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ORIGINAL PAPER

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 populations are of concern because green turtle abundance is considered to be an indicator of seagrass and coral reef ecosystem health and resilience (Jackson et al. 2001). However, green turtle conservation is severely hindered by the lack of reliable information on population status and trends due to sampling difficulties of large mobile animals in coastal and oceanic habitats (Chaloupka and Limpus 2001; Chaloupka and Balazs 2007). However, important information on sea turtle health, age, size composition, diet, reproductive status, population trends and cause-specific mortality can be derived from strandings of moribund or dead turtles (Limpus and Reed 1985; Bjorndal et al. 1994; Caillouet et al. 1996; Boulon 2000; Schwartz 2000; Bugoni et al. 2001; Zug et al. 2002; Work et al. 2004; Foley et al. 2005). Strandings are also commonly used to infer geographic distribution and abundance (MacLeod et al. 2004; Maldini et al. 2005) or the primary cause of declining populations exposed to anthropogenic hazards (Pinedo and Polacheck 1999; Lopez et al. 2002; Kreuder et al. 2003).

Five species of sea turtle are recorded from the Hawaiian Archipelago with the green turtle being the most abundant and resident year-round (Balazs and Chaloupka 2004a). The main nesting region for Hawaiian green turtles is French Frigate Shoals in the Northwestern Hawaiian Islands, where turtles nest mainly from June to August (Balazs and Chaloupka 2004a). The Hawaiian green turtle genetic stock is a spatially disjunct metapopulation resident in many coral reef and coastal foraging grounds dispersed throughout the Archipelago (Balazs and Chaloupka 2004b). The Hawaiian green turtle was seriously depleted by over-harvesting and nesting habitat destruction but is now on the way to recovery following protection under the US Endangered Species Act since the late 1970s (Chaloupka and Balazs 2007). Green turtle strandings in the Hawaiian Archipelago have increased over the past 20 years or more, a trend consistent with the increasing abundance of the recovering Hawaiian stock (Chaloupka and Balazs 2005).

However, there are many apparent causes of mortality attributed to these green turtle strandings other than natural mortality that warrants further investigation. So estimating cause-specific mortality trends could be useful for identifying potential impediments to the ongoing recovery of the Hawaiian green turtle stock. We present a comprehensive analysis of 22 years of green turtle strandings in the Hawaiian Archipelago (1982–2003) based on necropsy data. Specifically, the main purpose of our analysis was to (1) define the relative risk of anthropogenic hazards such as coastal fisheries and vessel traffic and (2) identify any temporal or spatial trends in these cause-specific mortality risks.

Materials and methods

Data set

Since 1982 the US National Marine Fisheries Service (NMFS, Pacific Islands Fisheries Science Center, Honolulu, Hawaii) maintains a comprehensive program of reporting and salvaging stranded sea turtles in the Hawaiian Archipelago, especially around the main Hawaiian Islands (Aguirre et al. 1998; Murakawa et al. 2000; Work et al. 2004). Stranded turtles are reported to the NMFS via a well-advertised telephone hotline with the specimens then recovered by NMFS personnel. Moribund turtles are clinically evaluated by two veterinarians and one biologist. Those judged to have poor prognosis for survival are euthanised (Work et al. 2004) with the remainder rehabilitated and released. Locations of stranding were recorded by island (Kauai, Oahu, Maui and Hawaii)—data from the two small islands of Molokai and Lanai near Maui were combined with Maui and referred to here as Maui.

The primary cause of stranding based on the most significant and severe gross lesion was determined via gross necropsy (Work et al. 2004). All stranded turtles were then grouped into eight stranding categories—boat strike, gillnet fishing gear, nets other than gillnets, hook-and-line fishing gear, fibropapillomatosis, shark attack, miscellaneous natural causes and unknown. The fishing gear related hazard categories were based on the fisheries known to interact with sea turtles in Hawaiian waters (Nitta and Henderson 1993). Boat strike strandings were turtles with gross evidence of linear to parallel carapace fractures indicative of propeller, skeg or hull strikes (Kreuder et al. 2003). Gillnet fishing gear, nets other than gillnets and hook-and-line fishing gear strandings were those where there was documented interactions or entanglement with the specific fishing gear. Fibropapillomatosis were those animals with gross evidence of external tumors (Work et al. 2004). Shark predation strandings were those turtles with recent evidence of traumatic amputation of body parts with or without irregular linear abrasions (Kreuder et al. 2003) or semicircular ablation of the carapace or plastron revealing contents of the coelomic cavity. Miscellaneous natural causes included all non-anthropogenic causes of mortality other than fibropapillomatosis or shark attack. Unknown were those causes for which a cause of death could not be determined. In the small number of cases (<2%) where a stranding had multiple possible causes only the primary cause was used in the analysis—for instance if a stranding was attributed to gillnet entanglement/shark attack then only gillnet entanglement was used in the analysis. Gender of stranded turtles was determined by visual inspection of gonads at necropsy. Straight carapace length (cm SCL) or curved carapace length (cm CCL) was measured for each turtle so all size measurements were converted to SCL using the following robust linear regression function derived by us from an independent sample of 1,323 Hawaiian green turtles: SCL = 1.245 + 0.913*CCL, $R^2 = 0.996$.

Statistical methods

Measures of association for count data (or probabilities) in the form of 2 × 2 contingency tables were carried out using χ^2 tests (Bishop et al. 1975). Mantel–Haenszel tests (Bishop et al. 1975) were used for multidimensional tables ($k \times 2 \times 2$ contingency tables) while exact binomial tests were used for single proportions such as strandings sex ratio (Fleiss 1981). Cause-specific mortality rates (conditional probabilities) were derived using cause-specific hazard probabilities and Bayes theorem (Fleiss 1981). Long-term trends and seasonality in the monthly strandings were modelled using nonparametric regression smoothing known as STL (Cleveland et al 1990), which is a time domain filtering procedure that decomposes a series into frequency components of variation—(1) trend, (2) seasonal and (3) residual. Nonparametric logistic regression (Hastie and Tibshirani 1990) was then used to model the probability of hazard-specific stranding or mortality given informative covariates or risk factors such as year, season, straight carapace size (cm SCL) and stranding location. All the logistic regression models comprised logit link, binomial error and cubic smoothing splines to model any nonlinear functional form (Hastie and Tibshirani 1990). All data and graphical analyses were carried out using the statistical modelling program R (Ihaka and Gentleman 1996).

Results

Stranding summary

Five species of sea turtle occurred in the 3,861 strandings reported in the Hawaiian Archipelago over the 22-year period from 1982 to 2003—3,732 green turtles (97%), 47 hawksbills (1.2%), 31 olive ridleys (0.8%), 5 leatherbacks, 1 loggerhead and 45 of unknown species identity. The relative occurrence of these five species in the strandings closely reflects the relative abundance in Hawaiian waters. Totally 74% of all the strandings were recorded from Oahu (Fig. 1), 12.6% from Maui (including Molokai and Lanai), 6.6% from the island of Hawaii, 4.2% from Kauai and the remainder (2.6%) from other islands throughout the Archipelago. Totally 99% of green turtle strandings recorded in the Archipelago occurred around the four main islands of Kauai, Oahu, Maui (including Molokai and Lanai) and Hawaii. However, most green turtle strandings occurred around Oahu (75%) with 50% of these reported from the northeast coast of Oahu (including Kaneohe Bay). Very few green turtle strandings were reported from the southwest coast of Oahu (4%).

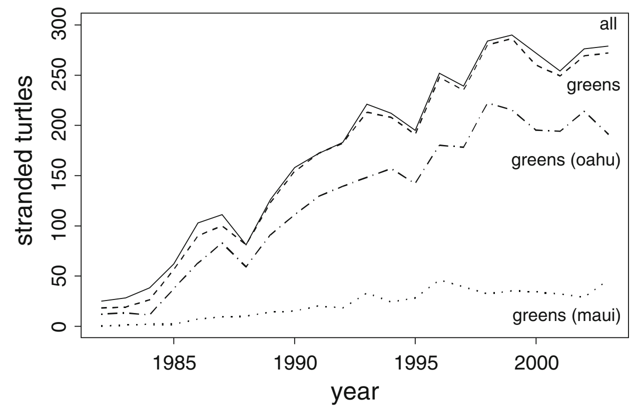

Fig. 1 Shows trends in reported annual strandings since 1982 for all five species (*solid curve*) and for greens throughout the Archipelago (*dashed curve*) or for greens around Oahu and Maui

Temporal trends in green turtle strandings

Strandings of green turtles increased since 1982 but levelled off by the late 1990s (Fig. 1). There were significant fluctuations in the monthly strandings of green turtles recorded for both Oahu and Maui but little temporal synchrony between the two islands (Fig. 2a). Strandings on Oahu (mean of all years) peaked between March and June with a secondary peak and in September (Fig. 2b). It appears that monthly strandings decreased over the 22 years in January and August but increased for most of the other months. Hence, there was a main historical seasonal peak but increasingly more green turtle strandings were recorded throughout the year in more recent times—perhaps reflecting a changing pattern in reporting or changing seasonality of the underlying hazards that cause the strandings.

Hazard-specific strandings and mortality

The tumour-forming disease, fibropapillomatosis, was the most frequent known cause accounting for ca. 28% of the green turtle strandings while hook-and-line fishing gear accounted for 7% (Fig. 3a). The cause of 49% of the green turtle strandings was undetermined because no lesions indicative of cause of death were seen or because carcasses were too decomposed precluding determination of cause of death (Hart et al. 2006). Totally 75% of the green turtle strandings were dead and stranding status (alive or dead) was significantly hazard-specific ($\chi^2_{0.05,21} = 964.7, P < 0.005$).

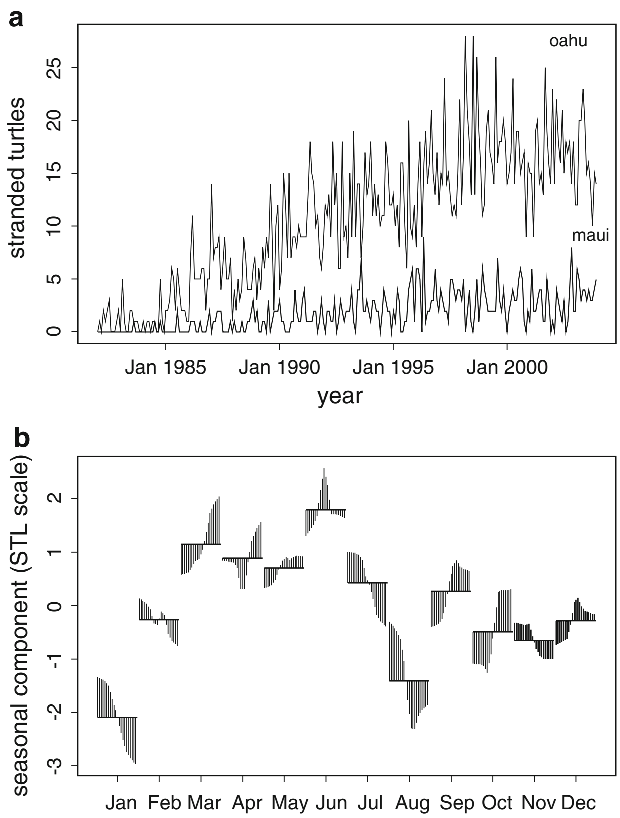

Fig. 2 *Chelonia mydas*. Panel **a** shows trends in monthly strandings since January 1982 for green turtles around Oahu and Maui. Panel **b** shows a seasonal cycle monthly subseries plot of estimated number of monthly green turtle strandings around Oahu from period 1982–2003. *Horizontal line* is fitted mid-mean value of seasonal component for each month. Fitted values for each year (*ends of vertical lines*) associated with each midmean show pattern of interannual variation of monthly subseries

The joint probability of being dead and having a given known stranding cause was highest for fibropapillomatosis and lowest for nets other than gill net (Fig. 3b). Boat strike and shark attack were the hazards most likely to result in a dead stranded green turtle (Fig. 3c). On the other hand, if a stranded green turtle was dead and the cause of death was known, then it most likely due to fibropapillomatosis than any of the fisheries-related hazards (Fig. 3d).

Size- and gender-specific green turtle strandings

Stranded green turtles SCL ranged from ca. 20 cm to ca. 100 cm (Fig. 4), which spans the full range of size from recruitment from an oceanic habitat to adult size in the neritic habitat (Balazs and Chaloupka 2004b). Stranded green turtles were predominately small juveniles ranging from 40 to 60 cm SCL, which corresponds to an estimated age range of ca. 12–15-year-old (Balazs and Chaloupka 2004b). Green turtle strandings from shark attack were significantly larger than strandings from other categories (Fig. 4a), perhaps because larger green turtles are more likely to be taken by sharks or that the remains of a larger turtle are more likely to be found washed up on a beach. On the other hand, median size of fisheries-related strandings (gillnet, hook-and-line) was significantly smaller than for all other hazards (Fig. 4a). There was no significant trend over the 22-year period (1982–2003) in the median size of stranded green turtles in the Archipelago nor was there any seasonal trend in the size of stranded green turtles (data not shown). The median size of green turtles that stranded (alive or dead) in either Maui or Kauai was generally larger than stranded greens around either Oahu or Hawaii (Fig. 4b). There was no gender bias in the Oahu green turtle strandings [exact binomial sex ratio test for $P = 0.50$ (or 50%), $n = 1009$, $P = 0.71$] but stranded male green turtles were significantly smaller than stranded female turtles. Stranding status (alive, dead) for green turtle strandings around Oahu was not a function of gender or sector (Mantel–Haenszel test: $\chi^2_{0.05,1} = 0.028$, $P = 0.87$).

Hazard-specific green turtle stranding probability

Figure 5 shows the probability of a fibropapillomatosis (tumour-forming disease) related stranding as a function of four informative covariates or cofactors—stranding year, season, green turtle size (cm SCL) and the main Hawaiian islands. The probability of a fibropapilloma related stranding increased significantly from the early 1980s, levelled off by the mid-1990s and began declining in recent years (Fig. 5a). Moreover, such strandings were significantly more likely to occur during winter (Fig. 5b). There was also a size-dependent effect with the probability of a fibropapilloma stranding increasing with turtle size (Fig. 5c). Fibropapilloma strandings were more likely to occur around Oahu and Maui than around either Kauai or Hawaii (Fig. 5d). The probability of a gillnet gear related stranding as a function of the four covariates (stranding year, season, size, island) increased significantly from the early 1980s and then declined significantly from the mid-1990s (Fig. 6a). There was no significant seasonal effect in gillnet strandings (Fig. 6b). Gillnet strandings were more likely for small turtles than for large turtles (Fig. 6c) and there was no significant spatial effect in gillnet stranding probability (Fig. 6d). The probability of a hook-and-line gear related stranding as a function of the covariates increased significantly from the early 1980s (Fig. 7a) and appeared more likely during the summer (Fig. 7b). Hook-and-line strandings were more likely for small (<40 cm SCL) or larger turtles >80 cm SCL (Fig. 7c) and there was no significant spatial effect (Fig. 7d).

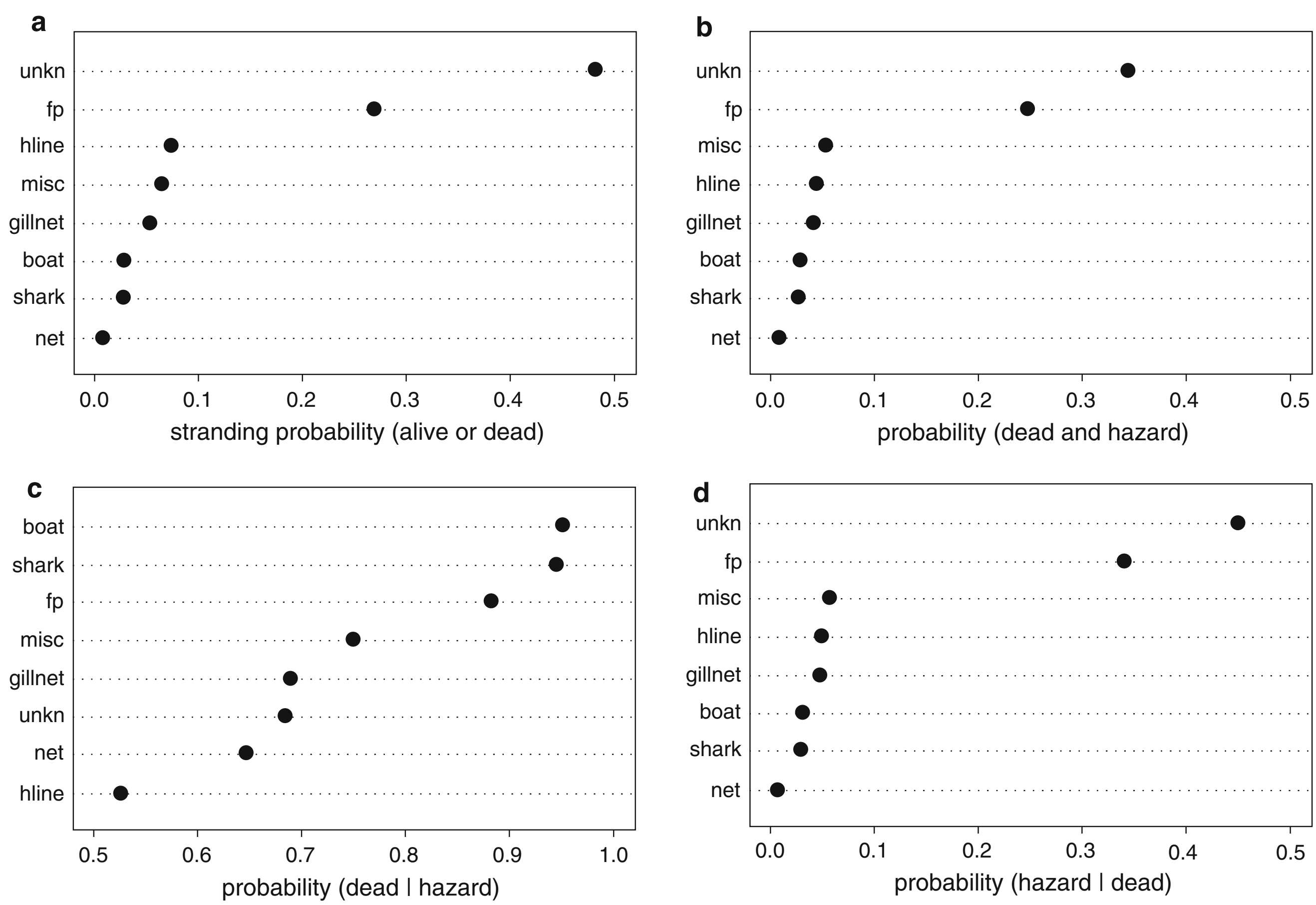

Fig. 3 *Chelonia mydas.* Hazard-specific strandings of 3,732 green turtles in the Hawaiian Archipelago (1982–2003). Panel **a** shows hazard-specific stranding frequency for green turtles (alive or dead). Panel **b** shows joint probability of a green turtle being both dead and attributed to a specific hazard. Panel **c** shows probability of a stranded green turtle being dead given a specific hazard. These hazard-specific mortality rates derived from probabilities in (**a**, **b**) as follows: *P*(dead/hazard) = *P*(dead and hazard)/*P*(stranding probability). Panel **d** shows conditional probabilities of a green turtle stranding being attributable to a specific hazard given that turtle was dead. Conditional probabilities in (**d**) derived from probabilities shown in (**a**) conditioned on probability of dead turtle stranding, which was *P*(dead) = 0.747. Conditional probabilities in (**c**, **d**) related by Bayes theorem. *fp* fibropapillomatosis (tumour-forming disease), *hline* hook-and-line, *misc* various pathological causes, *boat* boat strike, *net* other nets besides gillnets

Hazard-specific green turtle stranding mortality

Around 75% of all green turtles stranded were dead. Figure 8 shows the probability of a dead turtle stranding as a function of four informative covariates or factors—stranding year, turtle size, main island in the southeastern chain of the Hawaiian islands where nearly all strandings were recorded and the main hazard assumed to be the cause of the dead stranding. The probability of a dead green turtle stranding increased significantly from the early 1980s and then levelled off by the late-1990s (Fig. 8a). Meanwhile, the probability of a dead green turtle stranding decreased significantly with increasing turtle size (Fig. 8b). A dead stranded green turtle was more likely to be recorded from Maui and less likely to be recorded from Hawaii (Fig. 8c). When the data are conditioned on stranding year, stranding size, and stranding location then the hazards least likely to be the cause of a dead green turtle stranding are hook-and-line and gillnet fishing gear (Fig. 8d). Boat strike and shark attack were the hazards most likely to result in a dead stranded green turtle around the main Hawaiian islands (Fig. 8d), which is a finding that is consistent with the hazard-specific stranding mortality rates shown in Fig. 3c.

Discussion

Strandings can be a useful supplementary source of information on mortality trends and for helping to understand the health status of recovering marine populations (Kreuder et al. 2003). Most stranding mortality trend studies deal with marine mammal (Pinedo and Polacheck 1999; Lopez et al. 2002; Kreuder et al. 2003) or sea birds (Camphuysen 1998). There have been few analyses of sea turtle stranding

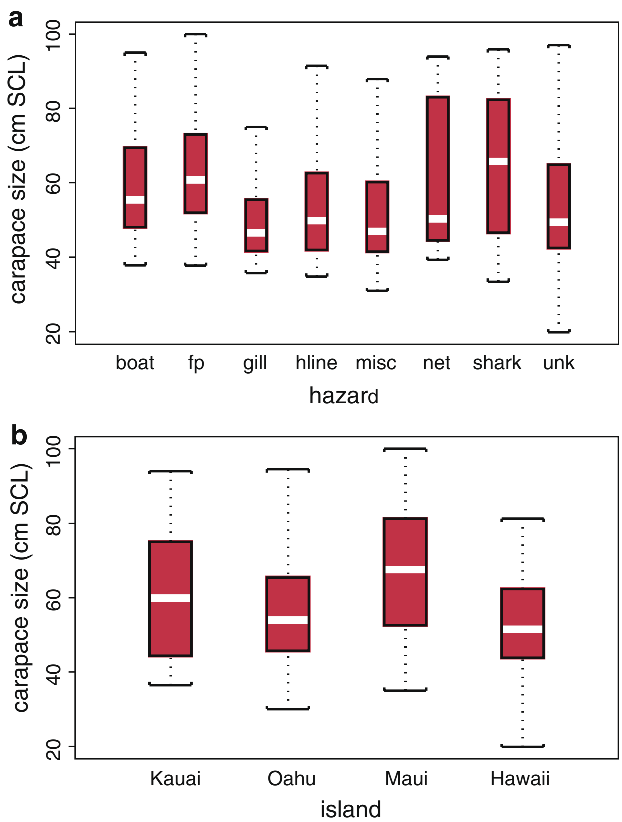

Fig. 4 *Chelonia mydas. Box plot* summaries of the hazard- or island-specific carapace size (cm SCL) distribution of the green turtles stranded (alive or dead) in the Hawaiian Archipelago from 1982 to 2003. Panel **a** shows the distribution for the eight hazard categories. Panel **b** shows carapace size distribution of the strandings for the four main islands. The *white horizontal bar* in each box shows 50th percentile (median) of carapace size for each hazard. Upper and lower boundaries of each box show 75th and 25th percentiles, respectively. Top and bottom cap of *dotted vertical lines* show 90th and 10th percentiles, respectively. *boat* boat strike, *fp* fibropapillomatosis, *gill* gillnet gear, *hline* hook-and-line gear, *misc* miscellaneous pathologies, *net* other fishing net gear besides gillnets, *shark* shark attack, *unk* unknown or inconclusive cause of stranding

trends (Caillouet et al. 1996; Boulon 2000; Schwartz 2000; Foley et al. 2005) and even fewer that were based on systematic postmortem examination (Work et al. 2004; present study). Stranding data are often overlooked as a source of demographic information on marine wildlife because of problems with sample coverage and difficulty in identifying the primary cause of stranding (Caillouet et al. 1996; Camphuysen 1998; Kreuder et al. 2003; MacLeod et al. 2004; Work et al. 2004). The data sets presented here are unique in that they cover a long time period (>20 years) and are based on a systematic examination of each stranding case. An important caveat is that our stranding categories were primarily based on gross necropsy findings, and it is possible given sufficient resources, that more detailed examinations of the carcasses might have revealed underlying pathology not identified in this study. Regardless, this would not have helped in cases where carcasses were decomposed.

The relative abundances of the five species of marine turtle strandings recorded in the main Hawaiian islands are consistent with known foraging and nesting activities in the Archipelago. Green turtles are the most abundant sea turtle in Hawaiian waters with nesting occurring mainly in the Northwestern Hawaiian Islands (Balazs and Chaloupka 2004a). Hawksbills are more common in the inshore waters of the islands of Hawaii and Maui (Balazs 1982), and nesting occurs around some of the main Hawaiian islands (Ellis et al. 2000). There are few records of olive ridleys nesting in the Hawaiian islands (Balazs and Hau 1986) and this turtle is rare in the inshore Hawaiian waters (Balazs 1982). Leatherback and loggerhead strandings are extremely rare since neither species nest or forage around the Hawaiian islands and so are probably just migratory transients. However, it is not known whether the green turtle strandings are a reliable indicator of the relative mortality risks attributable to various anthropogenic hazards. Whether most moribund or dead turtles wash ashore is unknown and clearly the reported strandings can only be some unknown fraction of all green turtle mortalities. Epperly et al. (1996) found that winter beach strandings might not be a reliable indicator of fishery-induced mortalities in North Carolina because the prevailing winter currents were offshore and so dead loggerhead turtles were less likely to wash ashore. Hart et al. (2006) speculated that perhaps ca. 20% of sea turtle mortalities due to gear-induced injury might strand along the North Carolina coast, depending on seasonal factors. It is unlikely that such findings apply year-round or to a broader range of coastal geographic settings (Lugo-Fernandez et al. 2001), such as around the main Hawaiian islands.

Strandings of green turtles around the main Hawaiian islands increased significantly since 1982 but levelled off by the late 1990s to ca. 200 per annum or ca. 15–20 per month. The slowing of the strandings rate for Oahu greens reflects the recovering trend in the Hawaiian green sea turtle stock since the 1970s, where the stock is now approaching carrying capacity (Chaloupka and Balazs 2007). However, the initial rapid increase in reported strandings rate from 1982 to 1988 may also reflect increasing public awareness during this period. The Hawaiian sea turtle strandings program was established in the late 1970s but the spatial and temporal coverage was considered inadequate until 1982 so that reporting bias at least for Oahu is considered a minor source of error in the green turtle strandings record. Moreover, the Oahu green turtle strandings rate from 1988 onwards was 5.4% pa (95% CI: 3.6–7.1%), which is consistent with the Hawaiian nesting population increase estimated 5.7% pa (95% CI:

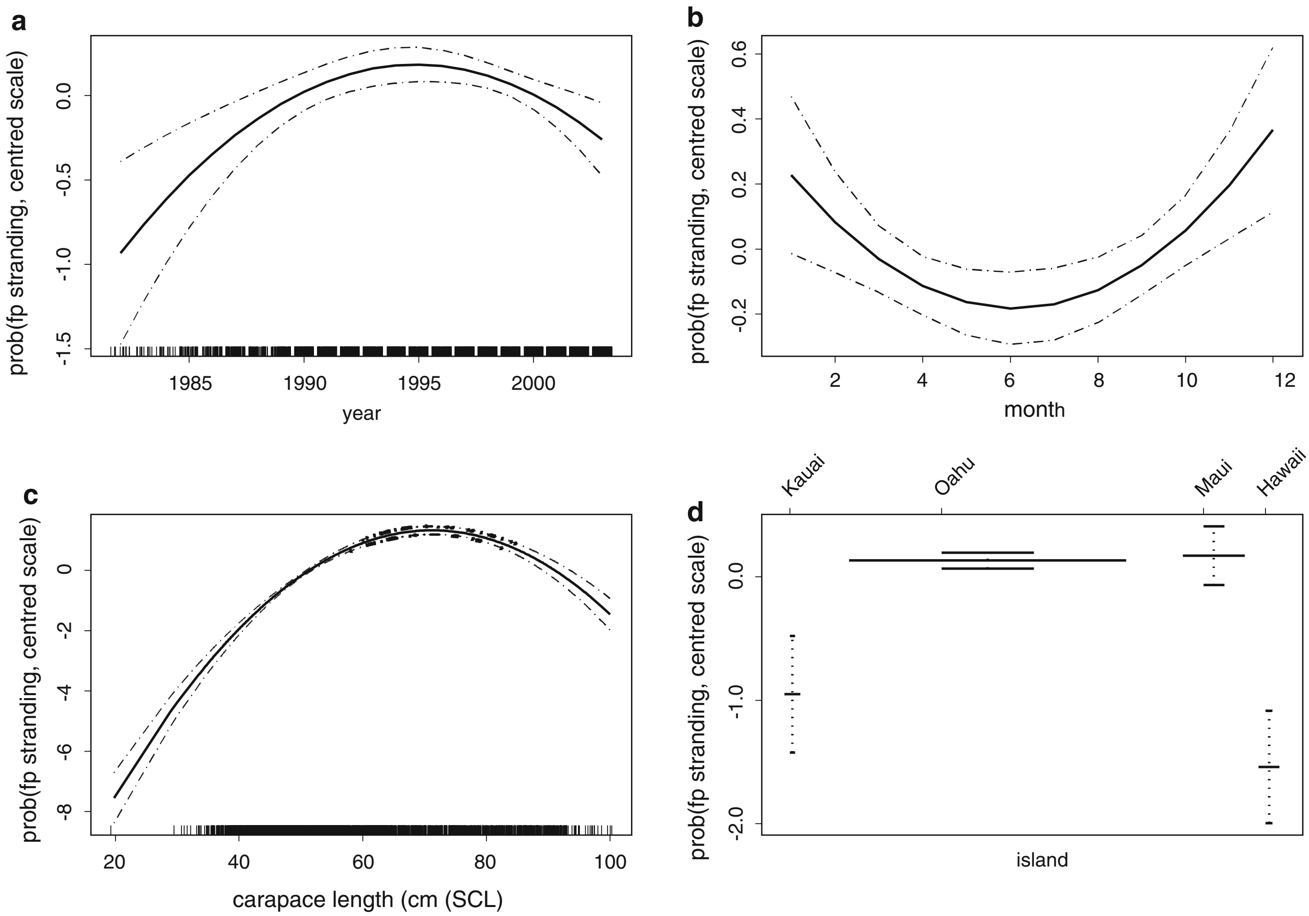

Fig. 5 *Chelonia mydas.* Graphical summary of a logistic regression model fit for probability of a fibropapilloma afflicted green turtle stranding conditioned on four predictors (year, month, carapace length, and island where stranding occurred). The response variable (probability of fibropapilloma afflicted stranding) is shown on *y*-axis in each panel as centred scale to ensure valid pointwise 95% confidence bands and comparison between predictors across panels. The expected predictor-specific function is shown in each panel by the *solid curve* while the 95% pointwise confidence bands are shown by the *dashed curves*. Panel **a** shows response variable as a function of stranding year conditioned on the other three predictors. Panel **b** shows response variable as a function of season conditioned on predictors. Panel **c** response variable as a function of size conditioned on predictors. Panel **d** response variables as a function of where stranding was recorded in the main Hawaiian islands conditioned on predictors. The *vertical bars* on the topside of the lower *x*-axis of (**a**, **c**) are known as a rug, which shows data distribution within each panel. Width of ISLAND categories in (**d**) are proportional to sample size with 95% confidence interval for each category shown by top and bottom cross bars with expected response shown by *middle cross bar*

5.3%–6.1%). Another plausible explanation for any increase in reported green turtle strandings around the main Hawaiian islands would be an increasing trend in exposure to various anthropogenic hazards. Most strandings were recorded from Oahu presumably reflecting the greater probability of a stranding being reported due to the larger human population on Oahu. Maui is the next most populous island and accounted for the next highest number of green turtle strandings record in accordance with previous findings (Work et al. 2004). The relatively lower strandings reported from the island of Hawaii relative to the amount of coastline, population and recreational fishing effort might be due to the much narrower coastal shelf around this island thus decreasing the probability of a dead or debilitated turtle washing onshore. We suspect that the stranding pattern around Oahu was not a function of reporting bias due to human population density but probably reflected the prevailing winds and surface currents (Work et al. 2004; Maldini et al. 2005).

The size class structure of stranded green turtles was consistent with the expected relative size-class structure of the Hawaiian green turtle metapopulation (Balazs and Chaloupka 2004b). The decreased probability of stranding with increasing turtle size could reflect fewer large turtles at sea, decreased probability of large turtles washing up on shore, or decreased probability of mortality from the factors listed here as turtles age. The smaller size of males suggests that female Hawaiian green turtles might grow faster than males at comparable sizes (or ages), as shown for other green turtle populations where gender is known

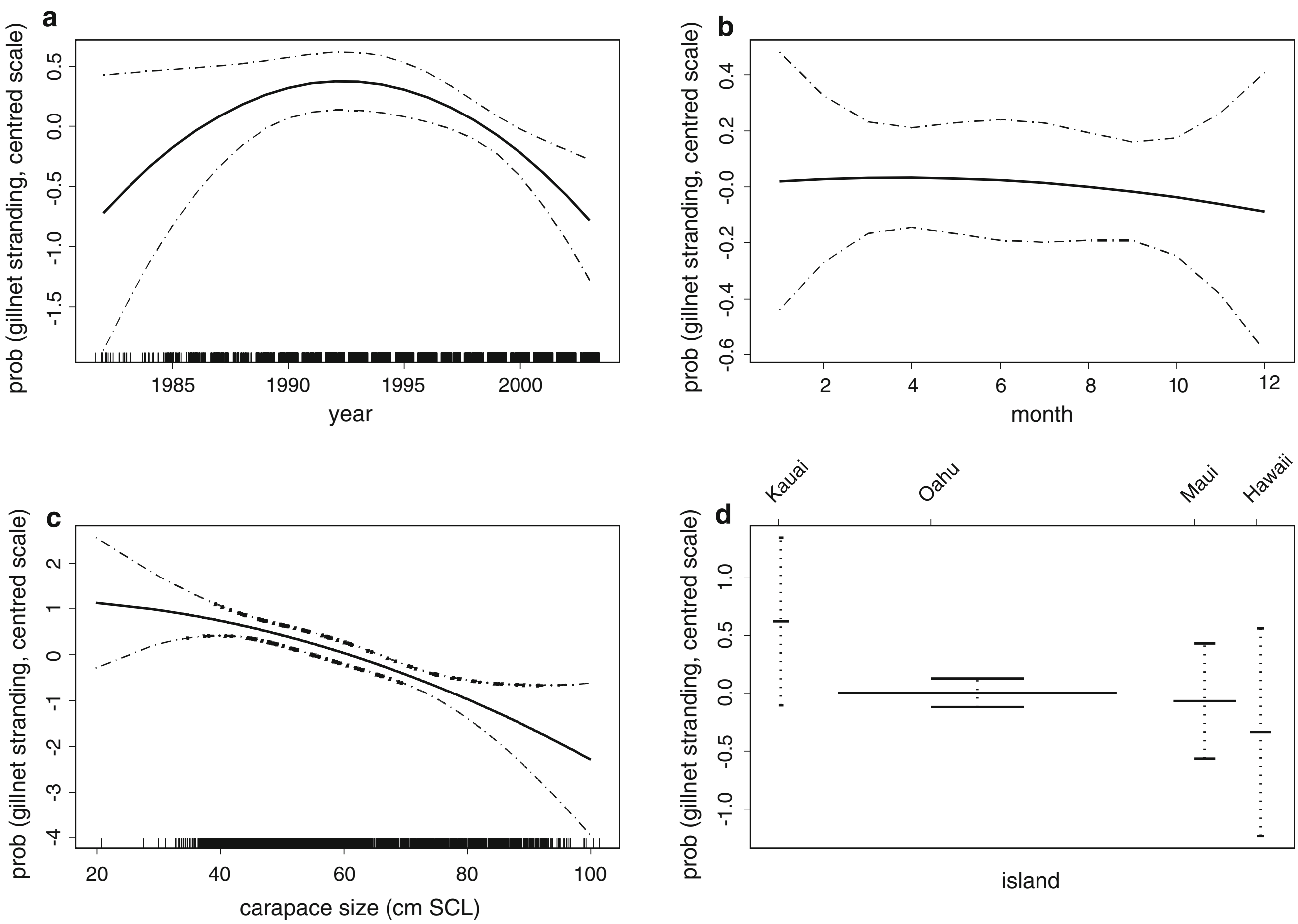

Fig. 6 *Chelonia mydas.* Graphical summary of a logistic regression model fit for the probability of a gillnet gear related green turtle stranding conditioned on four predictors (stranding year, stranding month, carapace length, island)—see Fig. 5 for abbreviated codes

using laparoscopic examination of gonads (Chaloupka et al. 2004). However, this remains to be confirmed for Hawaiian green turtles (Balazs and Chaloupka 2004b). On the other hand, there was no gender-bias in the green turtle strandings since males were as frequent in the strandings as females. This is consistent with Wibbels et al. (1993) who found a 1:1 primary sex ratio for the Hawaiian green turtle stock.

We conclude then that sea turtle strandings around the main Hawaiian islands reflects the relative species abundance in coastal Hawaiian waters as well as the general size- and gender-composition of the resident green turtle stock. Similarly, Maldini et al. (2005) found that the pattern of odontocete cetacean strandings around the main Hawaiian islands reflects well the species composition and relative abundance trends derived from live-animal surveys. So it is apparent that marine animal strandings can be a useful supplementary source of information about the geographic distribution and relative abundance of green turtles and some cetaceans in coastal Hawaiian waters. Importantly, the green turtle strandings in our study provide insight into the various sources of mortality for green turtles in coastal Hawaiian waters and the relative risks of exposure to anthropogenic hazards such as fishing gears and boat strike.

Fibropapillomatosis was the most common known cause of green turtle strandings and strandings were more likely around Oahu and Maui than the other main Hawaiian islands, which is consistent with the restricted geographic prevalence of this disease in the Hawaiian Archipelago (Balazs and Chaloupka 2004b; Work et al. 2004). Importantly, this disease does not appear to be affecting the recovery of the Hawaiian green turtle stock (Balazs and Chaloupka 2004a; Chaloupka and Balazs 2005). It has also been suggested that protuberant fibropapillomas increase the risk of entanglement and fishery-induced mortality (Foley et al. 2005). We found no such association between stranding status (alive or dead) and fibropapilloma-afflicted strandings with or without fishery-induced injuries (gillnet, hook-and-line, nets), irrespective of the main Hawaiian island where the stranding was recorded (Mantel–Haenszel $k \times 2 \times 2$ test: $\chi^2_{0.05,1} = 2.78$, $P > 0.09$; or collapsed over the 4-island factor for a single 2×2 table $\chi^2_{0.05,1} = 2.39$,

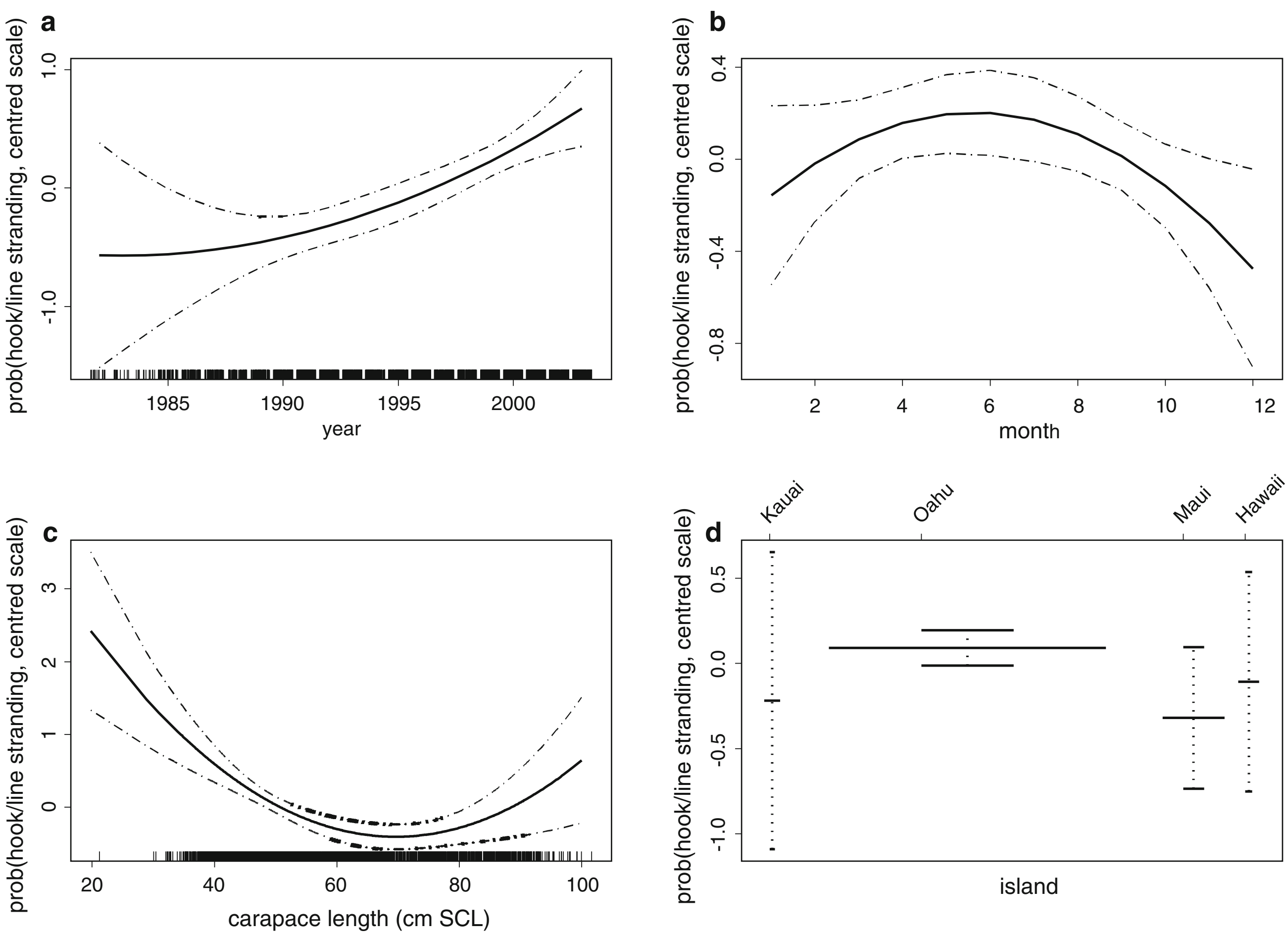

Fig. 7 *Chelonia mydas.* Graphical summary of a logistic regression model fit for the probability of a hook-and-line gear related green turtle stranding conditioned on four predictors (stranding year, stranding month, carapace length, island—see Fig. 5 for abbreviated codes

$P > 0.12$). In other words, we found no evidence that fibropapillomatosis increases the risk of fishery-induced mortality for Hawaiian green turtles.

Interaction with hook-and-line fishing gear was the second most common cause of a green turtle stranding around the main Hawaiian islands. Hook-and-line gear strandings were also more likely around Oahu than the other main Hawaiian islands probably reflecting higher per capita inshore fishing effort. Shrimp trawling (Caillouet et al. 1996) and gillnets (FAO 2004) are considered to be the major fishing gear hazards for sea turtles in coastal waters around the world. However, there are no coastal trawl fisheries in Hawaiian waters and we found that gillnet interactions were less likely than hook-and-line interactions in coastal Hawaiian waters. Moreover, most fishing effort in inshore Hawaiian waters is related to hook-and-line activities rather than net-related activities (Nitta and Henderson 1993). Nonetheless, gillnet fishing gear poses a significant risk to green turtles in Hawaiian waters because of the much higher specific mortality rate than hook-and-line gear.

Three of the hazards were found to have a significant temporal trend in the probability of a stranding—fibropapillomatosis, gillnet fishing gear and hook-and-line fishing gear. Despite increasing initially, the probability of fibropapillomatosis strandings has declined since the mid-1990s. Moreover, Chaloupka and Balazs (2005) have shown that the severity of this disease has declined since the late 1990s for a green turtle population resident around Molokai near Maui. The probability of gillnet gear strandings has also declined significantly since the mid-1990s. Meanwhile, the probability of hook-and-line gear strandings has increased significantly since the early 1990s. Even though this hazard had the lowest specific mortality rate, if the risk of hook-and-line strandings continues to increase then management intervention might be warranted.

The probability of a stranding attributable to gillnet and hook-and-line gear decreased significantly with increasing turtle size. Such fishing gear could be size-selective or juvenile turtles could be more likely to become debilitated from fishing gear interaction (resulting

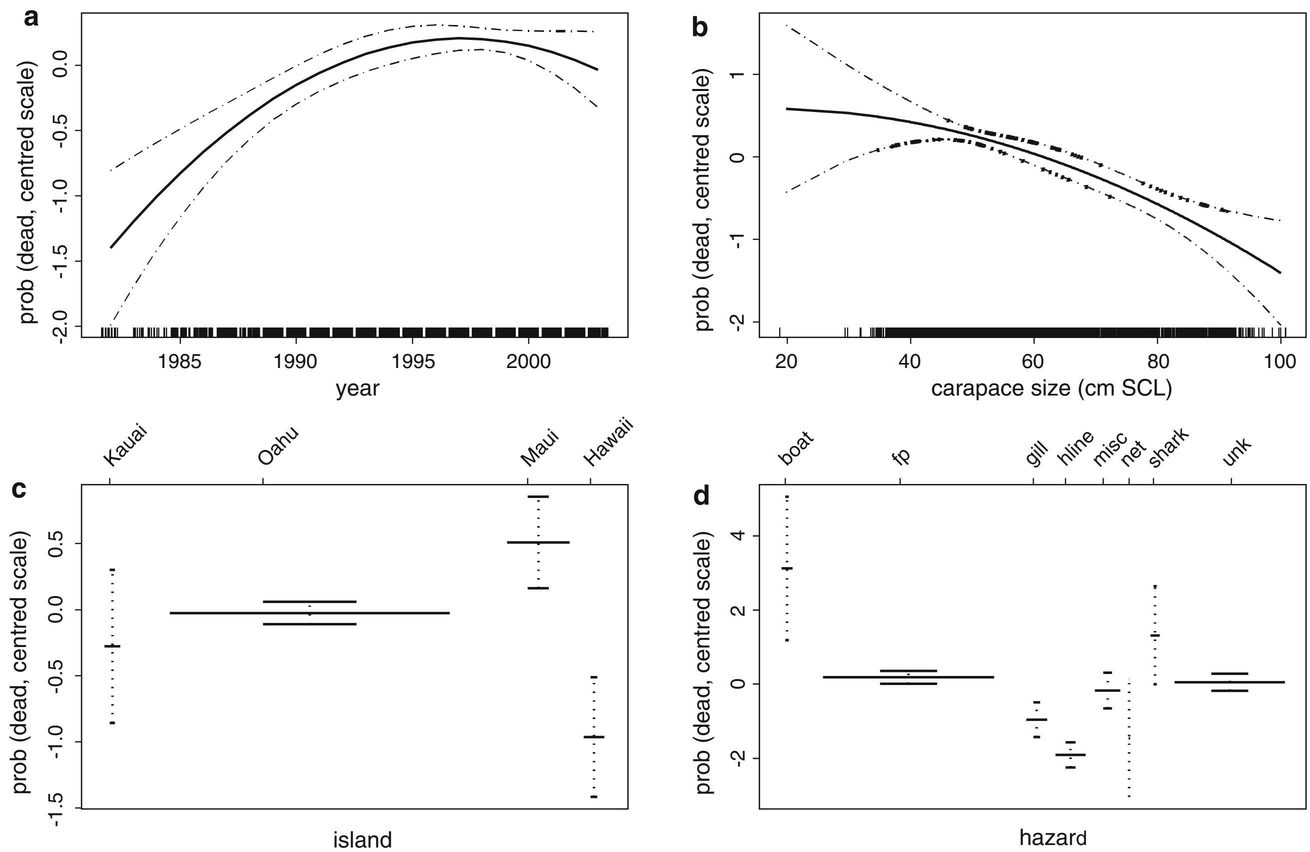

Fig. 8 *Chelonia mydas.* Graphical summary of a logistic regression model fit for the probability of a dead green turtle stranding (response variable) conditioned on four predictors (stranding year, carapace length, island where stranding occurred, and specific hazard). Panel **a** shows response variable as a function of stranding year conditioned on the other three predictors. Panel **b** shows response variable as a function of turtle size conditioned on predictors. Panel **c** shows response variable as a function of where stranding was recorded in the main Hawaiian islands conditioned on predictors. Panel **d** shows response variable as a function of hazard conditioned on predictors

in a stranding). However, a more likely explanation is that gear-induced strandings reflect the higher relative abundance of juveniles expected for this recovering stock. Recall that most causes of stranding were unknown and that the criteria for attributing fishing gear as a cause of stranding demanded physical evidence of gear interaction. It is likely that some turtles die from fishing gear interaction through drowning leaving no external marks. However, drowning is an extremely difficult cause of death to determine for stranded marine animals (Kreuder et al. 2003). So stranded sea turtles that drown due to incidental capture in fishing gear may have no conclusive cause of death or could be mistakenly attributed to some other cause. Therefore, our study may underestimate the impacts of fishing gear on the Hawaiian green turtle stock.

However, assuming that there was no hazard-specific stranding bias (for instance a boat strike stranding was no more likely to wash ashore and be found than a gillnet stranding), then green turtle strandings attributable to fishing gear interactions were not common in the Archipelago. Moreover, while the specific mortality rate for fibropapillomatosis was 88% it was significantly lower at 69% for gillnet fishing gear and 52% for hook-and-line fishing gear. These conditional probabilities or specific mortality rates provide a basis for evaluating the relative risks of exposure to specific anthropogenic hazards and to help assess the cost-benefits of imposing hazard-specific mitigation strategies. So while hook-and-line gear interactions was one of the more common causes of green turtle strandings, it was the least likely hazard to cause a dead stranded green turtle in Hawaiian waters. Furthermore, boat strike rather than fisheries interactions was the most likely human-related cause of a dead green turtle stranding around the main Hawaiian islands. It is possible that a sick turtle or a turtle that died from some other cause was then subsequently struck by a boat and sorting this out would require more detailed postmortem exams on freshly dead turtles (Work et al. 2004). Boat strike was also reported as a major cause of sea turtle strandings around the US Virgin Islands although sample sizes in that study were small (Boulon 2000).

Seasonal trends were also evident for some hazard-specific strandings, which might be due to environmental factors (Hart et al. 2006). For instance, temporal fluctuations in sea surface temperature and food supply were proposed to account for trends in loggerhead sea turtle strandings along the US northeast Atlantic coast (Schwartz 2000). On Oahu there was a peak historical season of green turtle strandings from March to June and a secondary peak in September perhaps reflecting seasonal abundance of turtles or seasonality of onshore winds or currents. Fibropapilloma strandings were more likely during winter. This could be due to winter storms washing debilitated turtles onshore or to temperature-dependent immunosuppression in affecting tumoured turtles more severely (see Zapata et al. 1992). Foley et al. (2005) also found that stranded green turtles with fibropapillomatosis were more common during winter in Florida. There was also a summer peak in fishing gear related strandings (gillnets, hook-and-line, nets) that could be due to increased fishing activity during that time of year.

The identification of the various sources of green turtle mortality in Hawaiian waters is essential for understanding the health and long-term population recovery of the Hawaiian green turtle stock (Chaloupka and Balazs 2005; Chaloupka and Balazs 2007). Temporal and spatial trends in green turtle strandings can provide important information on disease threats and trends in mortality risk attributable to anthropogenic hazards such as coastal fisheries. For instance, the declining risk of exposure to fibropapilloma disease and gillnet fishing gear bodes well for the long-term health and recovery of the once-depleted Hawaiian green turtle stock (Chaloupka and Balazs 2007). However, more comprehensive information on ageclass- and sex-specific green turtle abundance in Hawaiian waters, and direct estimates of coastal fishing effort, are now needed to support improved risk assessment of such hazards in coastal Hawaiian waters.

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