

THE BOOK OF

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Enjoying and Learning
about Hawai'i's Sea Turtles

PETER BENNETT AND URSULA KEUPER-BENNETT

Abstract—Skeletochronological data on growth changes in humerus diameter were used to estimate the age of Hawaiian green sea turtles ranging from 28.7 to 96.0 cm straight carapace length. Two age estimation methods, correction factor and spline integration, were compared, giving age estimates ranging from 4.1 to 34.8 and from 3.3 to 49.4 yr, respectively, for the sample data. Mean growth rates of Hawaiian green sea turtles are 4–5 cm/yr in early juveniles, decline to a relatively constant rate of about 2 cm/yr by age 10 yr, then decline again to less than 1 cm/yr as turtles near age 30 yr. On average, age estimates from the two techniques differed by just a few years for juvenile turtles, but by wider margins for mature turtles. The spline-integration method models the curvilinear relationship between humerus diameter and the width of periosteal growth increments within the humerus, and offers several advantages over the correction-factor approach.

Age and growth of Hawaiian green sea turtles (*Chelonia mydas*): an analysis based on skeletochronology

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Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock

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Abstract

The green sea turtle is one of the long-lived species that comprise the charismatic marine megafauna. The green turtle has a long history of human exploitation with some stocks extinct. Here we report on a 30-year study of the nesting abundance of the green turtle stock endemic to the Hawaiian Archipelago. We show that there has been a substantial long-term increase in abundance of this once seriously depleted stock following cessation of harvesting since the 1970s. This population increase has occurred in a far shorter period of time than previously thought possible. There was also a distinct 3–4 year periodicity in annual nesting abundance that might be a function of regional environmental stochasticity that synchronises breeding behaviour throughout the Archipelago. This is one of the few reliable long-term population abundance time series for a large long-lived marine species, which are needed for gaining insights into the recovery process of long-lived marine species and long-term ecological processes.

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Keywords: Green sea turtle; Abundance; Population recovery; French Frigate Shoals; Hawaii

1. Introduction

The green turtle (*Chelonia mydas*) has a circum-tropical distribution with distinct regional population structures (Bowen et al., 1992) and is the most abundant large marine herbivore (Bjorndal, 1997). Globally, the green turtle has been subject to a long history of human exploitation with some stocks now extinct and others in decline (Frazier, 1980; Witzell, 1994). Yet despite being recognized as globally threatened (National Research Council, 1990) there are few reliable assessments of abundance status and trend of any green turtle stock (Chaloupka and Limpus, 2001). Reliable long-term estimates of population abundance trends are needed to support recovery planning (Foin et al., 1998), model sea turtle demography (Chaloupka, 2002) and are essential for developing a better understanding of long-term ecological processes (Inchausti and Halley, 2001).

For sea turtles, such population abundance estimates are based preferably on foraging ground capture-mark-

recapture programs that can provide more detailed sex- and age-class-specific demographic information (Limpus and Chaloupka, 1997; Chaloupka and Limpus, 2001, 2002). However, capture-mark-recapture programs in the marine environment for large and highly mobile species such as sea turtles are very difficult and expensive to conduct and so are rarely undertaken (Limpus and Chaloupka, 1997; Bjorndal et al., 2000). Nearly all assessments of sea turtle population abundance have been based on trawl based catch-per-unit-effort estimation, aerial survey based density estimation or, more commonly, by monitoring the number of females that come ashore each year to nest at stock-specific rookeries (see review in Chaloupka and Limpus, 2001).

Monitoring beach nesting is by far the easiest and least expensive means to assess green turtle population abundance but short-term surveys (<10 years) are inadequate for several reasons (Chaloupka and Limpus, 2001). Most notably because green turtles are long-lived (Limpus and Chaloupka, 1997; Zug et al., 2002) and females skip several nesting seasons due to nutritional constraints (Bjorndal, 1997). Hence, long-term nesting beach surveys are essential if this form of assessment of

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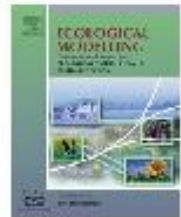
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Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago

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Abstract The somatic growth dynamics of green turtles (*Chelonia mydas*) resident in five separate foraging grounds within the Hawaiian Archipelago were assessed using a robust non-parametric regression modelling approach. The foraging grounds range from coral reef habitats at the north-western end of the archipelago, to coastal habitats around the main islands at the south-eastern end of the archipelago. Pelagic juveniles recruit to these neritic foraging grounds from ca. 35 cm SCL or 5 kg (~6 years of age), but grow at foraging-ground-specific rates, which results in quite different size- and age-specific growth rate functions. Growth rates were estimated for the five populations as change in straight carapace length (cm SCL year⁻¹) and, for two of the populations, also as change in body mass (kg year⁻¹). Expected growth rates varied from ca. 0–2.5 cm SCL year⁻¹, depending on the foraging-ground population, which is indicative of slow growth and decades to sexual maturity, since expected size of first-time nesters is ≥80 cm SCL. The expected size-specific growth rate functions for four populations sampled in the south-eastern archipelago displayed a non-monotonic function, with an immature growth spurt at ca. 50–53 cm SCL (~18–23 kg) or ca. 13–19 years of age. The growth spurt for the Midway atoll population in the north-western archipelago occurs at a much larger size (ca. 65 cm SCL or 36 kg), because of slower immature growth rates that might be due to a limited food stock

and cooler sea surface temperature. Expected age-at-maturity was estimated to be ca. 35–40 years for the four populations sampled at the south-eastern end of the archipelago, but it might well be >50 years for the Midway population. The Hawaiian stock comprises mainly the same mtDNA haplotype, with no differences in mtDNA stock composition between foraging-ground populations, so that the geographic variability in somatic growth rates within the archipelago is more likely due to local environmental factors rather than genetic factors. Significant temporal variability was also evident, with expected growth rates declining over the last 10–20 years, while green turtle abundance within the archipelago has increased significantly since the mid-1970s. This inverse relationship between somatic growth rates and population abundance suggests a density-dependent effect on somatic growth dynamics that has also been reported recently for a Caribbean green turtle stock. The Hawaiian green turtle stock is characterised by slow growth rates displaying significant spatial and temporal variation and an immature growth spurt. This is consistent with similar findings for a Great Barrier Reef green turtle stock that also comprises many foraging-ground populations spanning a wide geographic range.

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Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock

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ABSTRACT

The Hawaiian green sea turtle genetic stock is endemic to the Hawaiian Archipelago. This stock was depleted over the past century mainly due to over-exploitation that ceased during the 1970s following protection under the US Endangered Species Act. Nesting trends suggest the stock has been recovering but no formal stock assessment has been undertaken. So, we used a Bayesian state-space surplus-production model to describe Hawaiian green turtle population dynamics given limited data and uncertainty about sea turtle demography. Data series comprised commercial landings of green turtles reported from the Archipelago (1944–1973) and nester abundance recorded at the primary rookery on East Island, French Frigate Shoals (1973–2004). The model incorporated process and observation error and was fitted using Markov chain Monte Carlo simulation with a mix of informative and non-informative priors. We estimated that the Hawaiian green turtle stock was ca. 20% of pre-exploitation biomass when monitoring and protection began in the 1970s. The stock is estimated to be now ca. 83% of pre-exploitation biomass with an intrinsic growth rate ca. 5.4% pa (95% Bayesian credible interval: 3.1–8.9%). Rebound or recovery potential (also exploitation rate at MSP) of this stock was estimated to be 3.4% (1.6–6.2%), which is consistent with estimates for other long-lived late-maturing marine species. So, this once-seriously-depleted green turtle stock is well on the way to recovery and a limited harvest might now be demographically feasible. These findings are relevant for supporting informed public policy debate on the restoration of indigenous hunting rights in the Archipelago. Parameter estimates and model structure from the Bayesian surplus-production model were incorporated in an interactive easy-to-use stochastic simulation model to help support policy analysts in stock recovery planning and to explore sustainable harvest potential.

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1. Introduction

The green sea turtle, *Chelonia mydas*, is the most abundant large long-lived marine herbivore (Bjorndal, 1997) and has a long history of human exploitation for meat and eggs (Parsons, 1962). The Hawaiian green turtle stock is increasing in abundance following severe depletion due to nesting

habitat destruction (Amerson, 1971) and over-exploitation of eggs and turtles (Balazs and Chaloupka, 2004a). Green turtles resident in Hawaiian waters comprise a single genetic stock (Bowen et al., 1992) that is dispersed over numerous coral reef and coastal foraging grounds throughout the Hawaiian Archipelago (Balazs and Chaloupka, 2004b). Adult female turtles resident in these foraging grounds migrate every few years

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TWO PREVIOUSLY UNREPORTED BARNACLES COMMENSAL WITH THE GREEN SEA TURTLE, *CHELONIA MYDAS* (LINNAEUS, 1758), IN HAWAII AND A COMPARISON OF THEIR ATTACHMENT MODES

BY

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ABSTRACT

Two species of barnacles found living in the skin of green sea turtles, *Chelonia mydas*, and not previously recorded in Hawaii are reported and their attachment mechanisms compared. These findings bring to five the total number of barnacles commensal with Hawaiian sea turtles and to 50 the number of shallow-water cirripedes known in Hawaii. Identified as *Stomatolepas elegans* and *Platylepas decorata*, both species live embedded in the soft skin of the limbs, neck, and tail of their host. *Stomatolepas elegans* is perhaps a recent arrival in Hawaii with this being the first report of it, or any member of the genus, occurring with hawksbill turtles, *Eretmochelys imbricata*. We found the barnacle embeds by penetrating the epidermis of sea turtles and then anchors in connective tissue of the dermis by way of small spikes extending from the shell. Conversely, *P. decorata* invades host tissue less deeply, lacks anchoring devices, and becomes encapsulated only by epidermis. Species diagnoses were made by light and scanning electron microscopy and by comparison with other members in each genus.

RÉSUMÉ

Deux espèces de cirripèdes vivant dans la peau des tortues vertes marines *Chelonia mydas* et inconnues jusqu'à ce jour d'Hawaii sont étudiées et leur mécanismes de fixation comparés. Ces trouvailles portent à cinq le nombre total de cirripèdes commensaux des tortues marines d'Hawaii et à 50 le nombre d'espèces de cirripèdes d'eaux peu profondes connues à Hawaii. Identifiées comme *Stomatolepas elegans* et *Platylepas decorata*, les deux espèces vivent enfoncées dans la peau molle des membres, du cou et de la queue de leur hôte. *Stomatolepas elegans* est peut-être d'arrivée récente à Hawaii, ceci étant la première mention de sa présence, comme la première mention de ce genre, vivant avec les tortues imbriquées, *Eretmochelys imbricata*. Nous avons trouvé que le cirripède s'enfonce en pénétrant dans l'épiderme des tortues de mer et s'ancre ainsi dans le tissu conjonctif du derme au moyen de petites pointes venant de la coquille. Inversement, *P. decorata* envahit le tissu-hôte moins profondément, n'a pas de système d'ancrage et s'encapsule seulement dans l'épiderme.

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Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian Archipelago (1982–2003)

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Abstract We investigated cause-specific temporal and spatial trends in sea turtle strandings in the Hawaiian Archipelago. Five species of sea turtle were recorded in 3,861 strandings over a 22-year period (1982–2003). Green turtles comprised 97% of these strandings with size and gender composition reflecting the demographic structure of the resident green turtle population and relative green turtle abundance in Hawaiian waters. The cause of strandings was determined by necropsy based on a complete gross external and internal examination. Totally 75% of the 3,732 green turtle strandings were from Oahu where strandings occur year-round. The most common known cause of the green turtle strandings was the tumour-forming disease, fibropapillomatosis (28%) followed by

hook-and-line fishing gear-induced trauma (7%), gillnet fishing gear-induced trauma (5%), boat strike (2.5%), and shark attack (2.7%). Miscellaneous causes comprised 5.4% of strandings whereas 49% of green turtle strandings could not be attributed to any known cause. Green turtle strandings attributable to boat strike were more likely from Kauai and Oahu while fibropapilloma strandings were more likely from Oahu and Maui. Hook-and-line gear strandings were more likely from Oahu due to higher per capita inshore fishing effort. The specific mortality rate (conditional probability) for fibropapillomatosis was 88%, 69% for gillnet gear and 52% for hook-and-line gear. The probability of a dead green turtle stranding increased from 1982 but levelled off by the mid-1990s. The declining mortality risk was because the prevalence and severity of fibropapillomatosis has decreased recently and so has the mortality risk attributable to gillnet gear. Despite exposure to disease and inshore fishing gears, the Hawaiian green turtle stock continues to recover following protection since the late 1970s. Nevertheless, measures to reduce incidental capture of sea turtles in coastal Hawaiian fisheries would be prudent, especially since strandings attributable to hook-and-line fishing gear have increased steadily since 1982.

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Introduction

The green sea turtle (*Chelonia mydas*) is the most abundant large marine herbivore in the world and has been subject to a long history of human exploitation (Frazier 1980; Parsons 1962) leading some populations to be extirpated or depleted (Parsons 1962). Declining

RESEARCH
PAPER



Encouraging outlook for recovery of a once severely exploited marine megaherbivore

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ABSTRACT

Aim To critically review the status of the green sea turtle (*Chelonia mydas*) using the best available scientific studies as there is a prevailing view that this species is globally endangered and its marine ecosystem functions compromised.

Location Ogasawara (Japan), Hawaii (USA), Great Barrier Reef (Australia), Florida (USA), Tortuguero (Costa Rica).

Methods We compiled seasonal nesting activity data from all reliable continuous long-term studies (> 25 years), which comprised data series for six of the world's major green turtle rookeries. We estimated the underlying time-specific trend in these six rookery-specific nester or nest abundance series using a generalized smoothing spline regression approach.

Results Estimated rates of nesting population increase ranged from c. 4–14% per annum over the past two to three decades. These rates varied considerably among the rookeries, reflecting the level of historical exploitation. Similar increases in nesting population were also evident for many other green turtle stocks that have been monitored for shorter durations than the long-term studies presented here.

Main conclusions We show that six of the major green turtle nesting populations in the world have been increasing over the past two to three decades following protection from human hazards such as exploitation of eggs and turtles. This population recovery or rebound capacity is encouraging and suggests that the green turtle is not on the brink of global extinction even though some stocks have been seriously depleted and are still below historical abundance levels. This demonstrates that relatively simple conservation strategies can have a profound effect on the recovery of once-depleted green turtle stocks and presumably the restoration of their ecological function as major marine consumers.

Keywords

Chelonia mydas, conservation, green sea turtle, marine, stock recovery.

INTRODUCTION

Human exploitation and habitat destruction have caused major declines in the abundance of marine megafauna such as leatherback sea turtles (Spotila *et al.*, 1996), Steller sea lions (Trites & Donnelly, 2003), great whales (Roman & Palumbi, 2003), pelagic sharks (Baum & Myers, 2004) and dugong (Marsh *et al.*, 2005). There is increasing concern that the widespread decline of the marine megafauna will have unexpected and grave consequences for fisheries productivity (Pauly *et al.*, 1998), the stability

of marine food web dynamics (Estes *et al.*, 1998) and the long-term viability of the world's coastal ecosystems (Jackson *et al.*, 2001). In particular, Pandolfi *et al.* (2003) found that the long-term degradation of coral reef ecosystems was always preceded by a significant loss of the large herbivores and predators that comprise the marine megafauna. However, it is believed that these degraded marine ecosystems might retain the capacity for recovery as most megafauna populations in these ecosystems still exist, although at vastly reduced levels of abundance (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003).

Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations

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Abstract

The diving behavior of an adult female and two adult male green turtles was recorded during their roundtrip breeding migration from Laniakea, Oahu, to French Frigate Shoals in the Northwestern Hawaiian Islands. These data represent the first detailed records of diving behavior of green turtles as they migrate to their breeding grounds. All three turtles exhibited a biphasic diving behavior. During the daylight hours, diving depth was shallow (1–4 m) and duration was short (1–18 min). It was assumed that the turtles were moving deliberately toward their destination during this time. Between 1900 and 1930 h daily, the turtles began a diving pattern consisting of deep dives with a mean maximum dive depth of 35–55 m and a mean duration of 35 to 44 min. The shallow diurnal diving began between 0600 and 0700 h, after the nocturnal deep-diving pattern ended. The adult female made two dives in excess of 135 m and one male made several dives in excess of 100 m. These are the deepest dives ever recorded for a naturally diving green turtle. It took an average of 36 days for the turtles to make the trip to French Frigate Shoals and an average of 30 days to make the return trip. The deep nocturnal diving was unexpected and this behavior is in need of further investigation.
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Keywords: Diving; Hawaiian Islands; Migration; Sea Turtles; TDR

1. Introduction

Diving plays a central role in the lives of all air-breathing marine vertebrates, including sea turtles. With the advent of small, reliable data-loggers that can record diving behavior, there has been a profusion of studies examining the dive performance of a range of marine animals including mammals, reptiles and birds. For sea turtles, most dive studies focus on the interesting period between successive clutches, as instruments can be deployed relatively easily and removed when turtles are ashore nesting (Hays et al., 2002). More difficult is obtaining dive information when turtles are away from their nesting beaches, for example, on foraging grounds or while migrating. Some satellite tags allow dive information to be relayed from such environments (e.g., Hochscheid et al., 2005a,b; Myers et al., 2006), but higher resolution, continuous dive data could potentially be supplied from data-loggers that are not constrained by the limited bandwidth of the Argos satellite system (McMahon et al., 2007).

Satellite tracks of Hawaiian green turtles (*Chelonia mydas*) returning from their breeding grounds have shown that they take between 20 and 50 days to make the 800–1100 km trip with an average speed between 1.5 and 2 km/h (Balazs, 1994; Balazs et al., 1994; Balazs and Ellis, 2000). This is a generalized picture of their behavior during the migration necessitated by the long time interval between accurate Argos fixes and the lack of fine resolution diving data. As a consequence, we do not know if the turtles are traveling at the same rate of speed throughout the day, if they are swimming at the surface or at depth, and if they are feeding during the trip. Displacement studies at Ascension Island (Hays et al., 2001) have shown that adult green turtles exhibit diel variations in diving patterns during their breeding migration. There are currently, however, no published accounts of migration tracks or diving behavior for green turtle migrations to their breeding grounds. This is a result of the difficulty of determining when a turtle will migrate to breed without using techniques such as laparoscopy for gonad evaluation involving a relatively large number of animals.

Our study examines the diel diving behavior of three adult green turtles during their roundtrip breeding migrations between

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Composition of Hawaiian green turtle foraging aggregations: mtDNA evidence for a distinct regional population

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ABSTRACT: To examine the stock composition of Hawaiian foraging populations and evaluate current life-history hypotheses, mtDNA control region sequences from immature and adult green turtles that forage around the Hawaiian Islands were compared to potential source nesting populations across the Pacific. We examined the stock composition of the feeding ground (FG) populations at 5 index sites across the Hawaiian Archipelago, as well as animals stranded in areas outside these index sites. Six haplotypes, based on mtDNA sequences, were observed among the 788 green turtles sampled around the Hawaiian Islands. Stock mixture analysis shows that the Hawaiian FG populations comprise one genetic stock derived from the nesting population at French Frigate Shoals (FFS), based on a mean estimate of 99.9% from FFS as opposed to other potential source stocks. We identified only 3 turtles with haplotypes not found at FFS, indicating that Hawaiian FGs might occasionally, albeit rarely, be visited by animals from rookeries outside the Hawaiian Archipelago, both in the eastern and western Pacific. These findings lead us to conclude that the numerous foraging aggregations around the Hawaiian Islands can be considered part of a distinct regional population for management. The finding that FGs scattered across a distance of over 2400 km belong to one genetic stock is unique among sea turtles, and allows Hawaiian green turtles to be assessed separately from other Pacific stocks with respect to risk. We explore the unique population ecology of Hawaiian green turtles with reference to the complex life history of this marine megaherbivore.

KEY WORDS: Population genetics · Control region · Mitochondrial DNA · mtDNA · Sea turtles

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INTRODUCTION

The green turtle *Chelonia mydas* occurs throughout the many coral reef and coastal foraging grounds (FG) within the Hawaiian Archipelago, which consists of more than 130 islands and reefs spanning approximately 2400 km (see Fig. 1). The only significant nesting assemblage occurs at French Frigate Shoals (FFS), a mainly uninhabited reef with several sand islets located in the middle of the archipelago (see Fig. 1), although it appears that some nesting occurred at the southeastern end of the archipelago prior to European settlement (Balazs 1985a), and low-level nesting occurs elsewhere

in the northwestern Hawaiian Islands. The FFS nesting population of threatened green turtles has been monitored since 1973 and is one of the few populations in the Pacific that appears to be increasing in numbers (Balazs & Chaloupka 2004a, 2006, Hays 2004, Chaloupka & Balazs 2007), along with Ogasawara (Japan), and Heron Island (Australia) (Chaloupka et al. 2008). Although the Hawaiian nesting population is genetically distinct from other Pacific stocks (Dutton et al. unpubl. data), there is no genetic information on stock composition among FGs within the Hawaiian Archipelago. This reflects a more general limitation in the way sea turtle populations are defined, assessed, and managed. Popu-

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Dietary Shifts by Green Turtles (*Cbelonia mydas*) in the Kāne'ohē Bay Region of the Hawaiian Islands: A 28-Year Study¹

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Abstract: The green turtle, *Cbelonia mydas*, has modified its feeding behavior to include the increasing abundance of nonnative algae growing in the greater Kāne'ohē Bay area of O'ahu in the Hawaiian Islands. Changes in diet of the green turtle are correlated with an increase in abundance of seven species of nonnative algae between 1977 and 2005. Turtles were found to be eating 130 species of marine vegetation, and the three most common were the nonnative species *Acanthopora spicifera*, *Hypnea musciformis*, and *Gracilaria salicornia*. These three abundant and nutritious food sources are now an important part of the turtle diet in addition to native species found in and near Kāne'ohē Bay. *Cbelonia mydas* behavior has shifted to include these new seaweeds within 10 years of their introduction to the region. The turtles have also gradually included an additional four less-prolific slow-growing nonnative algal species (*Eucheuma denticulatum*, *Gracilaria tikvahiae*, *Kappaphycus striatum*, and *Kappaphycus alvarezii*), but the time it has taken turtles to include these species has been longer, 20–30 years, after the seaweeds were introduced. During this same 28-year time period numbers of *C. mydas* have increased throughout the Hawaiian Islands.

THE FEEDING BEHAVIOR and diet of the herbivorous green turtle, *Cbelonia mydas* (L.), have been the subject of 28 years of research conducted between 1977 and 2005 throughout the Hawaiian Archipelago and especially in the vicinity of Kāne'ohē Bay, Hawai'i (Figure 1). The green turtle has shown a remarkable ability to rebound from decline, largely due to conservation measures, such as protection from harvesting and other forms of take under the U.S. Endangered Species Act, and now the population is recovering (Balazs and Chaloupka 2004a, 2006). However, a decline in the somatic growth rates of the turtles indicates that the population may

be approaching carrying capacity and now available food may be limiting growth at some locations (Balazs and Chaloupka 2004b). Shifts in the diet of the green turtle in Kāne'ohē Bay may be fortuitous for the turtles and their continuing recovery. This paper focuses on the ability of green turtles to modify their feeding behavior and take advantage of additional algal food sources.

Although understanding all aspects of green turtle biology is critical for the recovery of the species (Hirth 1997), one of the more important conservation topics involves turtle feeding behavior, which includes knowledge of the species of algae, sea grasses, animals, and other items *C. mydas* is eating, and eventually protecting the most important foraging sites and food species they are utilizing (Balazs 1980, Hirth 1997, Russell et al. 2003). It has been known for many years that *C. mydas* feeds on a wide variety of marine vegetation (Balazs et al. 1987, Russell and Balazs 1994, Arthur and Balazs 2008). Data from the feeding habits of *C. mydas* have also been used to discover changes in the feeding behavior of *C. mydas*, which include nonnative species in its diet, and to follow the spread of *Hypnea musciformis*, a nonnative species, from its

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Ecosystem structure and processes at Kaloko Honokōhau, focusing on the role of herbivores, including the green sea turtle *Chelonia mydas*, in reef resilience

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ABSTRACT: The formal protection of the Hawaiian green turtle *Chelonia mydas* in the 1970s has led to significant increases in the number of individuals recorded throughout the archipelago. Reduced growth rates and poor body condition of individuals at a number of foraging sites, including Kaloko-Honokōhau National Historical Park (Kaloko), suggest that some aggregations have reached carrying capacity. To better understand the ecological structure and processes of the reef system at the park, we developed an ecosystem model that synthesized available data on Kaloko for the year 2005 and included 26 groups, spanning the entire trophic web. Model results showed that the combined grazing pressure of the different herbivore functional groups (i.e. reef fish, sea urchins, and green turtles) in Kaloko matched total algal production. Sea urchins exerted the strongest control over algal resources, partly because of their large biomass in park waters. Results confirmed that the Kaloko green turtle aggregation has reached carrying capacity. Green turtles help maintain low algal cover, and thus resilience of reefs in the face of disturbances, and should be explicitly included in studies of ecosystem dynamics on reefs. Our work also provides a 'current-condition' baseline for Kaloko, and a valuable tool for the assessment of the future marine ecosystem impacts of projected urban expansion plans around the park.

KEY WORDS: Marine turtles · Ecosystem-based management · Ecopath · Coral reef · Herbivory · Phase shift · Nutrient enrichment · Kona coast · Hawaii

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INTRODUCTION

Grazing by herbivores is one of the major processes structuring benthic coral reef communities. Studies highlighting the role of herbivores in promoting reef resilience and recovery to coral-dominated states,

where disturbance has led to increased algal biomass (e.g. Bellwood et al. 2004), have focused almost exclusively on fish and sea urchins (Hay 1984a, Carreiro-Silva & McClanahan 2001, Mumby et al. 2006a, Paddock et al. 2006, Albert et al. 2008). Numerous Caribbean reefs have transitioned from

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NOTE

Estimating carrying capacity at the green turtle nesting beach of East Island, French Frigate Shoals

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ABSTRACT: Many sea turtle populations are at a fraction of their historical abundance, and understanding ecological processes, under current and climate change scenarios, is critical for establishing recovery goals. In the Hawaiian Islands, the nesting population of the green turtle *Chelonia mydas* on East Island, French Frigate Shoals, has been recovering at a rate of 5.7 % per year. Climate change models, however, predict a loss in nesting habitat on East Island of up to 30% due to sea level rise by 2100. Therefore, the objective of the present study was to determine the carrying capacity of East Island for hatchlings and nesting females under current conditions and predictions of sea level rise. In the simulation model, density-dependent nest destruction was the primary factor regulating population size. Carrying capacity was reached between 1.9 and 2.1 million hatchlings at current conditions; carrying capacity was approached when 80 000 to 120 000 nests were laid on the beach, representing 20 000 to 30 000 nesting females. With a rise in sea level, carrying capacity was reached when 60 000 to 100 000 nests were laid on the beach. The current mean estimate of 300 nesting females per year, over the past 10 yr, at East Island represents 1.3 to 2% of the females that would nest at carrying capacity. The beach at East Island is well below carrying capacity and is capable of supporting a larger nesting population. However, the availability of suitable coastal habitats may play a bigger role in regulating the Hawaiian green turtle population than available nesting habitat.

KEY WORDS: Carrying capacity · Green turtles · *Chelonia mydas* · Nesting · Climate change · French Frigate Shoals · Hawaii

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INTRODUCTION

Populations of green sea turtles *Chelonia mydas* have declined worldwide, and many populations are considered to be at a fraction of their historical abundance and environmental carrying capacity (Jackson et al. 2001, Seminoff 2004, Tiwari et al. 2006). However, recent analyses of global trends in green turtle nesting populations demonstrated a promising, and sometimes remarkable, increase over the past decades at several nesting rookeries (Bjorndal et al. 1999, Seminoff 2004, Trøeng & Rankin 2005, Broderick et al. 2006, Chaloupka et al. 2008). Among the rookeries that have responded positively to long-term protection is the green turtle population on East Island in French Frigate Shoals (Balazs 1976), which lie within the

remote Northwestern Hawaiian Islands (Fig. 1), an area designated as the Papahānaumokuākea Marine National Monument in 2007. Prior to the mid 20th century, green turtles were heavily exploited for their eggs and meat in the Hawaiian Islands, and their nesting habitats destroyed, resulting in a severe population decline (Balazs 1980, Balazs & Chaloupka 2004a). However, protection was strengthened in the late 1970s by the State of Hawaii and the US Endangered Species Act (Bennett & Keuper-Bennett 2008), and the green turtle population has since been recovering rapidly at a rate of 5.7 % per year (Balazs & Chaloupka 2006, Chaloupka et al. 2008) over the past 35 yr.

Although green turtles nest throughout the Northwestern Hawaiian Islands, about 90 % of the nesting takes place in French Frigate Shoals (Balazs 1980).

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FIRE

THE GREEN SEA TURTLE
AND THE FATE OF THE OCEAN

IN THE

TURTLE

HOUSE

OSHA GRAY DAVIDSON



IMMUNE STATUS OF FREE-RANGING GREEN TURTLES WITH FIBROPAPILLOMATOSIS FROM HAWAII

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ABSTRACT: Cell mediated and humoral immune status of free-ranging green turtles (*Chelonia mydas*) in Hawaii (USA) with and without fibropapillomatosis (FP) were assessed. Tumor and non-tumor turtles from Kamehame Bay (KB) on the island of Oahu and from FP-free areas on the west (Kona/Kohala) coast of the island of Hawaii were sampled from April 1998 through February 1999. Turtles on Oahu were grouped (0-3) for severity of tumors with 0 for absence of tumors, 1 for light, 2 for moderate, and 3 for most severe. Turtles were weighed, straight carapace length measured and the regression slope of weight to straight carapace length compared between groups (KB0, KB1, KB2, KB3, Kona). Blood was assayed for differential white blood cell count, hematocrit, in vitro peripheral blood mononuclear cell (PBMC) proliferation in the presence of concanavalin A (ConA) and phytohaemagglutinin (PHA), and protein electrophoresis. On Oahu, heterophil/lymphocyte ratio increased while eosinophil/monocyte ratio decreased with increasing tumor score. Peripheral blood mononuclear cell proliferation indices for ConA and PHA were significantly lower for turtles with tumor scores 2 and 3. Tumor score 3 turtles (KB3) had significantly lower hematocrit, total protein, alpha 1, alpha 2, and gamma globulins than the other four groups. No significant differences in immune status were seen between non-tumored (or KB1) turtles from Oahu and Hawaii. There was no significant difference between groups in regression slopes of body condition to carapace length. We conclude that turtles with severe FP are immunosuppressed. Furthermore, the lack of significant difference in immune status between non-tumored (and KB1) turtles from Oahu and Kona/Kohala indicates that immunosuppression may not be a prerequisite for development of FP.

Key words: Cell proliferation assay, *Chelonia mydas*, fibropapillomatosis, green turtle, hematology, immunology, protein electrophoresis.

INTRODUCTION

Fibropapillomatosis (FP) is an often-fatal neoplastic disease of marine turtles that causes external fibroepithelial and internal fibromatous tumors. Fibropapillomatosis was first documented in green turtles (*Chelonia mydas*) from Florida (USA) (Smith and Coates, 1938) and has since been reported in loggerheads (*Caretta caretta*) and olive ridleys (*Lepidochelys olivacea*) (Herbst, 1994). While many factors have been suspected to cause FP, recent findings appear to incriminate herpes viruses (Herbst et al., 1998; Quackenbush et al., 1998; Lackovich et al., 1999).

Fibropapillomatosis has a worldwide distribution in marine turtles (Herbst, 1994). In Hawaii (USA), FP is found in

green turtles that aggregate in coastal residential foraging pastures of algae and sea grass associated with all islands. The one exception is the Kona/Kohala (west) coast of the island of Hawaii where FP has historically been rarely seen (Balazs, 1991; Balazs et al., 2000b). In Hawaii, FP affects immature green turtles most severely, and the prevalence can reach >50% in some aggregations (Murakawa et al., 2000). Current genetic evidence indicates that green turtles throughout Hawaii belong to a single population (Bowen et al., 1992).

Various investigators have theorized immunosuppression as a contributing or predisposing cause of FP. Aguirre et al. (1995) concluded that green turtles with FP were immunosuppressed based on lymphopenia

Bacteraemia in free-ranging Hawaiian green turtles *Chelonia mydas* with fibropapillomatosis

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ABSTRACT: Past studies of free-ranging green turtles *Chelonia mydas* with fibropapillomatosis (FP) in Hawaii have shown that animals become immunosuppressed with increasing severity of this disease. Additionally, preliminary clinical examination of moribund turtles with FP revealed that some animals were also bacteraemic. We tested the hypothesis that bacteraemia in sea turtles is associated with the severity of FP. We captured free-ranging green turtles from areas in Hawaii where FP is absent, and areas where FP has been endemic since the late 1950s. Each turtle was given an FP severity score ranging from 0 (no tumours) to 3 (severely affected). A fifth category included turtles that were stranded ashore and moribund with FP. We found that the percentage of turtles with bacteraemia increased with the severity of FP, and that the majority of bacteria cultured were *Vibrio* spp. Turtles with severe FP were more susceptible to bacteraemia, probably in part due to immunosuppression. The pattern of bacteraemia in relation to severity of disease strengthens the hypothesis that immunosuppression is a sequel to FP.

KEY WORDS: Bacteria · Bacteraemia · *Chelonia mydas* · Green turtle · Haematology · *Vibrio*

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INTRODUCTION

Fibropapillomatosis (FP) is a globally distributed neoplastic disease of marine turtles. The disease causes external and internal tumours and debilitation that mainly affects immature animals (Herbst 1994). Although factors such as contaminants (Aguirre et al. 1994a), parasites (Dauby & Morris 1995, Aguirre et al. 1998), and marine toxins (Landsberg et al. 1999) have been suspected of contributing to FP, herpesviruses appear to be a common denominator (Herbst et al. 1998, Quackenbush et al. 1998, Lackovich et al. 1999, Lu et al. 2000). However, attempts to culture this virus in the laboratory have been unsuccessful, and Koch's postulates have not been fulfilled.

In Hawaii, prevalence of FP in immature green turtles *Chelonia mydas* fluctuates between 40 and 60%

depending on where and how animals are sampled. The disease is present in turtles from all the main Hawaiian islands except the Kona/Kohala (west) coast of the island of Hawaii, where FP has historically been rare (Balazs 1991, Murakawa et al. 1999, Balazs et al. 2000).

The pathophysiology of FP in green turtles remains elusive. Debilitation from tumour loads involving the eyes and mouth (Balazs et al. 1997) certainly explains why animals with severe FP strand or become emaciated. However, severe debilitation also occurs in turtles with few external or internal tumours. Aguirre et al. (1995) concluded that turtles with severe FP were stressed and immunosuppressed based on haematology and blood cortisol levels. Work & Balazs (1999) and Work et al. (2001) showed, through immune function tests and haematology, that immunosuppression in

Retrospective pathology survey of green turtles *Chelonia mydas* with fibropapillomatosis in the Hawaiian Islands, 1993–2003

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ABSTRACT: We necropsied 255 stranded green turtles *Chelonia mydas* with fibropapillomatosis (FP) from the Hawaiian Islands, North Pacific, from August 1993 through May 2003. Of these, 214 (84%) were euthanized due to advanced FP and the remainder were found dead in fresh condition. Turtles were assigned a standardized tumor severity score ranging from 1 (lightly tumored) to 3 (heavily tumored). Tumors were counted and measured and categorized as external, oral, or internal and tissues evaluated by light microscopy. Turtles in tumor score 2 and 3 categories predominated, and tumor score 3 turtles were significantly larger than the other 2 categories. More juveniles stranded than subadults or adults. Total cross-sectional area of tumors increased significantly with straight carapace length (SCL). Frequency distribution of total number of external tumors per turtle was significantly skewed to the right, and there were significantly more tumors at the front than rear of turtles. Eighty percent of turtles had oral tumors, and 51% of turtles with oral tumors had tumors in the glottis. Thirty-nine percent of turtles had internal tumors, most of them in the lung, kidney and heart. Fibromas predominated in lung, kidney and musculoskeletal system whereas myxofibromas were more common in intestines and spleen. Fibrosarcomas of low-grade malignancy were most frequent in the heart, and heart tumors had a predilection for the right atrium. Turtles with FP had significant additional complications including inflammation with vascular flukes, bacterial infections, poor body condition, and necrosis of salt gland. Turtles with oral tumors were more likely to have secondary complications such as pneumonia. Most turtles came from the island of Oahu (74%) followed by Maui (20%), Hawaii, Molokai, and Lanai (<3% each). On Oahu, significantly more turtles we necropsied stranded along the northwestern and southeastern shores.

KEY WORDS: Green turtle · *Chelonia mydas* · Fibropapillomatosis · Pathology · Epizootiology

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INTRODUCTION

The Hawaiian Islands in the North Pacific have 2 species of marine turtles that live in coastal areas, the hawksbill *Eretmochelys imbricata* and the far more numerous green turtle *Chelonia mydas*. Since green turtles were listed as threatened and protected in 1978, numbers of nesting females at French Frigate Shoals, the primary nesting ground located in the northwestern Hawaiian Islands, have increased steadily (Balazs

& Chaloupka 2004). However, health issues continue to be of concern to the management and recovery of the Hawaiian green turtle population (Balazs & Pooley 1991, Aguirre et al. 1996, Work et al. 2003).

Most research on health of green turtles in Hawaii has focused on fibropapillomatosis (FP), a neoplastic condition first described in green turtles from Florida (Smith & Coates 1938). FP is manifested by external and internal tumors (Herbst 1994), and in more severely affected turtles by anemia, leukopenia and heterophilia

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EPIZOOTIOLOGY OF SPIRORCHIID INFECTION IN GREEN TURTLES (*CHELONIA MYDAS*) IN HAWAII

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ABSTRACT: We describe the epizootiology of spirorchiid trematode infections in Hawaiian green turtles (*Chelonia mydas*) by quantifying tissue egg burdens in turtles submitted for necropsy and by assessing antibody response to crude adult worm and egg antigens among a variety of age groups. *Hapalotrema* sp. and *Laeredius* sp. predominated in turtles infected with spirorchids. Tissue egg burdens decreased with increasing size and increased with deteriorating body condition of turtles. No relationship was found between tissue egg burdens and sex or fibropapillomatosis status. Tissue egg burdens increased in turtles from southeast to northwest in the main Hawaiian Islands (Hawaii to Kauai). Hatching and captive-reared turtles had significantly lower levels of antibodies against crude worm and egg antigens. Based on tissue egg burdens and antibody status, we hypothesize that immature turtles become infected with spirorchids shortly after recruiting into coastal foraging pastures from the pelagic environment, that infection levels decrease with age, and that spirorchids detrimentally affect the body condition of sea turtles independent of tumor burden. The low intensity of infection in turtles with the endemic trematode *Carettaicola hawaiiensis* suggests either that turtles are less susceptible to infection with this parasite or that the parasite is outcompeted by species of *Hapalotrema* and *Laeredius*. Given that the 2 latter species are found in the Pacific and other oceans, they are not likely endemic and were probably introduced into Hawaii through an undetermined route.

The major health issue affecting green turtles (*Chelonia mydas*) in Hawaii is fibropapillomatosis (FP), a neoplastic disease that is a significant cause of strandings (Murakawa et al., 1999; Work et al., 2004) and that presents complications such as immunosuppression (Work and Balazs, 1999; Work et al., 2001) and bacteremia (Work et al., 2003). A high percentage of turtles with FP in Hawaii (Dailey, 1992; Aguirre et al., 1998) and the Pacific (Gordon et al., 1998) are also infected with blood flukes. Blood flukes (spirorchids) could play an etiologic role in FP (Dailey and Morris, 1995), but more recent evidence implicates an FP-associated turtle herpesvirus (FPTHV) as the most probable cause of the disease in Hawaii (Quackenbush et al., 1998) and Florida (Lackovich et al., 1999). However, given that most turtles that strand with FP are infected with spirorchids and that these parasites can cause significant pathology (Aguirre et al., 1998; Work et al., 2004), understanding their epizootiology may shed light on their role in the health of sea turtles, thereby aiding conservation efforts to recover the species.

Four species of spirorchids in 3 genera (*Laeredius*, *Hapalotrema*, and *Carettaicola*) have been described from Hawaiian green turtles (Dailey et al., 1992, 1993). Adult worms infect the vessels of various organs, where they copulate and oviposit. Eggs migrate and lodge in tissues, where they elicit a granulomatous response in multiple organs. Adult worms can cause severe vasculitis (Aguirre et al., 1998; Work et al., 2004). Detection of infection with spirorchids in turtles usually is done at necropsy, when adult worms or eggs are observed either grossly or at microscopy. Antemortem detection of infection is more difficult and currently limited to serology. Graczyk et al. (1995) used enzyme-linked immunosorbent assays (ELISAs) to detect antibodies to adult worm antigens in Hawaiian green turtles and found 71% to be seropositive in Kaneohe, Oahu (where FP is enzootic), and 100% to be seropositive on the west coast (Kona) of the island of Hawaii, where FP rarely

occurs. Those authors concluded that no association existed between seropositivity to spirorchids and FP status. Herbst et al. (1998) used ELISA to examine green turtles from Florida for exposure to spirorchids and immunohistochemistry to measure antibodies against FPTHV; they also found no association between seropositivity to spirorchids and FP.

Serology is useful to detect exposure of sea turtles to spirorchids, but it does have limitations. Serology may not reflect the intensity of infection with spirorchids, nor will it indicate the relative role of individual species of flukes infecting turtles (Herbst et al., 1998). Existing studies (Graczyk et al., 1995; Herbst et al., 1998) have examined serology against adult worms in immature turtles within foraging habitats. However, a more complete picture of the epizootiology of infection with spirorchids in turtles might be gained by examining serology against both worms and eggs in other turtle life stages (hatching and adult). Finally, serological responses to spirorchids can be confounded if animals have concomitant infections with other helminths (Alarcon de Noya et al., 1996). Our objectives in the present study were, first, to evaluate the serological response of various age and health categories of sea turtles against spirorchid worm and egg antigen and, second, to examine the relationship between the intensity of infection with spirorchids in stranded turtles and serology, body condition, and FP burden.

MATERIALS AND METHODS

Free-ranging turtles were captured on a nesting beach or in coastal waters using tangle nets, SCUBA, or snorkeling. Turtles were bled from the cervical sinus (Owens and Ruiz, 1980) using 10-ml syringes and 20-gauge, 2.57-cm needles. Blood was collected in heparin (7 IU/ml), centrifuged at 300 g for 10 min, plasma harvested, and stored frozen (-70 C). Immature turtles were sampled from Kaneohe Bay, Oahu, (an FP enzootic area) and the west (Kona-Kohala) coast of the island of Hawaii (an area where FP is rarely observed). Hatchlings and nesting adults were sampled from French Frigate Shoals (FFS) in the northwestern Hawaiian Islands (Balazs and Chaloupka, 2004). Captive-bred and-reared, immature green turtles of Hawaiian origin were sampled from Sea Life Park (SLP), Oahu. Some of these turtles were then translocated within 2 mo of hatching to coastal holding ponds at the Mauna Lani Bay Resort (MLBR) on the Kona-Kohala coast of the island of Hawaii.

Stranded turtles that were moribund and judged to have poor prog-

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In vitro biology of fibropapilloma-associated turtle herpesvirus and host cells in Hawaiian green turtles (*Chelonia mydas*)

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Fibropapillomatosis (FP) of green turtles has a global distribution and causes debilitating tumours of the skin and internal organs in several species of marine turtles. FP is associated with a presently non-cultivable alphaherpesvirus Chelonid fibropapilloma-associated herpesvirus (CFPHV). Our aims were to employ quantitative PCR targeted to *pol* DNA of CFPHV to determine (i) if DNA sequesters by tumour size and/or cell type, (ii) whether subculturing of cells is a viable strategy for isolating CFPHV and (iii) whether CFPHV can be induced to a lytic growth cycle *in vitro* using chemical modulators of replication (CMRs), temperature variation or co-cultivation. Additional objectives included determining whether non-tumour and tumour cells behave differently *in vitro* and confirming the phenotype of cultured cells using cell-type-specific antigens. CFPHV *pol* DNA was preferentially concentrated in dermal fibroblasts of skin tumours and the amount of viral DNA per cell was independent of tumour size. Copy number of CFPHV *pol* DNA per cell rapidly decreased with cell doubling of tumour-derived fibroblasts in culture. Attempts to induce viral replication in known CFPHV-DNA-positive cells using temperature or CMR failed. No significant differences were seen in *in vitro* morphology or growth characteristics of fibroblasts from tumour cells and paired normal skin, nor from CFPHV *pol*-DNA-positive intestinal tumour cells. Tumour cells were confirmed as fibroblasts or keratinocytes by positive staining with anti-vimentin and anti-pancytokeratin antibodies, respectively. CFPHV continues to be refractory to *in vitro* cultivation.

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INTRODUCTION

Fibropapillomatosis (FP) is a neoplastic disease of marine turtles; it has a global presence and causes significant external (skin) and internal (organ) tumours (Herbst, 1994). FP is a major cause of stranding of green turtles (*Chelonia mydas*) in Hawaii (Aguirre *et al.*, 1998; Chaloupka *et al.*, 2008; Work *et al.*, 2004) and Florida (Foley *et al.*, 2005), but prevalence of the disease in Hawaii has been decreasing in recent years for unknown reasons. FP is transmissible using cell-free filtrates (Herbst *et al.*,

1995), and molecular studies consistently show alphaherpesviral DNA associated with tumour tissue in green, olive ridley (*Lepidochelys olivacea*) (Quackenbush *et al.*, 2001) and loggerhead (*Caretta caretta*) (Lackovich *et al.*, 1999) turtles in the Pacific and Atlantic oceans.

Both spontaneous and experimentally induced fibropapillomas have been characterized extensively on the basis of gross and microscopic morphology, revealing that lytic viral production, as evidenced by intranuclear inclusions with viral particles, is rare and limited to epidermal layers of the tumour (Herbst *et al.*, 1999). Greenblatt *et al.* (2004) found higher levels of Chelonid fibropapilloma-associated herpesvirus (CFPHV) *pol* mRNA expression in the

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SHORT COMMUNICATIONS

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Rise and Fall over 26 Years of a Marine Epizootic in Hawaiian Green Sea Turtles

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ABSTRACT: Estimates of chronic disease prevalence are needed to improve our understanding of marine disease epizootiology, which is poorly known for marine megafauna such as marine turtles. An emerging worldwide threat to green sea turtles (*Chelonia mydas*) is fibropapillomatosis (FP), which is a pandemic tumor-forming disease associated with herpesviruses. We report on a 26-yr FP epidemic in the Hawaiian Archipelago and show that apparent disease prevalence in the world's main endemic hot spot increased rapidly following a late 1980s outbreak, peaked during the mid-1990s, and then declined steadily ever since. While this disease is a major cause of sea turtle stranding in Hawaiian waters and can be fatal, we also show that long-term tumor regression can occur even for turtles with advanced FP. The endemic Hawaiian green turtle stock was severely depleted by overexploitation prior to protection under the US Endangered Species Act in 1978. This stock has increased significantly ever since, despite exposure to a major chronic disease epidemic that is currently declining.

Key words: *Chelonia mydas*, fibropapillomatosis, green sea turtle, marine epizootic.

Chronic and acute diseases are a major concern for the health of human populations and are subject to extensive research (Anderson and May, 1991). While our knowledge of acute disease impact on free-ranging marine wildlife is increasing (Harkonen et al., 2006), this is not the case for chronic diseases; this is mainly due to a paucity of long-term information on disease prevalence or incidence (Harvell et al., 1999; Lloyd-Smith et al., 2005). The green sea turtle (*Chelonia mydas*) is one of the long-lived late-maturing vertebrates that comprise the charismatic marine megafauna (Chaloupka et al., 2008a).

Many green turtle populations have been depleted by exploitation, leading to concern that the species might be globally endangered (Chaloupka et al., 2008a). An emerging worldwide threat to green turtles is fibropapillomatosis (Herbst, 1994), which is a pandemic disease associated with the presence of herpesviruses (Greenblatt et al., 2005).

Fibropapillomatosis (FP) is a neoplastic disease involving tumors in multiple cutaneous sites and connective tissue tumors in the viscera (Herbst, 1994; Fig. 1A). Fibropapillomatosis prevalence has apparently increased over the past 2–3 decades in green turtle populations in Australia, Indonesia, and the US (Herbst, 1994; Chaloupka and Balazs, 2005; Foley et al., 2005; Greenblatt et al., 2005). It is believed that FP might impair recovery of depleted populations (Herbst, 1994; Ene et al., 2005), especially the green turtle stock endemic to Hawaii (Balazs and Chaloupka, 2004; Chaloupka and Balazs, 2005). Despite a global distribution and high prevalence in some populations (Herbst, 1994), there has been no long-term assessment of FP for any marine turtle population (Chaloupka and Balazs, 2005). Long-term assessments of the prevalence of major chronic diseases like FP in marine vertebrates are critically needed to improve our understanding of marine disease epizootiology (Harvell et al., 1999).

We reviewed FP disease prevalence data for a green turtle population that has been monitored each year since 1982

Land Use, Macroalgae, and a Tumor-Forming Disease in Marine Turtles

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Abstract

Wildlife diseases are an increasing concern for endangered species conservation, but their occurrence, causes, and human influences are often unknown. We analyzed 3,939 records of stranded Hawaiian green sea turtles (*Chelonia mydas*) over 28 years to understand fibropapillomatosis, a tumor-forming disease linked to a herpesvirus. Turtle size is a consistent risk factor and size-standardized models revealed considerable spatial and temporal variability. The disease peaked in some areas in the 1990s, in some regions rates remained constant, and elsewhere rates increased. Land use, onshore of where the turtles feed, may play a role. Elevated disease rates were clustered in watersheds with high nitrogen-footprints; an index of natural and anthropogenic factors that affect coastal eutrophication. Further analysis shows strong epidemiological links between disease rates, nitrogen-footprints, and invasive macroalgae and points to foraging ecology. These turtles now forage on invasive macroalgae, which can dominate nutrient rich waters and sequester environmental N in the amino acid arginine. Arginine is known to regulate immune activity, promote herpesviruses, and contribute to tumor formation. Our results have implications for understanding diseases in aquatic organisms, eutrophication, herpesviruses, and tumor formation.

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Introduction

Combined with overexploitation, habitat loss, and climate change, emerging diseases pose major impacts to biodiversity worldwide [1,2]. Marine turtles suffer numerous population threats [3] with green sea turtles (*Chelonia mydas*) afflicted by fibropapillomatosis (FP) a debilitating tumor-forming disease [4]. While surveys show key green turtle populations are steadily growing [5,6], FP remains widespread and its origins are unknown. Here we present a spatial epidemiology from 28 years of disease records from the Hawaiian population of green turtles. We construct time series of disease rates, address the spatial scale of variability, and examine the role of land use and invasive macroalgae.

Early hypotheses of causal factors of the disease examined vascular trematodes and toxins but results were inconclusive [7,8]. A viral origin for FP became apparent after experiments successfully transmitted the disease using cell-free tumor extracts [9]. Later studies identified α -herpesviruses as the leading candidate after their DNA fragments were discovered in turtle tumors, but were absent in tumor-free turtles [10,11]. Subsequent results also showed sampled herpesviruses had low genetic variability [11,12] implying contact transmission, perhaps via ectoparasites [13].

Further advances to understanding this disease have been limited by the inherent complexities of epidemics and their ecosystems [14]. Infectious diseases involve individual susceptibility, exposure, infection, and immune response. These phases often

operate independently; interact in nonlinear ways; and vary demographically, geographically and through time. Mass-action models [15], for example, can predict the course of many diseases by their host population density. These models are intuitive, as communicable diseases often spread rapidly in dense populations. Understanding the variability of FP, however, is likely more complicated than transmission dynamics alone. In Hawaiian green turtles, for example, FP became prevalent in the 1980s, and apparently peaked in the 1990s [16,17] though the turtle population has grown continually [5]. Furthermore, recent phylogenetic analyses of the implicated herpesviruses show low mutability and coevolution with their turtle hosts over millions of years [12]. Investigating factors that can promote disease, such as environmental [18] or dietary conditions [19], may therefore provide insights.

Green turtles develop FP (Fig. 1) only after recruiting to nearshore habitat [17,20] indicating these environments are influential. Most Hawaiian green turtles hatch in the Northwestern Hawaiian Islands (NWHI, 900 km from Honolulu) and spend up to a decade in pelagic waters [21]. Juveniles recruit to nearshore waters at around 35 cm straight carapace length (SCL). Here turtles maintain spatiotemporal fidelity to specific macroalgae beds in shallow, nearshore sites [16,22]. After reaching ~80 cm SCL, individuals seasonally migrate to the NWHI to breed. There they spend months, afterwards return to their foraging sites in the Main Hawaiian Islands (MHI), and subsequently breed every 3–4 or more years [23]. Therefore all neritic green turtles are chronically and locally influenced by their local nearshore habitat in the MHI.

Abstract—Diet analysis of 52 loggerhead sea turtles (*Caretta caretta*) collected as bycatch from 1990 to 1992 in the high-seas driftnet fishery operating between lat. 29.5°N and 43°N and between long. 150°E and 154°W demonstrated that these turtles fed predominantly at the surface; few deeper water prey items were present in their stomachs. The turtles ranged in size from 13.5 to 74.0 cm curved carapace length. Whole turtles ($n=10$) and excised stomachs ($n=42$) were frozen and transported to a laboratory for analysis of major faunal components. Neustonic species accounted for four of the five most common prey taxa. The most common prey items were *Janthina* spp. (Gastropoda); *Carinaria cithara* Benson 1835 (Heteropoda); a chondrophore, *Veleva veleva* (Hydrozoa); *Lepas* spp. (Cirripedia), *Planes* spp. (Decapoda: Grapsidae), and pyrosomas (*Pyrosoma* spp.).

Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific

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Loggerhead sea turtles are circum-global, inhabiting temperate, subtropical, and tropical waters of the Atlantic, Pacific, and Indian Oceans. In the Pacific, loggerhead sea turtles have been found in nearshore waters of China, Taiwan, Japan, Australia, and New Zealand and are seen in offshore waters of Washington, California, and northwestern Mexico (Dodd, 1988; Pitman, 1990). Nesting in the North Pacific Ocean occurs in Japan; there is no known nesting in the eastern North Pacific (Márquez and Villanueva, 1982; Frazier, 1985; Bartlett, 1989). Trans-Pacific migrations of juveniles have been documented from mitochondrial DNA analyses of individuals found feeding off Baja California. Bowen et al. (1995) identified these Baja sea turtles as originating from Japanese rookeries, although a small percentage come from Australia. Recent research indicates that all loggerhead sea turtles found in the oceanic realm of the central North Pacific Ocean are of Japanese stock (Dutton et al., 1998). Tagging studies in Japan and the Eastern Pacific also demonstrate transpacific migrations of loggerhead sea turtles between the

east and west Pacific (Balazs, 1989; Resendiz et al., 1998; Uchida and Teruya¹).

Recent oceanic satellite tracking studies of loggerhead sea turtles indicate that they are active in their oceanic movements. These turtles follow subtropical fronts as they travel toward Japan from east to west across the Pacific Ocean, often swimming against weak geostrophic currents (Polovina et al., 2000; Polovina et al., 2004). One hypothesis discussed in Polovina et al. (2000; 2004) suggests that this species obtains prey items from the subtropical fronts along which they travel. A sharp gradient in surface chlorophyll is observed along the main frontal area where these turtles are commonly encountered. This frontal area, the transition zone chlorophyll front

¹ Uchida, S., and H. Teruya. 1991. A) Transpacific migration of a tagged loggerhead, *Caretta caretta*. B) Tag-return result of loggerhead released from Okinawa Islands, Japan. In International symposium on sea turtles '88 in Japan (I. Uchida, ed.), p. 169-182. Himeji City Aquarium, Tagarayama 440 Nishinobu-sue, Himeji-shi, Hyogo 670, Japan.



The Kuroshio Extension Bifurcation Region: A pelagic hotspot for juvenile loggerhead sea turtles

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Abstract

Satellite telemetry of 43 juvenile loggerhead sea turtles (*Caretta caretta*) in the western North Pacific together with satellite-remotely sensed oceanographic data identified the Kuroshio Extension Bifurcation Region (KEBR) as a forage hotspot for these turtles. In the KEBR juvenile loggerheads resided in Kuroshio Extension Current (KEC) meanders and the associated anti-cyclonic (warm core) and cyclonic (cold core) eddies during the fall, winter, and spring when the KEC water contains high surface chlorophyll. Turtles often remained at a specific feature for several months. However, in the summer when the KEC waters become vertically stratified and surface chlorophyll levels are low, the turtles moved north up to 600 km from the main axis of KEC to the Transition Zone Chlorophyll Front (TZCF).

In some instances, the loggerheads swam against geostrophic currents, and seasonally all turtles moved north and south across the strong zonal flow. Loggerhead turtles traveling westward in the KEBR had their directed westward movement reduced 50% by the opposing current, while those traveling eastward exhibited an increase in directed zonal movement. It appears, therefore, that these relatively weak-swimming juvenile loggerheads are not passive drifters in a major ocean current but are able to move east, west, north, and south through this very energetic and complex habitat.

These results indicate that oceanic regions, specifically the KEBR, represent an important juvenile forage habitat for this threatened species. Interannual and decadal changes in productivity of the KEBR may be important to the species's population dynamics. Further, conservation efforts should focus on identifying and reducing threats to the survival of loggerhead turtles in the KEBR.

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Keywords: Loggerhead turtle; Transition Zone Chlorophyll Front; Kuroshio Extension Bifurcation Region; Satellite altimetry; Nursery grounds habitat; Geostrophic flow

1. Introduction

The loggerhead turtle (*Caretta caretta*) is a threatened and declining species in the North Pacific, where its ecology and life history are not

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Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): Insights from satellite tag tracking and remotely sensed data

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Abstract

We analyzed satellite track data for 186 loggerhead sea turtles in the North Pacific Ocean using remotely sensed environmental data to characterize pelagic habitat. A large number of candidate habitat variables were merged to the satellite track data and statistically compared to background values over a large spatiotemporal grid which bounded overall occupancy. Five statistically significant variables were identified out of the 16 environmental variables examined. Two of these variables have strong seasonal, interannual, and spatial patterns (sea surface temperature and chlorophyll *a* concentration), while three others were primarily spatial (earth magnetic force, earth magnetic declination, and earth magnetic inclination). Habitat selectivity for these variables was quantified using preference curve methodology established in the foraging literature. The output from the selectivity curves was used to predict a multivariate loggerhead sea turtle habitat index across the pelagic North Pacific. This predicted habitat was ground-truthed with newly available satellite track data.

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Keywords: Biotelemetry; Habitat use; Oceanography; Remote sensing; Resource utilization; Satellite tracking; Sea turtles

1. Introduction

The spatial distribution of pelagic organisms is determined by physical-forcing mechanisms (winds, waves, currents, tides, etc.) coupled with active movement processes by the organisms. Large pelagic macrofauna such as nekton (by definition) possess good

swimming ability and can regulate their location actively. Despite the apparent homogeneity of the open ocean habitat, many scales of structure in the physical environment can be used by nektonic organisms to locate and maintain position in preferred habitat (Longhurst, 2006). The distribution and abundance of most studied nekton exhibit this type of patterned occupancy, i.e., they are not simply distributed randomly or uniformly throughout the open ocean. Sea turtles are one such group of nekton which displays structured pelagic distributions (Carr, 1987; Luschi et al., 2003; Polovina et al., 2000, 2006), presumably via some component of active orientation since even hatchling sea turtles possess good swimming ability (O'Hara, 1980; Davenport and

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Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies

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Satellite tags were attached to 34 non-reproductive loggerhead turtles (*Caretta caretta*) caught as bycatch in the Taiwanese coastal poundnet fishery from 2002 to 2008. Transmission durations ranged from 6 to 503 d (median 172 d), with 5860 d tracked in total. Horizontal track data were processed using the Bayesian state-space modelling to extract the most likely daily positions, taking into account ARGOS data quality and other forms of statistical error. A region of high occupancy in the East China Sea, covering 433 549 km² of coastal and pelagic area next to Taiwan, China, Japan, and South Korea, was characterized from the tracking data. Various attributes of this hotspot are described using satellite tracks and remotely sensed data. The tracks were merged with oceanographic data, emphasizing a new global dataset characterizing mesoscale eddies from satellite altimetry data. A proximity-probability approach coupled with odds ratio testing was used to infer orientation to eddy features. Comparisons against random points, simulated particle tracks, and drifter buoys were used to demonstrate turtle differential responses to eddies inside and outside the hotspot, depending on eddy features (i.e. cyclonic vs. anticyclonic, edges vs. centres). Turtles inside the hotspot utilize fewer strong cyclonic eddy edges than those outside.

Keywords: *Caretta caretta*, East China Sea, habitat, loggerhead turtle, mesoscale eddies, movement, pelagic behaviour, satellite tags.

Short-Range Movements of Hawksbill Turtles (*Eretmochelys imbricata*) from Nesting to Foraging Areas within the Hawaiian Islands¹

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Abstract: Hawksbill sea turtles, *Eretmochelys imbricata*, reside around the main Hawaiian Islands but are not common. Flipper-tag recoveries and satellite tracking of hawksbills worldwide have shown variable distances in post-nesting travel, with migrations between nesting beaches and foraging areas ranging from 35 to 2,425 km. Nine hawksbill turtles were tracked within the Hawaiian Islands using satellite telemetry. Turtles traveled distances ranging from 90 to 345 km and took between 5 to 18 days to complete the transit from nesting to foraging areas. Results of this study suggest that movements of Hawaiian hawksbills are relatively short-ranged, and surveys of their foraging areas should be conducted to assess status of the habitat to enhance conservation and management of these areas.

HAWKSBILL SEA TURTLES, *Eretmochelys imbricata* (L.), are found in nearshore habitats in tropical regions of all oceans. Hawksbill turtles are listed as Critically Endangered in the International Union for Conservation of Nature (IUCN) Redbook (Hilton-Taylor 2000) and as Endangered under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Washington, D.C., 1973) and the Endangered Species Act (U.S.A., 1973). The species has historically not been commonly harvested for consumption in the Pacific because the edible parts can sometimes be toxic (Fussy et al. 2007). Hawksbills in the Caribbean were not generally harvested for food before the

1900s because of toxicity, but as hawksbill numbers declined due to harvesting for scutes (Carrillo et al. 1999, Campbell 2003) toxicity also seemed to decline. McClenachan et al. (2006) suggested that this reduction in toxicity may be connected to the declines in hawksbill numbers because of an increased availability of less-toxic sponges on which hawksbills prefer to forage. Large numbers of hawksbills were taken in the Pacific, mainly for their scutes, which are the thickest and most decorative of all sea turtle scutes. Items that were fashioned from bonding, shaping, and carving these scutes include combs, jewelry, decorative art, and tools (Kaeppler 1978, Canin 1991, Hainshwang and Leggio 2006). Despite international protection, hawksbills are still being harvested and exploited for curios and for tortoiseshell, known in Japan as *bekko* (Canin 1991, MSNBC News Service 2007). Knowledge of hawksbill movements, locations, and habitat usage of critical marine foraging habitats can aid state and local entities to develop effective protection and management schemes for the species.

Before 1995, few studies had been conducted using satellite telemetry to determine post-nesting movements of hawksbill turtles. Knowledge about population size and distribution of hawksbills was obtained mostly from flipper-tagging and recapture programs. Records of flipper-tag recoveries have indi-

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