycatch described here and in Peckham et al. (2007a), it is likely that that the age distribution is highly skewed, with many fewer juveniles in the population than the 67000 expected from a stable stage distribution. Estimates of loggerhead abundance in BCS waters from aerial surveys corrected for submergence time suggest that upwards of 50% of larger juvenile loggerheads in the North Pacific population may utilize BCS waters. We therefore conclude that the high levels of fishing-related mortality reported here for BCS waters could have a profound impact on the trajectory of the North Pacific loggerhead population.

CONCLUSIONS

There have been a number of conservation success stories reported recently for sea turtles around the world, with increasing population sizes reported at rookeries of green, olive ridley, and Kemp's ridley turtles (Hays 2004, Broderick et al. 2006, Seminoff & Shanker 2008). However, the mortality rates reported here highlight pressing conservation threats that remain for many sea turtle populations.

The highly productive waters of BCS have been revered for decades and recognized for centuries for the abundance and diversity of megafauna they attract (Steinbeck & Ricketts 1941, Saenz-Arroyo et al. 2006). With perennially abundant prey including pelagic red

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crabs, sardine and squid (Aurioles-Gamboa 1995), it is unsurprising that loggerhead turtles and fishers alike frequent these waters. The unfortunate overlap between foraging loggerheads and fishers results in what may be the highest known rates of turtle bycatch and strandings worldwide. Given that estimated loggerhead mortality due to bycatch in 2 fleets observed at BCS exceeds 1500 loggerheads yr^{-1}, we conclude that reduction of this mortality may be essential for the persistence and recovery of the North Pacific population. Consistent decreases in small juvenile loggerheads foraging at BCS suggest that a decline in neophytes nesting in Japan that originated from BCS should be expected over the next 2 decades.

Based on the results of our observations of their bycatch in 2005 and 2006, one of the fishing fleets we observed (Santa Rosa) retired their bottom-set longline gear from the loggerhead high-use area prior to their 2007 season (Rodgers 2008), potentially sparing hundreds of loggerhead individuals from bycatch in 2007 alone. This extraordinary conservation action resulted from at least 2 factors: (1) perceived decreases in the profitability of the fleet's longlines and (2) increased awareness of the Pacific-wide impacts of their local bycatch due to outreach programs conducted with the Grupo Tortuguero at Santa Rosa from 2005 to 2007, including direct participation in this research (Peckham et al. 2007a,b). The action of the leaders of this fleet may serve as an example for both fishers and conservation practitioners alike.

Conservation action by state and federal agencies is urgently needed to reduce bycatch and hunting at the loggerhead high-use area off the Pacific coast of BCS, Mexico is recognized worldwide for its successful protection of assorted migratory species and it has established marine protected areas along the Baja California peninsula. A proposed Mexican federal refuge managed in partnership with local fishing leaders could ensure that both fishers' livelihoods and loggerheads are conserved through sustainable fishing practices in the loggerhead high-use area (Peckham et al. 2007a). Though the high-use area is well defined, additional, higher precision tracking could enable identification of critical habitat within the high use area (Schofield et al. 2007). Further research should focus on (1) quantifying bycatch in other small- and industrial-scale fleets that fish the loggerhead high-use areas; (2) determining cause of death of loggerhead carcasses through full necropsies; (3) monitoring trends in bycatch, strandings, and relative abundance in the region; and (4) assessing sightability and abundance, and incorporating the results reported here to derive survivorship rates of loggerheads at BCS. Given the response of the Santa Rosa fleet to their involvement in our participatory research (Rodgers 2008), further work should be conducted in partnership with local fisher leaders to continue to engage them in developing locally sustainable conservation solutions.

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DEMOGRAPHIC IMPLICATIONS OF ALTERNATIVE FORAGING STRATEGIES IN JUVENILE LOGGERHEAD TURTLES (CARETTA CARETTA) OF THE NORTH PACIFIC OCEAN

INTRODUCTION

Marine megafauna such as cetaceans, sea birds, sharks, and sea turtles are especially vulnerable to depletion as a result of their slow life histories (Heppell et al. 1999; Fujiwara and Caswell 2001; Baum et al. 2003). Since they are long-lived, slow-growing, and late to reproduce, their population growth is particularly sensitive to changes in growth and mortality of older juveniles and adults (Crowder et al. 1994; Crouse 1999; Heppell et al. 1999). Despite the demographic importance of large juveniles, their ecology and life history remain poorly understood for large marine vertebrates.

Delayed maturity, high mobility, and freedom from having to return to a central location to reproduce enable juvenile migratory megafauna to choose among ocean-wide habitats and foraging strategies. Because prey availability, predation risk, and other factors often vary among habitats, differential habitat use and corresponding foraging strategies may result in differential growth, survival and ultimately fecundity among individuals of the same species or population (Skulason and Smith 1995; Bolnick et al. 2003). Variation in the foraging strategies of juveniles and their

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resulting vital rates could have profound implications for the demography and conservation of migratory megafauna.

Loggerhead sea turtles exhibit several life history patterns that make them useful subjects for examining the effects of alternative foraging strategies. During their extremely long juvenile life stage that lasts upwards of three decades (Snover 2002; Heppell et al. 2003), the animals are opportunistically omnivorous and capable of transoceanic movements: they have no parental care or social structure; and they are not tied to a central location for reproduction, enabling them to choose from an ocean wide range of habitats (Bolten 2003). As juveniles, loggerheads use both oceanic and neritic habitats (Pitman 1990; Polovina et al. 2000; Bolten 2003; McClellan and Read 2007), and they have long been thought to undergo an ontogenetic habitat shift from oceanic to neritic habitats upon reaching a size threshold of ~48 cm (Carr 1987; Bjorndal et al. 2000; Bolten 2003).

Based on annual ring spacing in sectioned femurs, Snover (2002) found that large juvenile loggerheads in the Atlantic may experience as much as a thirty percent increase in growth rates after shifting from oceanic to neritic habitats, suggesting that foraging in neritic habitats is highly advantageous. This is presumably due to higher availability and quality of prey in neritic compared to oceanic habitats (Snover 2002). As a result of this difference in growth rate, habitat choice may have important indirect effects on demographic rates. But a growing body of evidence

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suggests that this ontogenetic shift may be facultative and reversible, and that some juveniles may remain in (or return to) oceanic habitats until reaching maturity, despite the potential growth advantages of neritic foraging (Polovina et al. 2006; McClellan and Read 2007).

Nesting loggerheads tracked from Japanese and West African rookeries show within-population differences in habitat use that are distinct enough to be classified as a trophic polymorphism (Hatase et al. 2002; Hawkes et al. 2006). In these populations, adult females that forage in productive neritic habitats are significantly larger than those foraging in oligotrophic oceanic habitats. Because growth is negligible once reproductive maturity is reached in sea turtles (Carr and Goodman 1970; Limpus and Limpus 2003), it is possible that individuals foraging in neritic habitats mature earlier or at larger sizes than those foraging in oceanic habitats (Hatase et al. 2002; Hawkes et al. 2006). Though not tested empirically, a reasonable hypothesis is that larger, neritic-foraging nesters may have greater lifetime reproductive output because they mature earlier and fecundity increases with size in loggerheads (Frazer and Richardson 1986; Tiwari and Bjorndal 2000; Broderick et al. 2003).

Juvenile loggerheads in the North Pacific depart from their Japanese rookeries as hatchlings and frequent two regions, the oceanic central North Pacific (CNP) and neritic habitats of the Baja California Peninsula, Mexico (BCP). Because the oceanographic factors that produce prey in the two regions are different (Espinosa-

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Carreon et al. 2004; Legaard and Thomas 2006; Palacios et al. 2006; Polovina et al. 2006), patterns of prey abundance and quality also differ between these regions. In the CNP, juvenile loggerheads feed opportunistically on patchily distributed epipelagic prey (Parker et al. 2005), and they move thousands of km each year tracking these prey through fronts and eddies (Polovina et al. 2000; Polovina et al. 2004; Polovina et al. 2006; Kobayashi et al. 2008). At the BCP, juvenile loggerheads frequent a coastal high-use area (Peckham et al. 2007), and they feed primarily on pelagic red crabs (Pleuroncodes planipes)(Ramirez-Cruz et al. 1991; Nichols 2003).

Given the probable advantages of neritic foraging in terms of both juvenile growth and adult fecundity (Hatase et al. 2002; Snover 2002; Hawkes et al. 2006; Hatase et al. 2007), alternative foraging strategies between juvenile loggerheads in the North Pacific could convey large differences in fitness. Here I evaluate this general hypothesis by directly comparing the diet, movement, habitat use, and size frequency of juvenile loggerheads between neritic BCP and oceanic CNP habitats.

METHODS

Satellite telemetry

The movements of loggerhead turtles were monitored using satellite transmitters deployed on 63 animals. In the CNP, observers on Hawaii-based longline fishing vessels attached Argos satellite-linked transmitters to twenty-three loggerhead turtles

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taken as bycatch from 1997-2001. At BCP, a total of 40 loggerheads were either

captured by hand from small fishing boats (38 individuals) or retrieved living from

bottom-set longlines (2 individuals), instrumented, and released as above. Satellite

transmitters were attached to turtle carapaces using polyester resin and fiberglass

cloth (Balazs et al. 1996) and monitored via the Argos satellite system. Portions of

this loggerhead satellite telemetry dataset have been used to examine distributional

relationships with oceanographic fronts (Polovina et al. 2000), diving behavior

(Polovina et al. 2003), and foraging behavior (Polovina et al. 2004), and to

characterize high-use areas (Polovina et al. 2006; Peckham et al. 2007), bycatch rates

(Peckham et al. 2007), and pelagic habitat utilization (Kobayashi et al. 2008). Here I

present fourteen new tracks in addition to tracks previously reported from the BCP

(Nichols et al. 2000; Peckham et al. 2007).

Movement analysis

Raw Argos-derived positions from all tracks were filtered based on a maximum rate

of travel of 5 km h-1. In order to obtain data that were equally spaced temporally,

consecutive ARGOS hits were interpolated every 12 h following the methods of

Tremblay et al. (2007). Multi-individual utilization distributions (UD) were

determined with a Gaussian kernel density analysis of the positions from tracks from

each habitat. From the combined dataset of all interpolated positions, an index of

turtle residence probability per unit area was derived as follows: 1) the number of

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locations per 5 km2 cell was calculated and 2) each of these totals was weighted by multiplying it by the number of individual turtles using that cell. In this way, cells frequented by more individuals for extended periods of time were given more importance, thus emphasizing multi-individual high-use areas. Contours representing various proportions of the whole probability surface were computed. The total area within each contour was then calculated.

Habitat use metrics were calculated by region as the mean of mean values for each track analyzed. Displacement was calculated as the straight line distance between release and furthest recorded locations. Straightness Index (SI) was calculated as the ratio of the straight line distance between the release location and last transmitted location over the total distance traveled between filtered points with a range of 0 (tortuous) to 1 (straight) (Batschelet 1981). All calculations took into account the curvature of the earth's surface. Sea surface temperature (SST) data from the NOAA/NASA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder product was merged at 0.05 degree, 8-day resolution to the satellite track data to calculate mean SST experienced by each turtle (http://www.nodc.noaa.gov/sog). Ocean surface chlorophyll-a pigment concentrations from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) were also merged at 0.1 degree, 8-day resolution with the satellite track data to calculate mean chlorophyll-a concentrations experienced by each turtle (http://oceancolor.gsfc.nasa.gov/SeaWiFS). Individual turtle track durations, displacement from release location, average speed, and

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straightness of tracks were compared between habitats using independent t-tests (SYSTAT 2007).

Diet

During the course of standardized stranding surveys conducted from 2003-2007 along the 44.3km Playa San Lázaro, Baja California Sur (Peckham et al. 2008), eighty-eight loggerhead stomachs were collected for diet analysis. Stomachs were removed from the stranded turtles, transported to a field facility, and frozen as soon after collection as possible. Gross observations of stomach contents were made, and all contents including both hard and soft parts were sorted to the lowest identifiable taxon. Frequency of occurrence of major components was calculated by dividing the number of stomachs in which the prey item occurred by the total number of turtle stomachs examined. Stomach contents of turtles from the BCP were compared with those reported from juvenile turtles of the CNP, which were processed in the same way (Parker et al. 2005). Morisita's index was used to evaluate the similarity of observed diets from the two regions on a scale from 0 (no overlap) to 1 (complete overlap)(Horn 1966; Barrett et al. 1990).

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Relative energetics and habitat quality of alternative foraging strategies

To compare relative diet quality and energetic costs between habitats, I compared the movement rates of turtles, mean energy density of prey, and SST and chlorophyll-a concentrations experienced by turtles in the two habitats. Dry weight energy densities (kJ g-1) were obtained from the literature for each species encountered or for the closest taxonomic order available. The mean value of the energy densities of all diet items present in more than 15% of stomachs was calculated as a measure of the relative energy quality of diets between regions. As ectotherms, the metabolic rate of loggerheads is strongly influenced by water temperature. Thus, I compared satellite-derived SST experienced by turtles as an index of thermal energetic costs between habitats. As proxies for primary production and, indirectly, prey abundance, I also compared satellite-derived chlorophyll-a concentrations between the two habitats. Relative rates of primary production are well correlated with secondary productivity (Smith et al. 1986; Ainley et al. 2005; Etnoyer et al. 2006; Polovina et al. 2006; Gremillet et al. 2008). Chlorophyll-a concentrations and SST experienced by each turtle were compared between habitats using independent t-tests (SYSTAT 2007). A Satterthwaite adjustment was used to address the large difference in variance in chlorophyll-a concentrations between CNP oceanic and BCP neritic habitats. All averages are reported as Mean ± SD in the text.

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Size distributions

Length frequency distributions were compared between turtles tracked from the CNP and BCP habitats in order to ascertain whether the observed difference in foraging strategy between regions was related to turtle size. Lengths reported as straight carapace length (SCL) were converted to curved carapace length (CCL) following the regression derived in Peckham et al. (2008; N=163, r2=0.93, P<0.001):

$$SCL = (0.932 \times CCL) + 0.369$$

Demographic analyses

To explore the possibility that variation in growth rate between juvenile strategies could affect overall population dynamics, I manipulated the demographic model used to make the 2001 NMFS-SEFSC loggerhead stock assessment (NMFS-SEFSC 2001). Because there is no specific parameter for growth rate in this stage-structured model, I lengthened the durations of the model's two "benthic juvenile" stages by 30%, simulating the decrease in growth rate expected for turtles that do not recruit to neritic habitats (Snover 2002) in order to determine the resulting effect on lambda. To explore the possibility that reduced predation pressure may counteract the energetic disadvantages of oceanic foraging by juvenile turtles, I further manipulated the model to determine what proportional changes in survivorship would balance the decreased growth rates expected to result from juveniles remaining in oceanic

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habitats until reaching maturity. To do so I systematically changed the duration of the two "benthic juvenile" stages from 10 – 50% and calculated the corresponding change in survivorship of those stages required to maintain a constant value of lambda.

RESULTS

The utilization distributions (UDs) of turtles tracked from the BCP versus the CNP were widely divergent (Fig. 1). The number of days turtles were tracked from each region were not significantly different (t = 0.912, df = 61, P = 0.365). The 40 BCP juveniles spent the majority of the mean 144 ± 98 days they were tracked in a geographically limited area on the continental shelf in the Bight of Ulloa, while the 23 CNP turtles ranged around the Central North Pacific during the mean 123 ± 75 days they were tracked. BCP tracked turtles were marginally larger than CNP tracked turtles (t = 1.951, df = 61, P < 0.056), and there was broad overlap in the length frequency of individuals tracked between regions (Table 1).

The UDs of the 40 turtles satellite tracked from the BCP were two orders of magnitude smaller across all UD contours than those from the 23 individuals from CNP (Figs. 1 and 2). CNP turtles on average traveled much further per unit time (Fig. 3). The linear fit of median cumulative distance traveled per day for CNP turtles had a slope of 19.21 versus 9.44 for BCP turtles. CNP turtles displaced significantly further (1,328 ± 867 km vs. 234 ± 272 km; t = -7.414, df = 61, P <

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0.000), faster (1.02 ± 0.32 vs. 0.40 ± 0.15 km hr-1; t = -10.259, df = 65, P < 0.000), and straighter (straightness index: 0.48 ± 0.18 vs. 0.14 ± 0.15; t = 8.038, df = 61, P < 0.000) than BCP turtles (Table 1).

Stomach contents of juvenile loggerheads in neritic habitats of the BCP differed from those in oceanic habitats of the CNP (Table 1, Parker et al. 2005). Prey items present most frequently in the stomachs of BCP turtles were fish - searobins, Prionotus spp (30% of stomachs), sand perches Diplectrum spp (23%), and lizardfish Synodus spp (11%), and crustaceans - the pelagic red crab, Pleuroncodes planipes (14%), Platymera gaudichaudii (6%) and Herisquilla ensigera (5%). When present in BCP stomachs, fish and crustaceans were generally found in large quantities. The most frequently occurring prey items in the stomachs of CNP turtles were pelagic gastropods – Janthina spp (75% of stomachs) and Carinaria cithara (50%) - and crustaceans that grow on loggerheads – hitchhiker crabs Planes spp. (56%) and gooseneck barnacles Lepas spp. (52%). The pelagic gastropods were found in great quantities, but the crustaceans were found in very low quantities and so are unlikely to be important prey items for CNP turtles, although they were present in a large proportion of stomachs. Salps and cnidarians occurred relatively frequently (21% and 25%, respectively). Similarity of prey species composition between the two regions was low (Morisita similarity index of 0.19).

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Juveniles foraging in BCP neritic habitats most likely enjoy an energetic advantage over those foraging in the oceanic CNP habitat. As reported above, within the BCP neritic habitat, turtles moved significantly slower (Table 1). The mean energy density of diet items was different between regions. The diet items of neritic foragers had a mean energy density of 18.1 kJ g-1, whereas the mean energy density of the diet items of oceanic foragers was 11.2 kJ g-1 (Table 2). Mean water temperatures experienced by turtles foraging in the CNP oceanic habitat ($19.74 \pm 1.77^\circ$C) were significantly cooler than those experienced in BCP neritic habitats ($24.00 \pm 1.88^\circ$C; t = 8.884, df = 61, P < 0.000; Table 3). Mean of mean chlorophyll-a concentrations experienced by turtles foraging in the CNP oceanic habitat (0.131 ± 0.038 mg m-3) were significantly lower than those experienced in BCP neritic habitats (0.828 ± 0.562 mg m-3; t = 7.81, df = 39.8, P < 0.000; Table 3). The variance in mean chlorophyll-a concentrations experienced by BCP turtles (0.562) was an order of magnitude higher than that experienced by CNP turtles (0.038), but the minimum mean chlorophyll-a concentration experienced by a BCP turtle (0.192 mg m-3) was greater than the maximum experienced by CNP turtles (0.188 mg m-3). Thus, all of the indices available in this study (prey quality, environmental productivity, movement, water temperature) suggest that BCP turtles enjoy a substantial energetic advantage over CNP oceanic foraging juveniles (Table 3).

The length frequencies of loggerheads tracked from the CNP (N = 23; 67.0 ± 11.2 cm CCL) and the BCP (N = 40; 71.4 ± 6.9 cm CCL) were not significantly different,

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but power to detect a difference was low (0.454). The 23 turtles captured from 1997-2000 in the CNP habitat were larger on average (67.0 ± 11.2 cm CCL.; Table 2) than the 63 loggerheads measured at BCS in 1999 (62.0 ± 13.0 cm CCL), though not significantly so (t = -1.695, df = 84, P < 0.094; (Gardner and Nichols 2001).

Manipulation of the 2001 NMFS-SEFSC loggerhead stock assessment model based on parameters measured and estimated for the North Atlantic loggerhead population suggest that differences in growth rate between the two juvenile strategies could impact lambda. When I lengthened the durations of the model's two "benthic juvenile" stages by 30% to simulate the decrease in growth rate expected for juveniles that remain foraging in oceanic habitats (Snover 2002), the model produced a decrease in lambda from 0.973 to 0.958. With all other parameters held constant, the relationship between changes in survivorship required to maintain a constant value of lambda was linear (Fig. 4); relatively small changes in annual survivorship balanced larger changes in growth rate of larger juveniles. Specifically, based on my manipulation of the model the 30% increase in the durations of the two "benthic juvenile" stages expected for juveniles remaining in oceanic habitats would be counteracted in terms of lambda by a 1.85% increase in average survivorship.

DISCUSSION

Juvenile loggerheads of the North Pacific tend to occur in one of two distinct habitats for extended periods, the oceanic waters of the Central North Pacific and the neritic

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waters of the Baja California Peninsula. The biological oceanography of these two habitats fundamentally differs in terms of temperature, productivity, and current regimes as well as the variability of each of these factors. The CNP oceanic habitat is characterized by lower primary production (0.01-1.00 mg m-3 chlorophyll-a), lower SST (5-26°C), and strong seasonal variability relative to the BCP habitat (Polovina et al. 2001; Kobayashi et al. 2008). Juvenile loggerheads in the CNP are associated with the Transition Zone Chlorophyll Front (TZCF) and the Kuroshio Extension Bifurcation Region (KEBR), dynamic mesoscale features characterized by elevated primary productivity (chlorophyll-a concentrations of 0.11-0.31 mg m-3) (Polovina et al. 2000; Polovina et al. 2001; Polovina et al. 2004; Polovina et al. 2006; Kobayashi et al. 2008) and associated secondary productivity (Polovina et al. 2006). Seasonally, the TZCF undergoes latitudinal shifts of ~1000 km (Polovina et al. 2001; Polovina et al. 2004), forcing oceanic predators such as loggerhead turtles to undertake seasonal migrations in order to take advantage of TZCF productivity (Polovina et al. 2001, Polovina et al. 2004). In addition, loggerheads must negotiate strong surface currents associated with the features such as the prevailing easterly geostrophic currents of 0.15 - 0.24 km hr-1 (Polovina et al. 2004). In contrast, juveniles foraging at BCP neritic habitats probably enjoy an energetic advantage by moving less distance through water of metabolically more favorable temperature in which they catch higher quality, more abundant prey (Table 3). The BCP neritic habitat occupied by loggerheads is located at the southern end of the highly productive California Current and characterized by year-round coastal upwelling

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conditions with mesoscale eddies, and fronts with seasonally variable sea surface temperatures (15-26°C), and high chlorophyll-a concentrations (0.2-19.0 mg m-3) (Espinosa-Carreon et al. 2004; Legaard and Thomas 2006; Gonzalez-Rodriguez 2008). Generally, primary production in the region remains high relative to the rest of the Pacific Ocean with chlorophyll-a concentrations rarely dropping below 1.0 mg m-3, and surface currents are weak and variable in direction (Espinosa-Carreon et al. 2004; Legaard and Thomas 2006; Gonzalez-Rodriguez 2008).

The differences in the biological oceanography of the two habitats result in proximal differences in turtle movement and diet. CNP turtles moved two orders of magnitude further (Figs. 1-2) and twice as fast (Fig. 3; Table 1) in comparison with BCP loggerheads, presumably in order to track the high productivity of the TZCF and KEC (Polovina et al. 2001; Polovina et al. 2006; Kobayashi et al. 2008). Concentrations of chlorophyll-a experienced by CNP turtles in this study were considerably higher (0.131 ± 0.038 mg m-3) than if they had remained in any one area of the CNP as small as that utilized by BCP turtles. In contrast, as a result of the higher overall primary productivity of the BCP neritic habitat, turtles foraging there experienced significantly higher concentrations of chlorophyll-a (0.828 ± 0.562 mg m-3) while moving significantly less.

Divergence in the UDs of turtles tracked from the BCP versus the CNP most likely reflect fundamental differences in the distribution, abundance, and quality of prey

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between the two regions (Fig. 1). The consistently higher primary productivity of the BCP neritic habitat likely translates into higher prey abundance for foraging loggerheads. Demersal fish and red crabs are abundant in the BCP neritic habitat, with red crabs present year-round at high densities (20-30 tons km-2) (Aurioles-Gamboa 1995; Robinson et al. 2004). In contrast, the TZCF habitat has lower primary production and productivity is generally patchy and ephemeral (Polovina et al. 2004; Parker et al. 2005; Kobayashi et al. 2008).

Because quantitative diet data were not available, my assessment of the relative energy density between habitats was necessarily qualitative. My approach probably overestimates the actual energy density for CNP oceanic foragers because: 1) high energy density items such as decapods, fish eggs, and cephalopods were found in low quantities, though present in 20-50% of stomachs (Parker et al. 2005), and 2) salps and scyphozoans are underestimated in loggerhead diet studies because they are digested quickly, leaving no identifiable remains (Plotkin et al. 1993). Thus, I found that CNP turtles foraged on a greater diversity of prey of considerably lower mean energy density. Based on optimal foraging theory, by which predators should maximize their intake of high quality prey (Stephens and Krebs 1986), the prevalence and diversity of low energetic quality prey in the diet of oceanic juveniles suggests that the higher quality prey consumed by neritic foragers are less accessible or nonexistent in the CNP oceanic habitat.

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While CNP juvenile loggerheads had to travel greater distances and at higher speeds to fulfill their nutritional requirements (Table 1), movements of oceanic species can also be influenced by current patterns (Gaspar et al. 2006; Shillinger et al. 2008). Overall geostrophic currents were similar in velocity between the two regions (0.0 – 0.7 km hr-1)(Polovina et al. 2004; Gonzalez-Rodriguez 2008), although Polovina et al. (2000, 2006) found that CNP turtles actively swim against dominant westward flowing geostrophic currents of 0.15 - 0.24 km hr-1 resulting in a 50% reduction in their net westward displacement, suggesting that CNP turtles expend considerably more energy in swimming than indicated by their observed travel rates of 1.02 ± 0.32 km hr-1. In contrast, the oceanography of the BCP shelf area is dominated by meanders, eddies, and filaments that result in variable direction of surface currents (Espinosa-Carreon et al. 2004; Soto-Mardones et al. 2004; Gonzalez-Rodriguez 2008). These currents in turn cause retention of nutrients, phytoplankton, and zooplankton, including pelagic red crabs (Aurioles-Gamboa 1992; Lavaniegos 1994; Robinson et al. 2004; Soto-Mardones et al. 2004; Gonzalez-Rodriguez 2008). Thus juvenile turtles foraging in the BCP region could be "retained" along with their pelagic red crab prey, resulting in reduced energy expended against geostrophic currents in comparison with CNP turtles. In fact, the observed tortuous and circumscribed tracks of turtles at BCP could result from relatively passive transport of turtles by local currents, suggesting that the observed mean travel rate for BCP turtles (0.40 ± 0.16 km hr-1) could represent some degree of passive transport rather

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than active swimming and could therefore be an overestimate of energy expenditure by BCP turtles.

Field studies of the effects of water temperature on energy budgets of juvenile loggerheads have not been conducted (Wallace and Jones 2008). The higher water temperatures experienced by turtles at BCP neritic habitats may confer higher metabolic rates (Lutz et al. 1989; Hochscheid et al. 2004). But higher water temperature also confers better energy assimilation for ectotherms including enhanced prey detection, prey capture, ingestion, digestion, and absorption of food (Congdon 1989; Dunham et al. 1989; Angilletta 2001). Higher water temperatures are reported to be energetically favorable for sea turtles, as long as they do not approach upper thermal limits (Bjorndal 1980). Thus, the higher water temperatures that turtles foraging at BCP habitats experienced may augment the energetic advantage by increasing food processing and assimilation efficiencies, although this may come at a cost of increased basal metabolic rate.

Alternative foraging strategies

The different oceanography between the CNP oceanic and BCP neritic habitats results in different loggerhead foraging strategies. Foraging plasticity associated with habitat choice has been found in a variety of marine turtles, including leatherbacks (Hays et al. 2004) and green turtles (Hays et al. 2002; Reich et al. 2007). It is well

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established that loggerheads take advantage of both oceanic and neritic habitats as both juveniles (Bolten 2003; McClellan and Read 2007) and adults (Hatase et al. 2002; Hawkes et al. 2006; Hatase et al. 2007). Thus it is not surprising that juvenile loggerheads in the North Pacific utilize different habitats and employ different foraging strategies in doing so.

An important and striking difference between North Pacific and North Atlantic loggerheads is that in contrast to the western North Atlantic, a portion of the juvenile loggerheads in the North Pacific appear to remain in oceanic habitats until reaching maturity without venturing into neritic habitats. Previous studies have hypothesized that loggerheads undertake an ontogenetic habitat shift by which younger juveniles initially utilize oceanic habitats and eventually recruit to neritic habitats when they reach a size threshold of ~48cm (Carr 1987; Bjorndal et al. 2001; Snover 2002; Bolten 2003). This argument was developed based on apparent size segregation between oceanic and neritic juveniles in the North Atlantic, with smaller individuals found exclusively in oceanic habitats (Bolten 2003). However, a recent tracking study shows that some juveniles continue to switch between neritic and oceanic habitats of the northwest Atlantic, suggesting that the ontogenetic shift is facultative rather than definite as originally theorized (McClellan and Read 2007).

As such, two hypotheses could account for the use of the two different regions of the North Pacific by juvenile loggerheads: 1) an ontogenetic habitat shift; or 2)

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alternative foraging strategies. It is unlikely that the pattern I have documented reflects an ontogenetic shift for two reasons: 1) If an ontogenetic shift occurs from CNP oceanic to BCP neritic habitats, a clear segregation in size frequencies would be expected between the two habitats, as has been demonstrated from the Atlantic (Bolten 2003). But turtles tracked in the CNP vs. the BCP were not significantly different in size (Table 1). Thus, the most likely explanation for the use of these two habitats is that they represent alternative foraging strategies for North Pacific juvenile loggerheads with juveniles remaining in either the oceanic or neritic habitats for extended periods, perhaps until reaching maturity. 2) none of 150+ juveniles captured and tracked to date from the CNP (Polovina et al. 2000; Polovina et al. 2004) or headstarted and released from Japan (Polovina et al. 2006) moved towards neritic habitats of either Mexico or Japan. Instead, juveniles tracked from the CNP actively maintained their positions in the oceanic habitats of the CNP, leading Polovina et al. (2006) to conclude that "a significant number of juveniles use pelagic habitat for their entire juvenile phase." Nor did any of 45 turtles tracked from the neritic habitats of the BCP move to occupy the oceanic habitats of the CNP, although five individuals migrated to or towards Japan, well south of the CNP foraging area (Nichols et al. 2000; Nichols 2003; Peckham et al. 2007). Thus I found that North Pacific loggerheads have two distinct, non-overlapping foraging strategies.

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Alternative life history strategies?

Given the apparent energetic advantages of neritic foraging (Table 3), extended residence by juvenile loggerheads in neritic vs. oceanic habitats is likely to produce differential vital rates including growth, age and size at maturity, fecundity, and survivorship. Age and size at maturity are strongly influenced by growth rates and are fundamentally important life history traits due to their effects on fecundity and survival (Stearns 1996). Growth rates are highly variable in reptiles and other taxa, due in part to resource limitation (Caswell 1983; Stearns and Koella 1986). Loggerhead turtle growth rates are highly variable across their range, and these differences have been attributed to several factors including quality and quantity of prey as well as foraging habitat (Van Buskirk and Crowder 1994; Klinger and Musick 1995; Bjorndal et al. 2003). Snover (2002) found that juvenile loggerheads grew up to 30% faster upon shifting to neritic from oceanic habitats in the Northwest Atlantic suggesting potential life history advantages to juveniles that forage neritically. Similarly, the energetic advantages enjoyed by juveniles foraging at BCP neritic habitats likely enable them to achieve higher growth rates than those foraging in CNP oceanic habitats.

These increased growth rates likely lead to either an earlier age or greater size at first reproduction. Because growth is negligible once reproductive maturity is reached (Carr and Goodman 1970; Limpus and Limpus 2003) and fecundity increases with

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size in sea turtles and loggerheads in particular (Frazer and Richardson 1986; Van

Buskirk and Crowder 1994; Tiwari and Bjorndal 2000; Broderick et al. 2003),

females that reach maturity at larger sizes should have higher fecundity. Loggerheads

may also benefit from larger adult size because smaller turtles are probably more

susceptible to predation by sharks (Heithaus et al. 2002; Bolten 2003). Earlier

maturation would also be advantageous due to the fewer years of mortality risk prior

to reproduction (Stearns 1996).

These differences in the size or age of first reproduction between the CNP and BCP

have important demographic implications. Based on the results of my manipulation

of the 2001 NMFS-SEFSC loggerhead stock assessment model, differences in

growth rates of 30% and their resulting differences in duration of the juvenile phase

alone between the two strategies could result in an approximately 1.5% reduction in

λ for oceanic foraging juveniles.

Demographic implications

All else equal, neritic foraging would seem to be the far better strategy for juvenile

loggerheads. But how then could an oceanic juvenile strategy with slower growth

rates, later maturity, smaller adult size and lower fecundity (or some combination of

these) be maintained? Juveniles maximize their fitness by increasing their probability

of survival to reproduce through a balance of optimizing growth rates and

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minimizing predation risk (Werner and Gilliam 1984; Mangel and Clark 1986). In many cases there are trade-offs in which habitats that afford higher growth rates come with higher predation risk (Lima and Dill 1990; Houston et al. 1993). Higher predation rates in neritic habitats have been assumed to cause smaller juvenile loggerheads to forego the advantages of neritic foraging until they are large enough to avoid predation (Carr 1987; Snover 2002; Bolten 2003). Predation risk of sharks limits the use of high quality foraging areas by sea turtles in habitats with intact predator communities (Heithaus et al. 2007; Heithaus et al. 2008), and higher predation rates have been observed in juvenile loggerheads newly arrived to neritic habitats in Australia relative to larger adults (Limpus and Limpus 2003).

My manipulation of the NMFS-SEFSC model should be interpreted with caution because the parameters of the model were derived from or estimated for the North Atlantic loggerhead population. Assorted life history parameters are known to vary between Atlantic and Pacific populations of loggerheads and other turtles (Van Buskirk and Crowder 1994; Wallace et al. 2006), and these differences could affect the magnitude of the effects I examine here. With that caveat, my results show that relatively small advantages in survivorship could counteract large costs in terms of decreased growth rates resulting from juveniles foraging in oceanic rather than neritic habitats. However, my manipulation of the model examined the effects of growth rate on stage duration, but did not factor in the additional advantages to higher growth rates including size at maturity and resultingly higher reproductive

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output expected from neritic foraging. Incorporating the advantages in reproductive output associated with neritic foraging into the model would clearly increase the margin of survivorship advantage required to justify the oceanic strategy.

Despite the conventional wisdom that oceanic habitats offer lower relative predation risk for sea turtles (Carr 1987; Bolten 2003), there are no comparable data on the relative predation pressures experienced by sea turtles or even data concerning predator density between neritic and oceanic habitats. Furthermore, predators concentrate at the same oceanographic features as turtles including high productivity fronts and eddies (Laurs et al. 1984; Polovina et al. 2001; Worm et al. 2003), so while the overall density of predators may be lower in the open ocean than in neritic habitats, predation risk for loggerheads at favored oceanic foraging features could actually be comparable to neritic habitats. In either case, the abundance of sharks and other large predators has been significantly reduced by fishing and bycatch throughout the world in recent decades (Baum et al. 2003; Myers and Worm 2003; Worm et al. 2005; Worm et al. 2006). Depletion of sharks has been very high in certain coastal habitats (Myers et al. 2007) including the BCP (Holts et al. 1998; Sala et al. 2004).

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Conservation implications

Bycatch of juvenile loggerheads was high at the CNP oceanic habitat in high-seas driftnets until they were banned in 1991 (Wetherall et al. 1993), and bycatch continues to be high in high-seas longlines (Lewison et al 2004). But currently bycatch is considerably higher in the BCP neritic habitats due to small-scale fisheries (Peckham et al. 2007; Peckham et al. 2008). If BCP neritic foraging juveniles realize higher growth rates, size and age at maturity and fecundity (or any one of these), they could have higher reproductive potential and therefore a greater per turtle potential contribution to lambda and population recovery. The question remains how survivorship varies between the two habitats and the relative contribution of animals in these two environments to the overall population trajectory of loggerheads in the North Pacific Ocean. The higher growth and fecundity and the high bycatch mortality rate together imply that conservation efforts directed at mitigating or even eliminating bycatch at the BCP loggerhead foraging high use area could offer considerable demographic leverage towards recovery of the overall population.

CONCLUSIONS

The fate of juvenile life history stages in sea turtles are important determinants of population change (Crouse et al. 1987; Crowder et al. 1994). As demonstrated here, the interaction of decades-long juvenile stages with ranges that span fundamentally different habitats can produce divergent life history strategies between juveniles of

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the same population. To evaluate the importance of these alternative life history strategies to population growth in loggerhead turtles, we need to more definitively determine juveniles' fidelity to oceanic or neritic habitats and the durations over which they inhabit them. Considered more broadly, my findings suggest that the ecologies of juveniles of other marine megafauna with delayed reproduction may play important roles in determining their population dynamics. Elucidating the juvenile ecologies of marine megafauna is thus an important priority for understanding their ecology and guiding their management.

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Table 1. Habitat use metrics for loggerhead turtles tracked via satellite telemetry from Central North Pacific and along the Baja California Peninsula, 1996-2007 (means of mean individual values).

	CNP Oceanic mean±SD	CNP Oceanic range	BCP Neritic mean±SD	BCP Neritic range	t-test P-value
N (turtles)	23		40		
CCL (cm)	67.0 (11.2)	51-89	71.4 (6.9)	59-91	0.056
Track duration (d)	123 (75)	9-270	144 (98)	10-424	0.365
Displacement (km)	1328 (867)	243-3828	234 (272)	32-1491	0.000
Mean speed (km hr-1)	1.02 (0.32)	0.6-1.9	0.40 (0.16)	0.10-0.90	0.000
Straightness Index (SI)	0.48 (0.18)	0.14-0.87	0.14 (0.15)	0.00-0.73	0.000

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Table 2. Percent occurrence of major prey items in loggerhead stomachs from the Baja California Peninsula (N = 89 stomachs) and the Central North Pacific (N=52; data from Parker et al 2005). Energetic values were obtained from the following sources: [1](Castro-González et al. 1998); [2](Castro-Gonzalez et al. 1995); [3](Chilton and Bull 1986); [4](Votier et al. 2004); [5](Szaniawska and Wolowicz 1986). Mean energetic values were calculated from all diet items occurring in more than 15% of stomachs.

	CNP Oceanic	kJ g^{-1}	BCP Neritic	kJ g^{-1}
Fish	7.7		85.2	20.1[1]
Decapod s	55.8	16.2[2]	31.8	16.2[2]
Cephalopods	21.2	20.7[1]	1.1	
Pelagic gastropods	75.0	15.2[3]	0.0	
Barnacles (*Lepas* spp.)	51.9	1.9[4]	0.0	
Anthropogenic debris	34.6	0.0	0.0	
Scyphozoa (*V. velella*)	25.0	2.9[1]	0.0	
Fish eggs	25.0	24[1]	0.0	
Pyrosoma	21.0	4.9[1]	0.0	
Amphipods	46.2	15.1[5]	0.0	
Mean kJ^{-1}		11.2		18.2

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Table 3. Relative advantage of energetic factors for loggerheads at CNP oceanic vs. BCP neritic foraging habitats

	CNP Oceanic	BCP Neritic	Energetic advantage
Prey abundance	low	high	Neritic
Prey quality (kJ^{-1})	11.2	18.2	Neritic
Movement rate (km hr^{-1})	1.02±0.32	0.40 ± 0.16	Neritic
SST (°C)	19.74±1.77	24.00 ± 1.88	Neritic
chlorophyll-a (mg m^{-3})	0.131 ± 0.038	0.828 ± 0.562	Neritic

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Figure 1. Utilization distributions of juvenile loggerhead turtles in the Central North Pacific (blue gradient) and at Baja California Peninsula (red gradient).
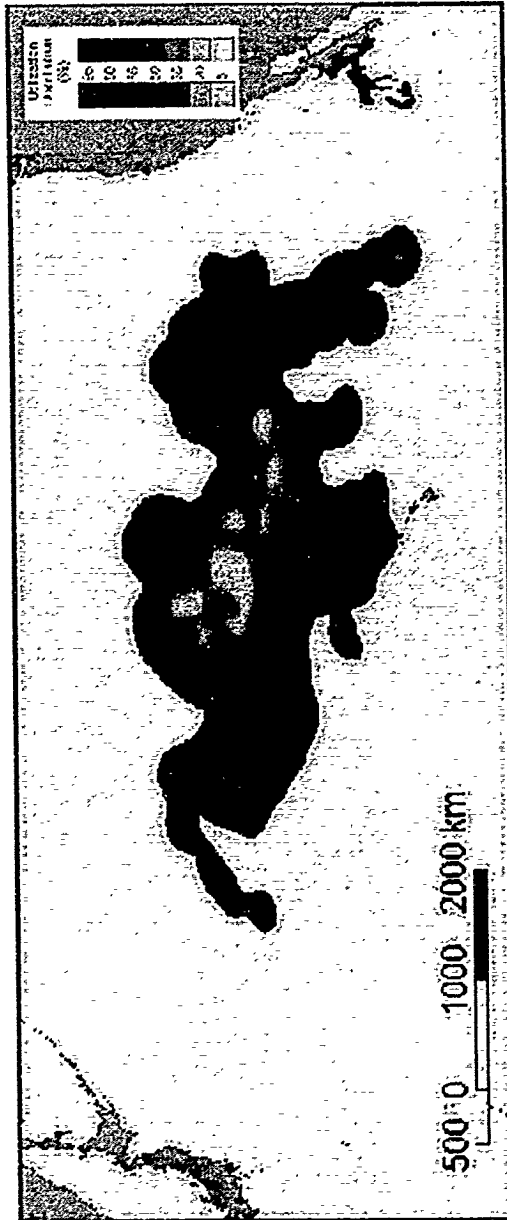
56

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Figure 2. Area of utilization distributions (UDs) of juvenile loggerheads at the Central North Pacific (blue) and Baja California Peninsula (red). Area of utilization distributions is two orders of magnitudes larger for CNP juveniles across all UD contours.
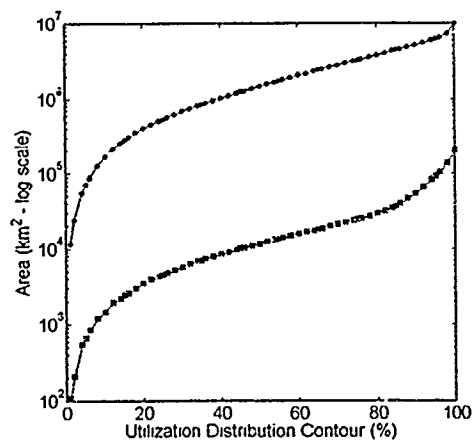

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Figure 3. Cumulative distance traveled by juvenile loggerheads satellite-tracked from Central North Pacific oceanic (blue; N = 23) and Baja California Peninsula neritic (red; N = 40) habitats. Bold lines represent linear fits of median values for each track by region.
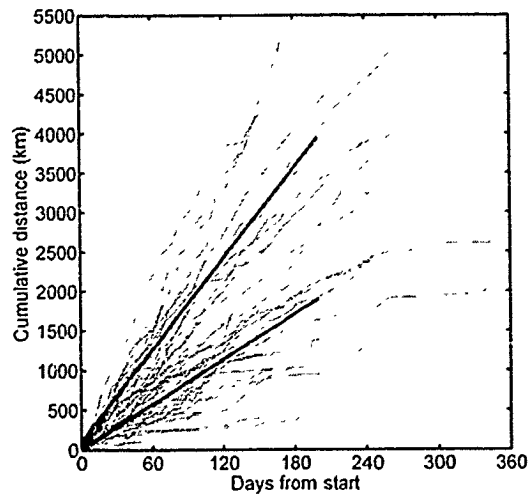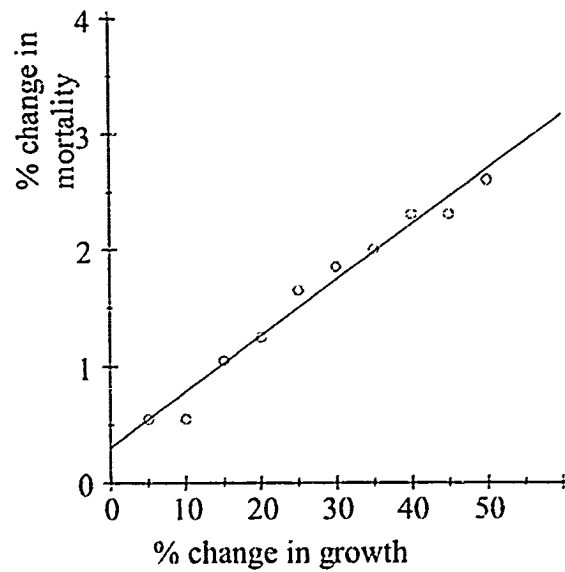

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Figure 4. Proportional change in juvenile mortality required to counteract proportional change in juvenile growth based on manipulation of the NMFS-SEFSC loggerhead stock assessment model.

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