Oceanic Diet and Distribution of Haplotypes for the Green Turtle, *Chelonia mydas*, in the Central North Pacific

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Abstract: A diet analysis was conducted on the gastrointestinal contents of 10 oceanic green turtles, *Chelonia mydas*, collected as bycatch mortalities in pelagic fisheries. Size distribution of the green turtles ranged from 30 to 70 cm curved carapace length (CCL). Prey items found indicated pelagic green turtles to be carnivorous with some omnivorous tendencies, foraging within the first 100 m of the water column. Most frequent identifiable prey items were zooplankton, pelagic crustaceans, and mollusks (listed in order of frequency of occurrence, which ranged from 80% to 40% frequency): *Pyrosoma* spp., *Lepas* spp. (goose barnacles), amphipods, *Carinaria* spp. (sea snails), and *Cavolinia* spp. (sea butterflies). Other coelenterates such as salps, ctenophores, and cnidarians (jellyfish) were also identified. Plastics and anthropogenic debris were commonly found (70% frequency, mean = 4% of gastrointestinal content by volume). The turtles examined consisted of two distinct morphotypes corresponding to the central Pacific and the eastern Pacific green turtle populations. Genetic analysis confirmed turtles of the central Pacific morphotype to be of Hawaiian origin and at least one of the eastern Pacific morphotype turtles to have a mtDNA haplotype found in the population nesting in the Revillagigedo archipelago off Mexico. Other eastern Pacific morphotypical turtles had a different common Mexican haplotype found among the nesting populations throughout Mexico and the Galápagos. Turtles of the central Pacific morphotype were distributed north of the Hawaiian Islands, and turtles of the eastern Pacific morphotype were all encountered south of Hawai’i, suggesting a dichotomy in the oceanic distribution of these two populations. Our records of green turtles as large as 70 cm CCL in pelagic waters suggest that some green turtles, mainly those with eastern Pacific green turtle morphology and mtDNA haplotype, delay their recruitment to nearshore (neritic) habitats or move back and forth between neritic and open ocean waters as adults.

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and Wildlife Service 1998b) (Figure 1). The lighter-colored morphotype is found worldwide, and a melanistic form is located mainly in the East Pacific (Groombridge and Luxmoore 1989, National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998a, b).

Hatchling green turtles emerge from their nests and enter the oceanic realm. Afterward, little is known about their ecological niche until they enter nearshore (neritic) benthic foraging grounds. According to a number of hypotheses, the recently hatched turtles stay in the open ocean, and this pelagic phase lasts between 5 and 10 yr (Zug et al. 2002, Reich et al. 2007). While in the pelagic phase, all turtle species are mainly carnivorous (Davenport and Balazs 1991, Parker et al. 2005, Reich et al. 2007, Boyle and Limpus 2008). However, little is known about C. mydas during this phase. It has been assumed that they associate with Sargassum drift lines in the Atlantic Ocean, similar to loggerhead post-hatchlings (Caldwell 1963, Carr and Meylan 1980). However, during a survey conducted by Witherington (2002) of juvenile Caretta caretta in Florida Current drift lines, no post-hatchlings of C. mydas were observed. The pronounced counter shading of the hatchlings suggests that posthatching C. mydas may dwell more in open waters rather than in and among algal mats (Bustard 1970, Musick and
Limpus 1997; but see Balazs [1986] regarding transitional plastron coloration). A recent study in the Atlantic suggests that green turtles likely do associate with algal mats; however their tendency to dive quickly with a burst of speed and hide within the algal mat makes it difficult to observe neonate turtles in the wild (Smith and Salmon 2009). Juvenile green turtles have been observed in association with floating *Macrocytis* spp. (kelp) mats in the eastern tropical Pacific (Pitman 1990, Nichols et al. 2001); however few juvenile green turtles have been sighted on the high seas in the central Pacific, except as fisheries bycatch.

Soon after recruiting to neritic habitats, *C. mydas* becomes mainly herbivorous (Bjorndal 1997). Most green turtles recruit to a benthic foraging habitat after the passage of their 5- to 10-yr pelagic phase when they reach sizes ranging from around 40–45 cm curved carapace length (CCL) in Australia (Limpus et al. 1994) to 35–45 cm straight carapace length (SCL) in Hawai‘i and 30–45 cm SCL in Baja California, Mexico (Balazs et al. 1987, Zug et al. 2002, Seminoff et al. 2003). Knowledge of *C. mydas* feeding ecology comes mainly from studies conducted on these neritic habitats (Mortimer 1982, Bjorndal 1985, Balazs et al. 1987, Burke et al. 1991, Seminoff et al. 2002). Sea grass and seaweed are the most preferred benthic forage when it is available (Pritchard 1977). Although nearly 95%–99% of the neritic green turtle diet is made up of plant matter, a small percentage can also consist of animal material such as jellyfish (Limpus 1978, Arthur and Balazs 2008), sea pens, sponges, or various other benthic invertebrates (Hays-Brown and Brown 1982, Burke et al. 1991, Ferreira et al. 2006, Amoroso and Reina 2007, Arthur and Balazs 2008).

The foraging ecology of pelagic turtles is a growing area of research. Salmon et al. (2004) reported the oceanic foraging habits of young captive-reared juvenile green turtles in the Atlantic Ocean. A diet analysis of stranded posthatchling turtles was also conducted along the east coast of Australia (Boyle and Limpus 2008), but few diet studies have been conducted on postneonate oceanic green turtles. In this paper, we report on the diet and sizes of oceanic green turtles in the central North Pacific region and discuss how this may relate to their genetic stock origin, morphotype, and life histories.

**MATERIALS AND METHODS**

We conducted diet analyses of gastrointestinal (GI) contents on 10 oceanic green turtles collected as bycatch mortalities in pelagic fisheries. Four of the green turtles were collected by National Marine Fisheries Service (NMFS) observers during 1990–1991 in the North Pacific high-seas drift-net fishery. Six other *C. mydas* were collected by NMFS observers during 1999–2004 in the Hawai‘i-based pelagic longline fishery. NMFS observers recorded the capture position, measured CCL (nearest 0.5 cm), and collected a skin sample from each turtle. Skin samples were taken from all turtles with a 6 mm skin biopsy punch and stored in salt and frozen until they could be transferred into DMSO solution (Dutton and Balazs 1995). Whole turtles were then sent to the Pacific Islands Fisheries Science Center (PIFSC) for necropsy. We noted the morphological characteristics of the green turtles during necropsy. We assigned a central or morphotypical *C. mydas* (CmM) morphology if the turtle had a typical oval carapace that ranged from light to dark brown in coloration and if the plastron was cream to orange in coloration (Carr 1952, National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998a, Wyneken 2001) (Figure 1A). We assigned an eastern tropical Pacific (ETP) morphology if the turtle had a black to black-gray, highly domed heart-shaped carapace and a grayish plastron (Carr 1967, Pritchard and Trenbuh 1984, Figueroa and Alvarado 1991, National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998b) (Figure 1B). The ETP (melanism) form also typically had thinner carapacial scutes than the CmM type (Figure 1A,B). We mapped the location of capture for each turtle using generic mapping tools as discussed in Ellis and Balazs (1998; see GMT in Wessel and Smith [1991]). We removed the GI contents and preserved them in a 10% formalin solution. Only stomach contents were col-
lected and saved from six of the 10 samples. Full GI tract contents, with stomach contents and intestinal contents saved separately, were collected from the remaining four turtles. We made gross observations of GI contents using a dissecting microscope and sorted the contents to the lowest identifiable taxonomic level. We identified major fauna and quantified the volume of each prey group in the stomach sample using the displacement method (Hellawell and Abel 1971). We used only data for the stomach samples for statistical analyses. Reported average values are followed by ±1 standard deviation.

We performed Principal Component Analysis and K-Means Clustering (Pearson’s correlation, Kruskal-Wallis comparison [two-tailed] and Levene’s test [XLSTAT 2010]) to compare foraging preferences between the CmM morphotype and the ETP morphotype (α = .05).

We conducted genetic analysis as described in Dutton et al. (2008) on tissue samples to obtain mtDNA sequences using the primers HDCM2 and LTCM2, designed to target 488 base pairs (bp) at the 5′ end of the control region of the mitochondrial genome (Lahanas et al. 1994). Sequences were aligned against reference data from the 384 bp segment of the mtDNA control region corresponding to the region reported in Dethmers et al. (2006) and Dutton et al. (2008) to identify haplotypes and assign most likely nesting stock origin.

RESULTS

Prey groups, mean percentage volume of prey, and frequency of occurrence for each prey group are listed in Table 1. The most commonly identifiable prey items were Pyrosoma spp., which we found in 80% of C. mydas stomachs, and we found unidentifiable material in 80% of all stomachs. One stomach contained 100% Pyrosoma, but among all turtles Pyrosoma averaged 35.2% (±42.4%) of the total prey volume. The results of the K-Means cluster analysis show that Pyrosoma make up an individual group, unidentified remains make up another individual group, and all other prey items are considered a third group (P < .0001, α = .5). We also commonly encountered Lepas spp. (goose barnacles, 70% frequency and 13.7% ± 22.3% by volume). We encountered cnidarians less frequently (jellyfish, siphonophores; 50% frequency and 1.9% ± 3.5% by volume for stomach only). Janthina spp. (violet snails) were present but occurred infrequently (30% frequency) and in low volumes (0.8% ± 1.9% of total volume). Anthropogenic debris, including small soft and hard plastic pieces, polypropylene line, and monofilament line, was common (70% frequency), averaging 4% of total volume, with a maximum volume of 11% in one sample. Algae were not commonly encountered (20% frequency), although Rhodophyta composed roughly 27% of the total volume for one sample, and Turbinaria ornata composed 7% of the total volume in another sample. Twenty-nine percent of the stomach contents by volume were unidentifiable as a result of the digestion process. The total volume of prey found in the stomach samples ranged from 24 to 315 ml. There were no significant differences in prey items between the two turtle morphotypes (Kruskal-Wallis, P = .114, Pearson correlation coefficient = 0.9). The distribution of the oceanic green turtles sampled ranged in an area from 5.6° to 33° N latitude and 159° E to 154° W longitude (Figure 2). All turtles were captured at a distance between 60 and 1,700 km from any landmass and over water depths between 1,890 and 5,780 m. The size distribution for green turtle specimens ranged from 30.0 to 70.5 cm CCL with a mean of 48.1 cm ± 12.4 (n = 10 turtles). All drift-net fisheries turtles were sampled north of the Hawaiian Islands. Longline-captured turtles were sampled both north and south of the Hawaiian Islands (Figure 2).

We determined mtDNA haplotypes for six of the 10 turtles, including two of the four drift-net-captured and four of the six Hawai‘i longline-captured turtles. The other four samples were too degraded for proper analysis (Figure 2). The two drift-net-captured turtles we were able to sequence had a common Hawaiian haplotype, CmP1 (Dutton et al. 2008), and the other two turtles had morphological characteristics consistent with the CmM morphotype. Three of six longline-captured turtles we sequenced had a common eastern Pa-
specific haplotype, CmP4 (Dutton et al. 2000, 2008), and all had the ETP morphotype. One of the longline specimens had a haplotype that occurs both in the Hawaiian and the eastern tropical Pacific nesting populations, CmP3 (Dutton et al. 2008), and that animal had the morphological characteristics of an ETP green turtle. Of the two longline-captured turtles we were unable to sequence, one had the typical CmM morphotype, and the other had morphological characteristics of an ETP green turtle (see Figure 2).

**Diet**

Our study analyzed *C. mydas* collected throughout oceanic environments in the central North Pacific and focuses on pelagic turtles (Figure 2). The prey items we describe in this study indicate that green turtles foraging on the high seas are opportunistic, mainly carnivorous, feeding at or near the surface (see Table 1). Gelatinous zooplankton (e.g., *Pyrosoma*, salps, ctenophores, and cnidarians) were common prey items, particularly *Pyrosoma atlanticum*, which was the most frequently and abundantly consumed prey item. Gelatinous zooplankton were observed in almost 80% of the stomachs we examined (Table 1). Unidentified remains were also a significant component of the diet, occurring in 80% of the stomachs. Other significant prey items included crustaceans, molluscs, and marine debris. The diet of green turtles in the oceanic environment appears to be diverse, with a focus on gelatinous zooplankton.
may also have made up part of the unidentified remains (28.9% ± 30.4% of total volume), because jellies are likely to be digested faster owing to their soft bodies, making clear identification difficult, especially when prey items were obtained from the intestinal tract. Although we did not quantify the volume of the intestinal contents of four of the 10 intestinal tract samples, we were able to easily identify and measure *Pyrosoma* bodies, shells from pelagic snails and barnacles, and debris for future analysis. Gelatinous zooplankton seems to be an important food source for all sea turtle species during their oceanic phase, because these foods have been documented as forage for green turtles as well as leatherbacks (Davenport and Balazs 1991), loggerheads (Parker et al. 2005), and olive ridleys (Work and Balazs 2002, 2010). Davenport and Balazs (1991) suggested that *Pyrosoma* and other gelatinous zooplankton are likely targeted as prey not for their gelatinous bodies but for their stomachs or “nuclei,” which are of higher nutritional value because they contain compacted phytoplankton, detritus, and microzooplankton. *Pyrosoma* were the most prevalent prey item that we found in eight out of 10 stomach samples.

Arenas and Hall (1991) reported a relationship between sea turtles and floating objects in the eastern tropical Pacific. We frequently observed goose barnacles (*Lepas* spp.), *Carinaria* spp. (sea snails), and sea butterflies (*Cavolinia* spp.) in our samples but not...
in large volumes. The goose barnacles would likely have been harvested from floating debris. Janthina spp., the violet snails, a prey group common in oceanic loggerhead diets (Parker et al. 2005), were not common in green turtle stomach samples we examined. Parker et al. (2005) also noted that Velella velella, by-the-wind sailors, was another common component of oceanic loggerhead diets, but this prey item was absent in all our green turtle stomach samples. Janthina spp. usually prey on Velella, and these species could likely be found together or individually. Velella often occur in large rafts of many hundreds of individuals (Wrobel and Mills 1998). However, because of the small sample size, the lack of Velella in this study should be further investigated to determine if this indicates a dietary preference, omission due to sample size, or just an absence of Velella in the area where the turtles were foraging.

Our finding of plastic in 70% of the stomachs we examined is consistent with many previous studies that document the ingestion of plastics by sea turtles (Balazs 1985, Allen 1992, Shaver and Plotkin 1998, Tomás et al. 2002). During necropsy, there were no apparent blockages or adverse impact due to the ingestion of the plastic debris (Work and Balazs 2002). Consumption of plastic debris may not have any immediate lethal effect on the turtle (McCauley and Bjorndal 1999), but the decrease in nutritional value of a diet composed of debris may lead to detrimental effects, such as suboptimal health. Studies show increasing amounts of floating plastics in both the Pacific and Atlantic oceans (Day et al. 1990, Moore et al. 2001, Pichel et al. 2007, Barry 2009, Gill 2010, McLendon 2010), which may lead to an increase in plastic consumption by turtles, but future studies need to be done to validate this hypothesis.

Our findings indicate that the turtles likely are opportunistically feeding on bait. A healthy fish or squid would be difficult for a turtle to chase down and catch, so it is more likely that only dead or injured specimens of this prey type would be ingested. The presence of saba (Scomber japonicus), a common bait used in the Hawai‘i-based longline fishery, and squid, Ommastrephes bartramii, the target species of the high-seas squid drift-net fishery (Wetherall et al. 1993), suggests that the oceanic green turtles were interacting with fishery gear and engaging in active dives for foraging purposes, and based on dives recorded for adult green turtles in the Hawaiian Islands these could have been as deep as or deeper than 135 m (Rice and Balazs 2008). However, we also found a spiny cowfish, Lactoria diaphana, which is not a bait item used in any fishery, in the stomach of a longline by-catch turtle. Although L. diaphana may be considered a reef fish, it is also known to live in the open ocean in both its juvenile and adult stages, confirmed from incidental records for adults of this species being noted in Micronesia from the stomachs of pelagic game fish (Myers 1999).

Some of the ingested items could have had land-based origins as well as an oceanic component. One turtle ingested some tree bark or wood. Whether the wood pieces were grazed from floating logs or from a neritic habitat is uncertain; however, logs and lumber have often been found in the open ocean and are often used as recruitment habitat for small fish, corals, and algae (Highsmith 1985, Jokiel 1989, Thil and Gutow 2005). Coralline rock material ingested could also have come from neritic habitat or been scraped off floating objects while the turtle was grazing on other prey items (Jokiel 1989). Another forage item typically thought of as land based was algae. Two morphotypical C. mydas specimens had algae as forage items. One drift-net–captured turtle had red algae (Rhodophyta) in its stomach contents, which could have been grazed as it ingested other prey items such as Lepas spp. The other turtle ingested a species of brown algae, Turbinaria ornata, which is commonly found growing attached to coral reef benches around the Hawaiian Islands. The longline-collected turtle was captured north of French Frigate Shoals (FFS), Northwestern Hawaiian Islands, where T. ornata is established on the reefs (Vroom et al. 2006) and has been recorded as forage for the few resident green turtles that live year-round at FFS (Balazs 1980). The turtle was within 200 km of FFS at the time it was captured, so it may have come upon a raft of floating Turbinaria, or it could
have foraged directly at FFS before returning to the pelagic zone because there was a low volume of *Turbinaria* in the intestine also.

**Genetics**

As noted, all drift-net–collected turtles were captured north of the Hawaiian Islands (Figure 2); those turtles were also all morphotypical (regular CmM type) *C. mydas* (Figure 1A). The one longline-collected turtle captured north of the Hawaiian Islands was a CmM type as well. Unfortunately, mtDNA haplotypes could not be obtained for all of the drift-net–caught turtles; although the genetic results we did obtain show that the regular CmM type green turtles belonged to the central Pacific (Hawaiian) genetic stock. However, because CmM morphotypes in this study were caught as far west as 155° E and we were unable to obtain genetic results from those specimens, it is possible that they may have come from western Pacific nesting beaches such as in Japan, Taiwan, or the Commonwealth of the Northern Mariana Islands or other numerous Pacific islands rookeries, rather than the Hawaiian archipelago (see Dethmers et al. 2006, Cheng et al. 2008). All of the longline-collected turtles captured south of the Hawaiian Islands had eastern Pacific morphology (ETP morphotype or melanistic type [Figures 1B, 2]). Genetic analysis for turtles with ETP morphotypes indicated that they typically had the CmP4 mtDNA haplotype, commonly found at all the eastern Pacific nesting beaches, including the Galápagos and Mexico (Dutton et al. 2008), but not at any of the central or western Pacific rookeries surveyed to date (Dethmers et al. 2006, Cheng et al. 2008, Dutton et al. 2008). Our results suggest that these two different morphotypes encountered as juveniles on the high seas are from two distinct stocks: the CmM type from central and possibly western Pacific stocks, and the ETP morphotype from eastern Pacific stocks. Of the ETP morphotypical greens, one was determined to have a mtDNA haplotype (CmP3 [Figure 2]) found in low numbers in the central Pacific (Hawaiian) and only one ETP rookery, Islas Revillagigedo (Dutton et al. 2008), indicating that this turtle likely originated from that offshore Mexican archipelago, because that particular haplotype has not been found in any other ETP nesting population. These results suggest that the biogeographic barrier that has been noted for a broad range of marine fish (Ebeling and Weed 1963, Hubbs and Wisner 1980, Collette and Aadland 1996, Lessios and Robertson 2006) also may extend to the pelagic distribution of oceanic green turtles in the Pacific (P.H.D., S. Hargrove, and G.H.B., unpubl. data).

It is possible that there are two different life history pathways at work for the two turtle morphotypes. One life history is the “normal” life history cycle, where small pelagic green turtles spend 5–10 yr (Zug et al. 2002, Reich et al. 2007) in the oceanic environment and then recruit to a neritic forage habitat in the Pacific at between 35 and 45 cm SCL. This life history seems to be followed more closely by CmM type green turtles. The other life history cycle has an extended oceanic period or perhaps has the turtles moving between neritic and oceanic habitats throughout their life history, and we propose that this life history pathway is being used more often by those turtles of ETP morphology and genetics. Hatase et al. (2006) suggested that adult female green turtles foraged in the pelagic while moving between neritic and nesting areas; however the tracking did not indicate a prolonged stay for these turtles in the oceanic realm. Senko et al. (2010) recently published evidence that a small percentage of immature East Pacific green turtles moved between neritic foraging areas, because the turtles were recaptured in foraging areas 80–300 km away from their original capture site. During that time, the turtle could have been traveling along the coast or it could have also gone back into pelagic habitat, foraging in the open ocean while it moved between neritic foraging sites. Other evidence to support this divergence in life history comes from a study done by Seminoff et al. (2008), in which postnesting females were tracked from the Galápagos Islands, where two of the seven turtles tracked spent time in the open ocean for over a month. These results bolster the hypothesis that oceanic foraging behavior
may be more prevalent throughout the life history of green turtles, especially ETP turtles, than the standard understanding of their life history suggests. The size range of the turtles in our study also indicates the likelihood of an extended pelagic stage, with five of the 10 greens sampled measuring larger than the average recruit size of 40–45 cm, four with ETP morphology and three genetically confirmed to be ETP animals. The occurrence of green turtles in Alaska (Hodge and Wing 2000) also suggests extended pelagic foraging. Green turtles recorded off Alaska are mainly from stranding of turtles on remote islands open to the Alaska Current. Most of these stranded turtles had the morphology of ETP green turtles and were larger than 60 cm CCL (Hodge and Wing 2000; PIFSC, unpubl. data). Although there may be sea grass or algae available along the Pacific Northwest coast for neritic foraging, prey items identified from the turtles that were necropsied indicated a pelagic diet (Carinaria spp. and Pyrosoma spp., PIFSC, unpubl. data).

Because of the small sample size in our study, additional research is needed to fully document the oceanic habitat and oceanic foraging ecology of the green turtle. Because sea turtles are rarely observed or scientifically sampled in the open ocean, obtaining information on the oceanic stage of the green turtle is mainly confined to a relatively few samples from fisheries bycatch. In fisheries as well as surveys in the Pacific, only 6%–9% of the turtles encountered over multiple years have been identified as green turtles (Wetherall et al. 1993, Alfaro-Shigueto et al. 2002, Donoso and Dutton 2010; R. Pitman unpubl. data). Total numbers of all turtle species caught in these fisheries could vary between a couple of hundred to a couple of thousand depending on year, area fished, fishing gear used, and many other variables. However, obtaining turtles from fisheries bycatch for scientific research is often hindered by lack of collection or Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) permits and also lack of adequate storage facilities aboard fishing vessels to properly preserve scientific samples. Research is also needed to more fully document the movements of green turtles with eastern Pacific morphology to the west of Mexico and south of the Hawaiian Islands to determine which nesting populations these turtles may originate from. These turtles are of particular interest because they exhibit a life history of an extended pelagic stage that is different from the usual understanding of green turtle life history, so more information about these turtles would be beneficial.

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