Four decades of green turtle (*Chelonia mydas*) strandings on Hawaiʻi Island (1983–2022): Causes and trends

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Abstract

Hawaiian populations of green turtles (*Chelonia mydas*) have increased since Federal and State protections were implemented in the mid 1970s, and reported stranding events have also increased. This study analyzed Hawaiʻi Island data: stranding location, date, size, sex, presence/absence of tumors, stranding status, and cause of stranding. A total of 754 stranded green turtles were reported from 1983–2022: 379 stranded on the east (windward) coast of Hawaiʻi Island and 375 on the west (leeward) coast. Strandings peaked in 2011 and 2018 and were highest from March to August. The most common known cause of stranding was hook-and-line fishing gear (21.4% of total strandings), followed by fibropapillomatosis (7.2%), human take (4.4%), miscellaneous (3.7%), boat impact (3.3%), shark attack (3.2%), and net (2.1%); however, 54.8% of strandings had no known cause. Stranded turtles on east Hawaiʻi Island had a higher frequency of fibropapillomatosis, whereas west Hawaiʻi stranded turtles showed higher incidence of shark attacks. These results provide the first analyses of stranding data from Hawaiʻi Island and provide information that can inform resource managers, policy makers, and the public about the various types and magnitudes of impacts, anthropogenic and natural, to green turtles so that mitigation measures can be put into practice.

Keywords: sea turtles, mortality, fishing gear, fibropapillomatosis, survey

1 Introduction

Green turtles (*Chelonia mydas*) are the most abundant large marine herbivores found throughout the world and in the Hawaiian Islands. Hawaiian populations of green turtles that were once depleted have increased since their 1974 protection under Hawaiian Law and their 1978 protection under the Endangered Species Act (Balazs and Chaloupka 2004). Green turtles migrate long distances during their lifetime, from nesting to foraging grounds (Balazs et al. 2015). In the Hawaiian Islands, 96% of nesting occurs on the sand islets at French Frigate Shoals, located in the Northwestern Hawaiian Islands (Marine Turtle Biology and Assessment Program 2022). Migration patterns and complicated life history patterns cause green turtles to occupy many habitats during their lifespans including pelagic

Note to publisher: The Hawaiian letter ʻokina is typeset in this manuscript as an open quote, e.g. Hawaiʻi, Oʻahu, Miloliʻi. In electronic publication, it should be rendered as unicode U+02BB MODIFIER LETTER TURNED COMMA.

environments during their early years and during migrations, as well coastal areas in their later years (Balazs 1980; Bolten 2003). Therefore, green turtles are susceptible to threats in both offshore and coastal environments (Bolten 2003).

Green turtles have experienced a long history of exploitation. The species was used for meat by indigenous coastal people around the world, as well as by European royals in the 18th and 19th centuries (Witzell 1994). Hawaiian green turtles have been additionally impacted by hunting at foraging grounds, by harvesting of both eggs and femails at nesting grounds, and by the destruction of their nesting habitat. Since protection began under the Endangered Species Act, a reduction in such exploitation has been observed (Balazs and Chaloupka 2004). However, large marine vertebrates, including green turtles, face other threats, and are often victims of bycatch, becoming accidentally entangled or hooked by commercial or recreational fisheries activities targeting other species (Lewison et al. 2004). Bycatch is harmful to green turtles because it can cause drowning, and internal/external injuries from hooks and line entanglements.

Fibropapillomatosis (FP) is another major threat to sea turtle populations. FP is a debilitating neoplastic disease associated with herpes virus found in turtles worldwide (Jacobson et al. 1991; Herbst 1994). The disease was first described in green turtles in the Florida Keys in 1938 and affects mostly immature turtles (Herbst 1994). FP is indicated by the presence of internal, external, and oral tumors. Oral tumors are unique to Hawaiian green turtles and are often found in the glottis, making survival difficult (Work et al. 2004). The presence of these tumors can impact the turtles' ability to breathe, swim, dive, forage, and see (Perrault et al. 2021). On Oʻahu, Maui, and Kauai from 1982-2003, FP was the most common cause of stranding, defined as a turtle that has been found dead, injured, or exhibits ill health or abnormal behavior (Chaloupka et al. 2008).

A variety of factors, both natural and anthropogenic, can cause sea turtle strandings. The majority of strandings involve sea turtles that died at sea and washed ashore; however, most stranded turtles show no cause of death (Hart et al. 2006). An unknown number of deceased turtles never reach shore. They are eaten by scavengers, sink, and/or decompose while in currents or eddies (Crowder et al. 1995; Hart et al. 2006). Therefore, the number of sea turtle strandings that is recorded is likely a minimal estimate (Hart et al. 2006). Stranding response programs can provide important insight into the health, welfare, and conservation status of sea turtle populations. Analyses of the data collected by these programs provide valuable information on mortality patterns and can aid regulatory managers (Crowder et al. 1995). Stranding data from Hawaiʻi Island have not been analyzed previously nor included in earlier studies in the Hawaiian Islands (Chaloupka et al. 2008). The knowledge gained from stranding patterns can be used to establish mitigation measures to reduce strandings and maintain healthy green turtle populations.

In the present study, a comprehensive analysis of 39 years of Hawaiʻi Island green turtle strandings is presented to (1) identify the causes of strandings affecting green turtles around Hawaiʻi Island, (2) assess trends in strandings, and (3) identify differences and similarities between strandings in west and east Hawaiʻi Island.

2 Methods

2.1 Data Collection

Data were collected on turtles stranded on Hawaiʻi Island from 1983–2022 by members of the Pacific Islands Fisheries Science Center under the US National Marine Fisheries Services, the University of Hawaiʻi at Hilo Sea Turtle Stranding Response Team, and the Hawaiʻi Preparatory Academy Sea Turtle Research Program. The database used in this study was compiled from records available at https://georgehbalazs.com/field-notebooks-by-george-h-balazs/hawaii/. The west and east coasts of Hawaiʻi Island are different in terms of climate (the windward east coast receives much more rainfall than the leeward west coast), terrain, currents, and population, so the data used in this study were analyzed for the island as a whole, as well as by west and east coast. West Hawaiʻi included locations from Miloliʻi north to Kawaihae, and east Hawaiʻi included locations from South Point north to Hawi (Figure 1).

For each stranded turtle, the following information was collected: date of stranding, stranding location, stranding status (alive/dead), and cause of stranding. Data on species, sex, straight carapace length (SCL), curved carapace length (CCL), and the presence or absence of tumors indicative of fibropapillomatosis were also recorded. SCL was used in size analyses because it was reported more frequently than CCL. In cases where CCL was recorded, but not SCL, CCL was converted to SCL using the following linear regression function: $\mathrm{SCL} = 1.245 + 0.913 \cdot \mathrm{CCL}$ (Chaloupka et al. 2008). Determination of size classes of turtles followed Balazs (1980): juvenile–post hatchling to 65 cm SCL; subadult–from 65 to 81 cm SCL; adult–greater than 81 cm SCL.

The primary cause of stranding was based on direct observation and/or necropsy when available. Causes of stranding were classified into eight categories used previously by Chaloupka et al. (2008): fibropapillomatosis (FP), hook-and-line fishing gear, net and gillnet fishing gear, boat impact, shark attack, human-take, miscellaneous, and unknown. FP strandings were turtles that had gross evidence of external tumors. Fishing gear strandings were identified by obvious signs of an interaction or entanglement with the particular gear (hook-and-line or net) (Boulon 2000; Chaloupka et al. 2008). Boat impact strandings were recognized by the presence of a crushed carapace or deep cuts originating from propellers or hulls of boats (Boulon 2000; Guimarães et al. 2021). Shark attack strandings included turtles with deep incisions or removal of soft tissue or body parts (Stacy et al. 2021). Human-take (take is defined under the Endangered Species Act as "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct") strandings were turtles with obvious evidence of having been butchered or poached, often accompanied with spear wounds (Boulon 2000). Miscellaneous strandings included turtles with natural, non-anthropogenic causes not fitting in any of the other categories (e.g., natural disasters, including weather and tsunami events; and internal diseases confirmed by necropsy), and unknown strandings were those for which no cause could be determined (Chaloupka et al. 2008).

2.2 Statistical methods

Chi-square goodness of fit tests were used to determine if there were equal proportions among months of stranding, stranding status, causes of stranding, and sex of stranded turtles for all of Hawaiʻi Island. When comparing west and east Hawaiʻi, contingency tables and chi-square tests of independence were used. All analyses were performed using the statistical software R version 4.2 (R Core Team 2022). Statistical significance was accepted at $p < 0.05$.

It is reasonable to model the occurrence of turtle stranding events as a Poisson process with a rate λ that potentially changes through time and space. If strandings are classified into groups, then there are two equivalent ways of modelling this: each class as an independent Poisson process with its own rate λ_i, or as a single overall process at rate λ that generates an event at time T, and this event is then

Table 1 Raw counts and proportions of stranding cause from 1983–2022 for Hawaiʻi island, separated into east and west sides. Fibropapillomatosis is abbreviated FP.

	East		West		Total	
Cause	n	%	n	%	n	%
Boat impact	9	2.4	16	4.3	25	3.3
FP	53	14.0	1	0.3	54	7.2
Hook/line	85	22.4	76	20.3	161	21.4
Human take	19	5.0	14	3.7	33	4.4
Misc.	5	1.3	23	6.1	28	3.7
Net	7	1.8	9	2.4	16	2.1
Shark attack	8	2.1	16	4.3	24	3.2
Unknown	193	50.9	220	58.7	413	54.8

distributed to a class by a categorical random draw from some class distribution π that potentially also depends on time T.

Of particular interest is the case where the categorical distribution π does not change with time, which is equivalent to saying that the ratios between the class rates λ_i are also constant. Probabilistically, the class is independent of the rate of the Poisson process. While the overall rate λ at which turtle strandings are observed depends on population size and human reporting patterns, this model allows us to investigate potential changes in the cause distribution π over time.

To this end, multinomial linear models with Poisson error structures were fit using the nnet package (Venables and Ripley 2002) and model selection was carried out using Akaike Information Criterion (Akaike 1974). These models produce a prediction function which may be interpreted as the class distribution $\pi(t)$, allowing us to compare models with and without a dependence on time.

3 Results

A total of 754 green turtles stranded on Hawaiʻi Island from June 1983 to June 2022. Of those strandings, 375 (49.7%) were located on the leeward or west coast of Hawaiʻi Island, while 379 (50.3%) were located on the windward side or east coast of Hawaiʻi Island (Figure 1, Table 2).

Of the 754 stranded turtles in the records, slightly over half had no known cause that could be determined (the "unknown" cause). The most common known cause of stranding was hook-and-line fishing gear, accounting for about 1 in 5 strandings.

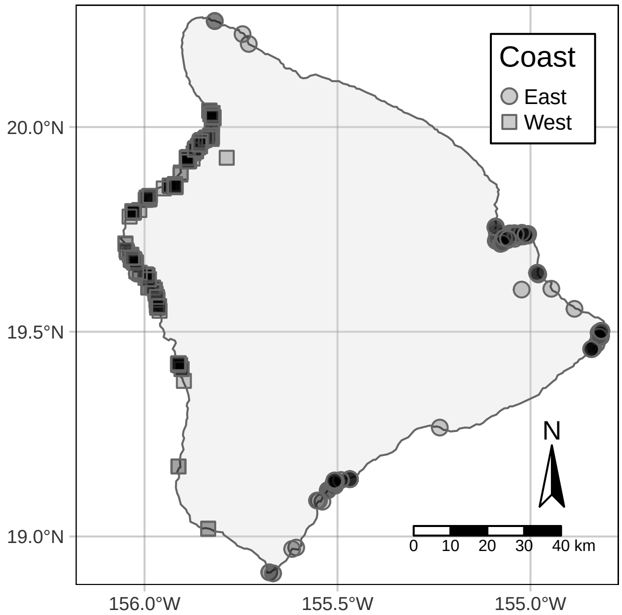

Fig. 1 Stranding locations and the division into eastern (windward) and western (leeward) sides of Hawai‘i island. Coastline map courtesy of United States Geological Service (USGS) and Hawai‘i Statewide GIS Program.

The distribution of causes is significantly different between the east and west coasts of the island (Chi-square test, $X_7 = 69.5$, $p < 10^{-10}$), with the effect being driven most strongly by the FP and Miscellaneous categories (Table 1).

3.1 Temporal trends

The number of strandings on Hawai‘i Island have fluctuated over the years but show an overall increase over time (Figure 2). Across both sides of the island, strandings were less frequent in winter, November–February, than in other months (Table 2). The highest totals were observed between March and August. Raw counts of hook-and-line fishing gear strandings have steadily increased over the years, and while strandings with FP as the chief cause of stranding have remained overall low, the number of FP-caused strandings was higher after 2000 (Figure 3). The second most common known cause of stranding in west Hawai‘i was miscellaneous, a category that includes a significant number of strandings associated with the 2011 Tōhoku tsunami, while in east Hawai‘i FP is the second leading cause (Table 1, Figure 3).

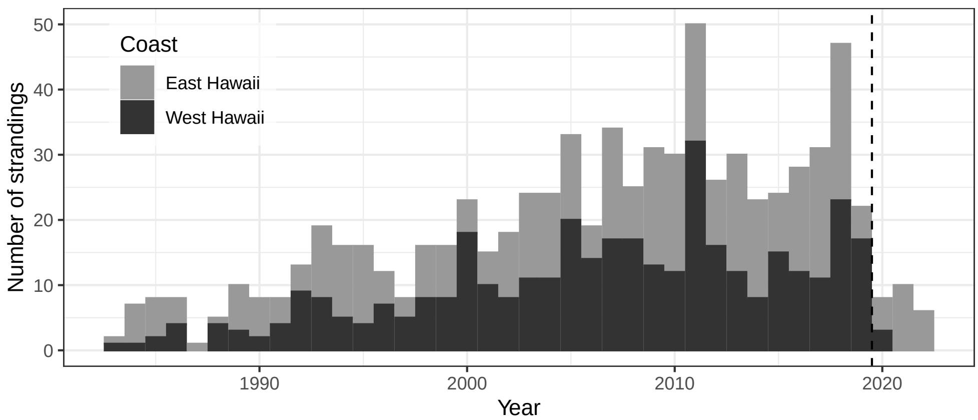

Fig. 2 Number of strandings from 1983–2022 for Hawaiʻi island, separated into east and west sides. Data for 2020 and beyond are incomplete due to COVID-19 disruptions to data collection.

Table 2 Strandings in each month for Hawaiʻi island, separated into east and west sides.

Coast	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
East	29	31	32	38	33	42	37	30	25	33	25	24	379
West	24	27	45	36	42	40	42	39	16	30	16	18	375
Total	53	58	77	74	75	82	79	69	41	63	41	42	754

To investigate changes in the relative rates of stranding causes, multinomial log-linear models were fit using date of record as a predictor. To reduce the variance of the fitted model parameters, the causes as recorded were consolidated into 3 categories: Human caused (hook-and-line, boat impact, human take, and net); predation, disease and weather (shark attack, FP, and Misc.); and the original unknown category. The 2011 Tōhoku tsunami-related strandings, as well as the records prior to 1985 were excluded from the model fit. The Akaike Information Criterion (AIC) is used to compare a series models of models using natural splines based on date of standing with increasing degrees of freedom. The AIC increases going from a null model (AIC 1300.9) with no dependence on year to a predictor function with 2 degrees of freedom (AIC 1304.7), and then slightly decreases again, so that a 4 degree of freedom model (AIC 1299.7) has an AIC 1.2 smaller than the null model. Figure 4 displays a 3-degree of freedom model (AIC 1301), with confidence bands constructed using the bootstrap. The null model is represented by dotted white lines, and apparently fits within the confidence bands of the model that includes dependence on year. These results show a lack of evidence that

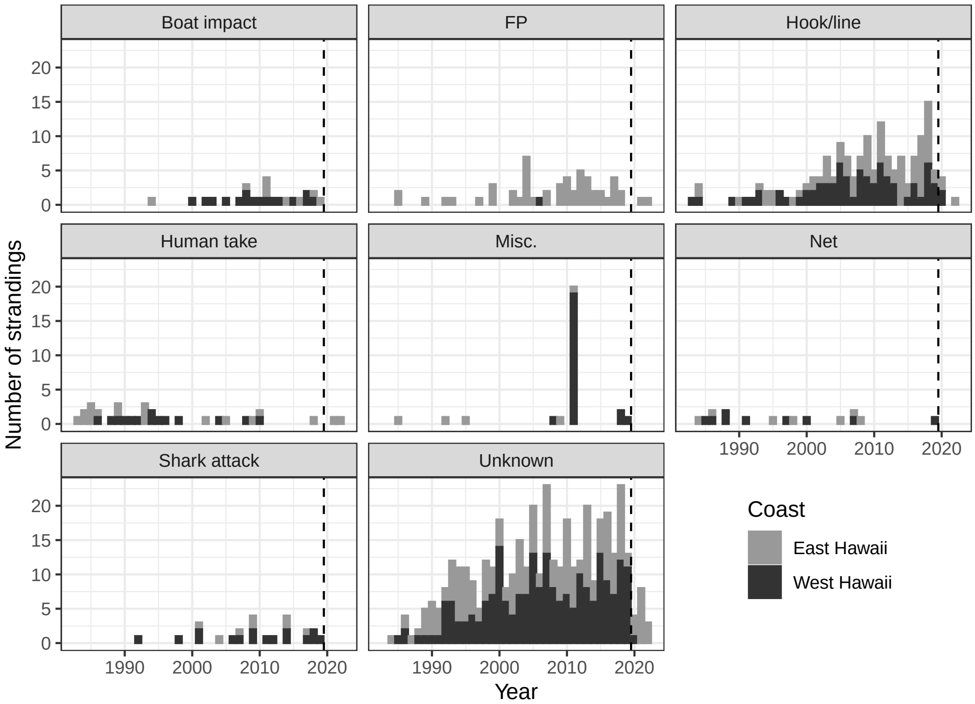

Fig. 3 Number of strandings from each cause, separated into east and west sides. Fibropapillomatosis is abbreviated FP. Data for 2020 and beyond are incomplete due to COVID-19 disruptions to data collection.

the date of stranding provides significant information about the relative rates of stranding among the three consolidated cause categories.

3.2 Size and gender

Stranded turtles in the records ranged from 19.8 cm to 99 cm straight carapace length (SCL), with a mean of 54.8 cm, across 381 juveniles, 88 subadults, and 19 adults. No carapace length measurement was recorded in 266 of the case reports. Turtles stranding in east Hawaiʻi ($\mu \pm \mathrm{SE} = 58.7 \pm 1$ cm SCL, $n = 227$) were significantly larger (t-test, $t_{378} = 6.29$, $p = 9 \times 10^{-10}$) than those in west Hawaiʻi ($\mu \pm \mathrm{SE} = 51.3 \pm 0.6$ cm SCL, $n = 261$) Figure 5 shows SCL distributions for each cause, and while the distribution of SCL is not independent of Cause (ANOVA, $F(7, 480) = 3.41$, $p = 0.0014$), the differences between the groups are small compared to the within-group variances. The records contain 154 female, 145 male,

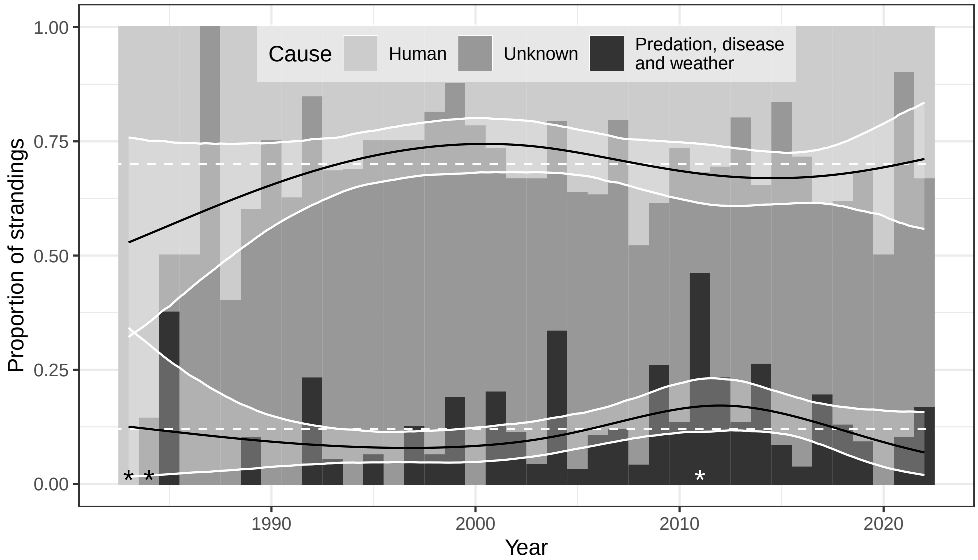

Fig. 4 A multinomial regression fit using natural splines with 3 degrees of freedom. 95% confidence bands are constructed by bootstrapping. Records from years with asterisks (*) are excluded from the model. The dotted white lines correspond to a model with no dependence on year.

Table 3 Fibropapillomatosis tumor presence in stranded turtles by side of Hawaiʻi island.

	Tumor		
Coast	Present	None	Not Recorded
East	141	143	95
West	9	317	49
Total	150	460	144

and 455 gender undetermined cases, also with marginally different distributions between side of the island (Chi-square, $X_2 = 6.4$, $p = 0.042$).

3.3 FP tumor presence/absence

As shown in Table 3, 460 records indicated the absence of FP tumors, 150 records presence of a tumor, and 144 records are missing this observation. Note that the presence of a FP tumor does not necessarily mean that the primary cause of stranding was recorded as FP. Tumor presence/absence is significantly associated

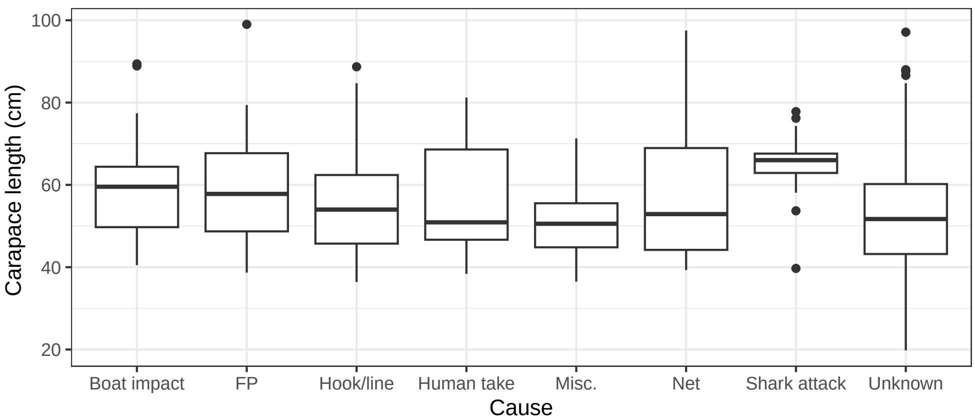

Fig. 5 Straight carapace length (SCL) was measured in 488 records, and and plotted for each stranding cause. Fibropapillomatosis is abbreviated FP. Boxplot outliers begin at 1.5 times the inter-quartile distance.

Table 4 Survival status of stranded turtles by cause. Fibropapillomatosis is abbreviated FP.

Cause	Alive	Dead	Not Recorded
Boat impact	12	13	0
FP	38	16	0
Hook/line	115	45	1
Human take	6	27	0
Misc.	23	5	0
Net	8	8	0
Shark attack	8	16	0
Unknown	149	251	13
Total	359	381	14

with side of the island, with turtles stranding in east Hawai‘i more likely to have tumors than those in west Hawai‘i (Chi-square test, $X_2 = 197$, $p < 10^{-10}$).

3.4 Stranding status

Of all the stranded turtles, 359 stranded alive, 381 stranded dead, and 14 turtles had no stranding status reported. Stranding status was found to be significantly associated with cause (Chi-square test, $X_7 = 93$, $p < 10^{-10}$). More turtles stranded alive than dead because of FP, hook-and-line, and miscellaneous, while boat impact, human take, shark attack, and unknown were causes more likely to result in dead stranded turtles. Net fishing gear strandings showed equal numbers

Table 5 Survival status of stranded turtles by month.

Month	Alive	Dead	Not Recorded
January	31	20	2
February	33	24	1
March	49	28	0
April	26	47	1
May	25	45	5
June	38	44	0
July	35	43	1
August	29	40	0
September	17	23	1
October	27	36	0
November	24	17	0
December	25	14	3

of turtles that stranded alive and dead (Table 4). More turtles stranded alive than dead in the months of November–March, while more turtles stranded dead than alive in the months of April–October (Table 5). Stranding status was also found to be significantly associated with stranding location (Chi-square test, $X_1 = 21.5$, $p = 3.5 \times 10^{-6}$). West Hawaiʻi had 146 turtles strand alive and 221 strand dead, while east Hawaiʻi had 213 turtles strand alive and 160 strand dead.

4 Discussion

Seven hundred fifty-four green turtles were recorded stranded on Hawaiʻi Island in the period 1983-2022, which represents an unknown fraction of total strandings on Hawaiian shores in that time. Stranding programs rely on reports from the public, and are therefore dependent on the density of human activity at the shoreline as well as public knowledge of the reporting procedures. However, if a location is regularly accessed by more than a few people, a stranding is likely to be reported, and it is reasonable to believe that this will happen independent of the variables observed in these records.

Strandings on Hawaiʻi Island showed an overall increase in rate between 1983 and 2022. Green turtle strandings have also increased on the other main Hawaiian Islands since 1982 (Chaloupka et al. 2008). One important reason for this increase is a positive one: Green turtle populations in the Hawaiian Islands have recovered significantly since their 1974 protection by the State of Hawaiʻi under Regulation 36 and their 1978 protection under the Endangered Species Act (Balazs and Chaloupka 2004; Bennett and Keuper-Bennett 2008). The increase in population size will directly lead to additional observed stranding events, even if the risk to an individual turtle remains constant over time (Boulon 2000). Additionally, the human population increase on Hawaiʻi Island and the rise in numbers of visitors at the shoreline increase the chance of encountering and reporting a stranding. In general, the locations of strandings shown in Figure 1 reflect beaches and other shoreline areas with easy public access. Increased public awareness of strandings and response programs and the greater use of cell phones and the internet probably have led to more reporting over time. However, the increase in reported strandings appears to slow in the early 2000s (Figure 2), stabilizing at approximately 25–30 per year. This trend was also noticed in studies covering the other main Hawaiian Islands (Chaloupka et al. 2008).

There are two years post 2005 which show an unusually large number of Green turtle strandings: 2011 and 2018. The peak in 2011 is associated with the March 2011 magnitude 9.0 Tōhoku earthquake off the coast of Japan and the subsequent tsunami, large waves, and hazardous currents that it caused around Hawaiʻi Island, and particularly its western shoreline (Cheung et al. 2013). The waves and currents associated with tsunamis bring marine life onshore with them and can wash turtles inland. Two hawksbill turtles were reported stranded in Hawaiʻi as a result of the 2011 earthquake (Brunson et al. 2022), and a 2009 tsunami in Samoa similarly led to 52 turtles stranding on land (Bell et al. 2011). The apparent downward trend of strandings after 2018 is probably not because fewer turtles stranded, but is rather due to human behavioral changes caused by the COVID-19 pandemic. Throughout the pandemic, people in general spent much less time in public locations, and for some periods, Hawaiʻi County and State beach parks were closed for recreational use by executive decree (County of Hawaiʻi, Office of the Mayor 2020; State of Hawaiʻi, Office of the Governor 2020). Similarly, tourism to the island and state was heavily restricted. All of these factors lead to a sharp drop in the number of people visiting Hawaiʻi Island coasts, and subsequent reports of strandings.

The highest rates of green turtle strandings occurred during the Hawaiian spring and summer months, from March–August. This is similar to the findings on Oʻahu where green turtle strandings were highest from March–June (Chaloupka et al. 2008), and for adult hawksbills in the Hawaiian Archipelago where strandings were highest from June–September (Brunson et al. 2022). Similarly, strandings of loggerhead, green, and leatherback turtles in Brazil were highest during the austral spring and summer seasons (Monteiro et al. 2016). Strandings on Hawaiʻi Island were lowest during the months of September, November, and December, but a secondary peak in the month of October was seen. This same peak was observed in the 2022 green turtle strandings on Maui (Cutt et al. 2023) and Oʻahu showed a similar secondary peak of strandings in September (Chaloupka et al. 2008). This trend of strandings seen in the Hawaiian Islands may indicate seasonal abundance of turtles, seasonal activity of humans, or seasonality of shoreline surf, currents, and winds (Chaloupka et al. 2008).

Hook-and-line fishing gear was the most common known cause of stranding of green turtles on Hawaiʻi Island as a whole. Fishing gear strandings show a similar qualitative pattern to the overall time series (Figure 3), increasing from 1983 to the mid 2000s and then apparently leveling off. Chaloupka et al. (2008) found a similar increase of hook-and-line fishing gear strandings since 1982. It is difficult to untangle the effects of the increased population of Hawaiian green turtles from the risk of hazard from fishing activity and gear, as both factors directly affect the rate of strandings observed.

Hawaiian green turtles are frequently reported with hooks intact and line entangled around their flippers and body. These interactions are often a result of lost and/or discarded fishing gear or fishers cutting the line when accidental hooking occurred, which illustrates the need for stronger management and preventatives (Nitta and Henderson 1993). Hook-and-line fishing gear strandings were also prevalent on Oʻahu, Maui, and Kauai, making up the second most common cause of stranding of green turtles (Chaloupka et al. 2008). Similar to the findings of the present study, fishing gear was the foremost cause of stranding for green turtles on Maui in 2022, with 81% of the total strandings showing interactions (Cutt et al. 2023).

However, the number of hook-and-line strandings may be even greater than estimated. Work et al. (2015) performed necropsies (postmortem autopsies) on stranded turtles throughout the Pacific and found that 48% of foreign body ingestion cases (mostly all associated with fishing gear) showed no external sign of fishing line interactions. Green turtle strandings resulting from interactions with fishing gear are prevalent around the world, including the U.S. Virgin Islands (Boulon 2000), Brazil (Guimarães et al. 2021), Taiwan (Cheng et al. 2019), and Greece (Panagopoulos et al. 2003). Fibropapillomatosis was the second most common cause of stranding in this study, whereas Chaloupka et al. (2008) found FP to be the main cause of stranding in green turtles in Oʻahu, Maui, and Kauai.

The relative rates of strandings by cause over time is of particular interest for managers and conservationists because it can indicate particular sources of danger to turtle populations. The overall rate of observation depends on population size and human reporting behavior in a complex way that is difficult to disentangle, but by looking at the distribution of causes over time we may be able to identify structural changes in the cause of strandings. While the record collection process kept eight categories of cause, for modelling purposes we reduced these to 3 broad categories: direct intentional and accidental human causes, such as boat impacts and fishing and hunting related injuries; natural events, predation, and disease; and unknown causes.

The distribution of these three consolidated causes has been relatively stable since the early 1990s (Figure 4), providing unconvincing evidence of any major shifts between the relative risks between direct human causes and the other categories. One way of interpreting this result is that the increased numbers of strandings over time can be explained entirely by the growth in turtle populations and increases in reporting by the public. While keeping the proportion of human-caused strandings constant over time may be regarded as a minor conservation success story, given the significant growth in human population and coastal activity over the same time period, humans remain a significant source of danger to turtles. There remains much room for improvement, in particular with regards to hook-and-line injuries.

The current study found that different sides of Hawaiʻi Island had different distributions of stranding cause. West Hawaiʻi Island had a higher proportion of shark attack and boat impact strandings, while east Hawaiʻi had more FP and human take strandings. Increased shark attack strandings on west Hawaiʻi may be because of the larger population of tiger sharks found along the west coast (Meyer et al. 2009). Tiger sharks are well-known predators of sea turtles, and green turtles are found regularly in their stomach contents (Witzell 1987; Lowe et al. 1996). West Hawaiʻi also has a large tourism industry, with many snorkel, diving, and manta ray and marine mammal watching tours operating in the same coastal waters that green turtles occupy. These tours, as well as commercial vessels, frequent the many shallow bays located in west Hawaiʻi that are important foraging habitats for green turtles. Increased boat presence accompanied with high vessel speeds, varying water depth, and times of poor visibility can all factor into a higher proportion of boat impact strandings on the west side of the island (Fuentes et al. 2021).

The majority of green turtles that stranded on Hawaiʻi Island were juveniles. Similarly, juveniles predominated the stranded green and hawksbill turtles throughout the Hawaiian Islands (Chaloupka et al. 2008; Brunson et al. 2022).

Juvenile green turtles were also the most common size class stranded in New Caledonia (Read et al. 2023), Australia (Flint et al. 2015), and Brazil (Monteiro et al. 2016). The high proportion of juveniles stranding may be a result of increased nesting populations at French Frigate Shoals leading to an increase in juveniles moving from nesting to foraging areas (Balazs and Chaloupka 2004). Juvenile turtles may be more immunologically naïve and susceptible to environmental stressors that could contribute to stranding (Flint et al. 2015).

Larger turtles stranded on east Hawaiʻi Island than on west Hawaiʻi, despite the fact that stranded turtles with the highest SCL values were the result of shark attacks. Bornatowski et al. (2012) found that the probability that a green turtle in Brazil stranded with a shark bite increased with size, and Chaloupka et al. (2008) reported the same trend for green turtles in the main Hawaiian Islands. Smaller green turtles are also frequently attacked by sharks, but may be completely consumed and thus do not wash ashore after such event. A spatial trend in size-classes was also reported by Chaloupka et al. (2008): larger turtles stranded on Maui and Kauai than on Oʻahu.

There was no gender-bias of stranded green turtles on Hawaiʻi Island: male and female strandings occurred with a 1:1.06 ratio. The lack of a gender-bias for green turtles was also shown in the main Hawaiian Islands (Work et al. 2004; Chaloupka et al. 2008). The present and prior studies are consistent with the 1:1 sex ratio of Hawaiian green turtles found by Wibbels et al. (1993). Unlike in the Hawaiian Islands, many green turtle populations around the world appear to have more females than males (Flint et al. 2010; Cheng et al. 2019; Read et al. 2023). Clutches of sea turtles are sensitive to temperature change, and an increase in the temperature during incubation can drastically change sex ratios of nests, leading to clutches of all females. As temperatures continue to rise as a result of climate change, the Hawaiian population of green turtles may eventually see the same skew seen in other locations around the world (Hawkes et al. 2009).

More than 60% of the stranded turtles on Hawaiʻi Island had no tumors indicative of FP, although this is likely an overestimate of the true value, as not every turtle in this study underwent a necropsy that could reveal the presence of internal tumors that would otherwise go unreported. However, the overall reduction of FP prevalence has been documented previously in Hawaiian green turtles. Twenty-one of 66 turtles observed with tumors in one summer were then seen later with no tumors (Bennett et al. 2000). The low population of turtles with FP on Hawaiʻi

Island is consistent with the 2022 stranding report for green turtles on Maui, in which only one case of FP was reported (Cutt et al. 2023).

Turtles were more likely to have FP on east Hawaiʻi, whereas FP was very rare on green turtles that stranded on west Hawaiʻi. The west (Kona) coast of Hawaiʻi Island had no diagnosed cases of FP for many of the years that FP was prevalent in the other Hawaiian Islands (Balazs 1991; Aguirre and Balazs 2000; Work et al. 2001). In Florida, turtles with tumors are more likely to become entangled in fishing line, thus the higher percentage of hook-and-line strandings that occurred on east Hawaiʻi may be a result of higher FP presence (Foley et al. 2005). However, Chaloupka et al. (2008) found no correlation between FP and fishing gear strandings in the other main Hawaiian Islands. Similar to the spatial variation in FP infection on Hawaiʻi Island, FP was more often found in Oʻahu and Maui than on Kauai (Chaloupka et al. 2008). Green turtles that stranded on the western (Gulf) coast of Florida (51.9%) were more likely to have tumors than turtles that stranded on the eastern (Atlantic) coast (11.9%) (Foley et al. 2005). In Australia, FP varied in prevalence from 0 to 11.6% at 15 sites all along the Queensland coast (Jones et al. 2022).

A variety of factors have been hypothesized for the varying prevalence of FP in different locations and may be the reason for the contrasting FP abundance on west and east Hawaiʻi Island. For example, FP in Florida was greatest in areas with the greatest habitat degradation and pollution, most shallow water areas, and lowest wave-energy level, indicating that one or more of these conditions may affect FP (Foley et al. 2005). In Brazil, highly urbanized areas have a higher FP prevalence than lightly urbanized areas (Bastos et al. 2022). Additionally, FP may be related to water temperature, with higher water temperatures correlated with greater FP prevalence (Manes et al. 2022). An important factor that could contribute to the absence of FP on west Hawaiʻi is the precipitation pattern on the leeward side of the island. The windward (east) side, experiences abundant, consistent rainfall and has large rivers and many streams (Juvik et al. 1998). Heavy rain may bring more land-based pollutants to rivers, and the discharge from these rivers located in urbanized areas may disrupt the immune system of green turtles, making them more susceptible to FP (Manes et al. 2022). Despite the low rainfall and lack of flowing surface water in west Hawaiʻi, coastal waters can experience nutrient pollution via submarine groundwater discharge, which could impact green turtle health (Abaya et al. 2018a,b; Panelo et al. 2022).

The relatively even distribution of turtles that stranded alive (359) versus dead 381 on Hawai'i Island in the present study is markedly different from the findings of Chaloupka et al. (2008), where on O'ahu, Maui, and Kauai approximately 75% of green turtles stranded dead. In the present study, stranding status was found to vary temporally, by cause, and spatially. Green turtles were more likely to strand alive in the winter months (November–March), and dead in the summer months (April–October). Additionally, more turtles stranded dead than alive because of boat impacts, human take, and shark attacks, similar to other Hawaiian Islands, where boat impact and shark attack were the hazards most likely to result in a dead turtle (Chaloupka et al. 2008). Shark attacks often cause the loss of appendages and boat impacts usually cause damage to the head, appendages, and/or the carapace, all serious injuries that lead to significant mortality. The present study found that turtles that stranded as a result of FP were more likely to strand alive than dead, unlike findings of Chaloupka et al. (2008). More turtles stranded dead than alive on west Hawai'iand more turtles stranded alive than dead on east Hawai'i, probably because shark attacks and boat impacts are more common on west Hawai'i, while FP is reported almost exclusively on eastern shores. Chaloupka et al. (2008) found that the probability of mortality in a stranding decreased with turtle size, and this pattern is also observed in this data across the two sides of Hawai'i Island.

Despite the large percentage of unknown causes of stranding, this long-term data set provides important information on Hawai'i Island green turtle strandings. Continued monitoring of turtle strandings and careful data collection on stranded individuals is critical to the conservation of green turtles.

The considerable contribution of hook-and-line fishing gear to strandings highlights the continuing need for additional mitigation efforts, such as barbless hooks and effective line removal techniques (https://dlnr.hawaii.gov/dobor/marineanimalhotline/), focused on green turtle interactions with fisheries.

5 Compliance with Ethical Standards

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This is an observational study compiled from publicly available records. No ethical approval is required. All data analyzed during this study are included in this published article and its supplementary information files.

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References

Abaya L, Wiegner T, Beets J, Colbert S, Kaile‘a M, Kramer L (2018a) Spatial distribution of sewage pollution on a Hawaiian coral reef. Mar Poll Bull 130:335–347. https://doi.org/10.1016/j.marpolbul.2018.03.028

Abaya L, Wiegner T, Beets J, Colbert S, Kaile‘a M, Kramer L, Most R, Couch C (2018b) A multi-indicator approach for identifying shoreline sewage pollution hotspots adjacent to coral reefs. Mar Poll Bull 129:70–80. https://doi.org/10.1016/j.marpolbul.2018.02.005

Aguirre A, Balazs G (2000) Blood biochemistry values of green turtles, *Chelonia mydas*, with and without fibropapillomatosis. Comp Haematol Int 10:132–137. https://doi.org/10.1007/s005800070004

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723. https://doi.org/10.1109/TAC.1974.1100705

Balazs G (1980) Synopsis of biological data on the green turtle in the Hawaiian islands. NOAA Tech Memo, NMFS-SWFC-7, pp 1–141

Balazs G (1991) Current status of fibropapillomatosis in the Hawaiian green turtle, *Chelonia mydas*. In: Balazs G, Pooley S (eds) Research plan for marine turtle fibropapilloma. NOAA Tech Memo, NMFS-SEFSC-436, pp 112–114

Balazs G, van Houtan K, Hargrove S, Brunson S, Murakawa S (2015) A review of the demographic features of hawaiian green turtles (*Chelonia mydas*). Chelonian Conserv Biol 14:119–129. https://doi.org/10.2744/CCB-1172.1

Balazs GH, Chaloupka M (2004) Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. Biol Conserv 117:491–498. https://doi.org/10.1016/j.biocon.2003.08.008

Bastos KV, Machado LP, Joyeux JC, Ferreira JS, Militão FP, de Oliveira Fernandes V, Santos RG (2022) Coastal degradation impacts on green turtle's (*Chelonia mydas*) diet in southeastern Brazil: nutritional richness and health. Science of The Total Environment 823:153593. https://doi.org/10.1016/j.scitotenv.2022.153593

Bell LA, Ward J, Ifopo P (2011) Marine turtles stranded by the Samoa tsunami. Marine Turtle Newsletter 130:22–24

Bennett P, Keuper-Bennett U (2008) The book of honu: enjoying and learning about Hawaii's sea turtles. University of Hawaii Press, Honolulu

Bennett P, Keuper-Bennett U, Balazs GH (2000) Photographic evidence for the regression of fibropapillomas afflicting green turtles at Honokowai, Maui, in the Hawaiian islands. In: Kalb H, Wibbels T (eds) Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech Memo, NMFS-SEFSC-443, pp 37–39

Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, vol 2. CRC Press, New York, pp 243–257

Bornatowski H, Heithaus MR, Batista CM, Mascarenhas R (2012) Shark scavenging and predation on sea turtles in northeastern Brazil. Amphibia-Reptilia 33(3-4):495–502. https://doi.org/10.1163/15685381-00002852

Boulon R (2000) Trends in sea turtle strandings, US Virgin Islands: 1982 to 1997. In: Abreu-Brogbois F, Briseno-Duenas R, Marquex-Millan R, Sarti-Martinez L (eds) Proceedings of the Eighteenth International Sea Turtle Symposium. NOAA Tech Memo, NMFS-SEFSC-436, pp 261–263

Brunson S, Gaos AR, Kelly IK, Van Houtan KS, Swimmer Y, Hargrove S, Balazs GH, Work TM, Jones TT (2022) Three decades of stranding data reveal insights into endangered hawksbill sea turtles in Hawaii. Endanger Species Res 47:109–118. https://doi.org/10.3354/esr01167

Chaloupka M, Work TM, Balazs GH, Murakawa SK, Morris R (2008) Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian archipelago (1982–2003). Mar Biol 154:887–898. https://doi.org/10.1007/s00227-008-0981-4

Cheng IJ, Wang HY, Hsieh WY, Chan YT (2019) Twenty-three years of sea turtle stranding/bycatch research in Taiwan. Zool Stud 58:44. https://doi.org/10.6620/ZS.2019.58-44

Cheung KF, Bai Y, Yamazaki Y (2013) Surges around the Hawaiian islands from the 2011 Tōhoku tsunami. J Geophys Res: Oceans 118:5703–5719. https://doi.org/10.1002/jgrc.20413

County of Hawaiʻi, Office of the Mayor (2020) Mayor's COVID-19 Emergency Rule No. 2. Published April 17, 2020, Hilo, Hawaiʻi, https://records.hawaiicounty.gov/WebLink/DocView.aspx?id=104042&dbid=1, accessed 25 August 2023

Crowder LB, Hopkins-Murphy SR, Royle JA (1995) Effects of turtle excluder devices (TEDs) on loggerhead sea turtle strandings with implications for conservation. Copeia 1995:773–779. https://doi.org/10.2307/1447026

Cutt T, Browne C, Mungai M, Gardner M (2023) MOC marine institute sea turtle program, 2022 impact report. https://georgehbalazs.com/wp-content/uploads/2023/03/2022-MOCMI-Turtle-Report.pdf, accessed 25 August 2023

Flint J, Flint M, Limpus CJ, Mills PC (2015) Trends in marine turtle strandings along the East Queensland, Australia coast, between 1996 and 2013. J Mar Sci 2015:848923. https://doi.org/10.1155/2015/848923

Flint M, Patterson-Kane JC, Limpus CJ, Mills PC (2010) Health surveillance of stranded green turtles in Southern Queensland, Australia (2006–2009): an epidemiological analysis of causes of disease and mortality. EcoHealth 7:135–145. https://doi.org/10.1007/s10393-010-0300-7

Foley AM, Schroeder BA, Redlow AE, Fick-Child KJ, Teas WG (2005) Fibropapillomatosis in stranded green turtles (*Chelonia mydas*) from the eastern United States (1980–98): trends and associations with environmental factors. J Wildl Dis 41:29–41. https://doi.org/10.7589/0090-3558-41.1.29

Fuentes MM, Meletis ZA, Wildermann NE, Ware M (2021) Conservation interventions to reduce vessel strikes on sea turtles: a case study in Florida. Mar Policy 128:104471. https://doi.org/10.1016/j.marpol.2021.104471

Guimarães SM, de Almeida LG, Nunes LA, Lacerda PD, de Amorim CES, Burato M, Baldassin P, Werneck MR (2021) Distribution and potential causes of sea turtle strandings in the State of Rio de Janeiro, Southern Brazil. Herpetol Conserv Biol 16:225–237

Hart KM, Mooreside P, Crowder LB (2006) Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. Biol Conserv 129:283–290. https://doi.org/10.1016/j.biocon.2005.10.047

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. Endanger Species Res 7:137–154. https://doi.org/10.3354/esr00198

Herbst LH (1994) Fibropapillomatosis of marine turtles. Annu Rev Fish Dis 4:389–425

Jacobson ER, Buergelt C, Williams B, Harris RK (1991) Herpesvirus in cutaneous fibropapillomas of the green turtle *Chelonia mydas*. Dis Aquat Org 12:1–6. https://doi.org/10.1111/csp2.12755

Jones K, Limpus CJ, Brodie J, Jones R, Read M, Shum E, Bell IP, Ariel E (2022) Spatial distribution of fibropapillomatosis in green turtles along the Queensland coast and an investigation into the influence of water quality on prevalence. Conserv Sci Prac 4:e12755. https://doi.org/10.1111/csp2.12755

Juvik SP, Juvik JO, Paradise TR (eds) (1998) Atlas of Hawaii. University of Hawaii Press, Honolulu

Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol Evol 19:598–604. https://doi.org/10.1016/j.tree.2004.09.004

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fish 47:203–211

Manes C, Pinton D, Canestrelli A, Capua I (2022) Occurrence of fibropapillomatosis in green turtles (*Chelonia mydas*) in relation to environmental changes in coastal ecosystems in Texas and Florida: a retrospective study. Animals 12:1236. https://doi.org/10.3390/ani12101236

Marine Turtle Biology and Assessment Program (2022) PSD Marine Turtle Biology and Assessment Program Metadata Portfolio. https://www.fisheries.noaa.gov/inport/item/2708, accessed 25 August 2023

Meyer CG, Clark TB, Papastamatiou YP, Whitney NM, Holland KN (2009) Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. Mar Ecol Prog Ser 381:223–235. https://doi.org/10.3354/meps07951

Monteiro DS, Estima SC, Gandra TB, Silva AP, Bugoni L, Swimmer Y, Seminoff JA, Secchi ER (2016) Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil. Mar Biol 163:1–19. https://doi.org/10.1007/s00227-016-3018-4

Nitta ET, Henderson JR (1993) A review of interactions between Hawaii's fisheries and protected species. Mar Fish Rev 55:83–92

Panagopoulos D, Sofouli E, Teneketzis K, Margaritoulis D (2003) Stranding data as an indicator of fisheries induced mortality of sea turtles in Greece. In:

Margaritoulis D, Demetropoulos A (eds) First Mediterranean Conference on Marine Turtles. Barcelona Convention–Bern Convention–Bonn Convention (CMS), Nicosia, Cyprus, pp 202–206

Panelo J, Wiegner T, Colbert S, Goldberg S, Abaya L, Conklin E, Couch C, Falinski K, Gove J, Watson L, Wiggins C (2022) Spatial distribution and sources of nutrients at two coastal developments in South Kohala, Hawaiʻi. Mar Poll Bull 174:113143. https://doi.org/10.1016/j.marpolbul.2021.113143

Perrault JR, Levin M, Mott CR, Bovery CM, Bresette MJ, Chabot RM, Gregory CR, Guertin JR, Hirsch SE, Ritchie BW, Weege ST, Welsh RC, Witherington BE, Page-Karjian A (2021) Insights on immune function in free-ranging green sea turtles (*Chelonia mydas*) with and without fibropapillomatosis. Animals 11:861. https://doi.org/10.3390/ani11030861

R Core Team (2022) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Read T, Farman R, Vivier JC, Avril F, Gossuin H, Wantiez L (2023) Twenty years of sea turtle strandings in New Caledonia. Zool Stud 62:01. https://doi.org/10.6620/ZS.2023.62-01

Stacy BA, Foley AM, Shaver DJ, Purvin CM, Howell LN, Cook M, Keene JL (2021) Scavenging versus predation: shark-bite injuries in stranded sea turtles in the southeastern USA. Dis Aquat Org 143:19–26. https://doi.org/10.3354/dao03552

State of Hawaiʻi, Office of the Governor (2020) Fifth Supplementary Proclamation (for COVID-19). Published April 16, 2020, Honolulu, Hawaiʻi, https://dod.hawaii.gov/hiema/fifth-supplementary-proclamation-covid-19/, accessed 25 August 2023

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edn. Springer, New York

Wibbels T, Balazs GH, Owens DW, Amoss MS (1993) Sex ratio of immature green turtles inhabiting the Hawaiian archipelago. J Herpetol 27:327–329

Witzell WN (1987) Selective predation on large cheloniid sea turtles by tiger sharks (*Galeocerdo cuvier*). Jpn J Herpetol 12:22–29

Witzell WN (1994) The origin, evolution, and demise of the US sea turtle fisheries. Mar Fish Rev 56:8–23

Work TM, Rameyer RA, Balazs GH, Cray C, Chang SP (2001) Immune status of free-ranging green turtles with fibropapillomatosis from Hawaii. J Wildl Dis 37:574–581. https://doi.org/10.7589/0090-3558-37.3.574

Work TM, Balazs GH, Rameyer RA, Morris RA (2004) Retrospective pathology survey of green turtles *Chelonia mydas* with fibropapillomatosis in the Hawaiian islands, 1993–2003. Dis Aquat Org 62(1-2):163–176. https://doi.org/10.3354/dao062163

Work TM, Balazs GH, Summers TM, Hapdei JR, Tagarino AP (2015) Causes of mortality in green turtles from Hawaii and the insular Pacific exclusive of fibropapillomatosis. Dis Aquat Org 115:103–110. https://doi.org/10.3354/dao02890