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Four Decades of Green Turtle (*Chelonia mydas*) Strandings on Hawai'i Island (1983–2022): Causes and Trends

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Received 11 January 2023 / Accepted 11 March 2024 / Published 26 June 2024 Communicated by Benny K.K. Chan

The Hawaiian population of green turtles (Chelonia mydas) has increased since Federal and State protections were implemented in the mid 1970s, and reported stranding events have also increased. This study analyzed Hawai'i Island data: stranding location, date, size, sex, presence/ absence of tumors, stranding status, and cause of stranding. A total of 754 stranded green turtles was reported from 1983–2022: 379 stranded on the east (windward) coast of Hawai'i 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. Statistical modeling did not provide convincing evidence of temporal changes in the distribution of strandings across three consolidated cause categories: human-caused; predation, disease, and weather; and unknown. Stranded turtles on east Hawai'i Island had a higher frequency of fibropapillomatosis, whereas west Hawai'i stranded turtles showed higher incidence of shark attacks. These results provide the first comprehensive analyses of stranding data from Hawai'i 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. Our findings allow for comparison with other green turtle populations worldwide.

Key words: Sea turtles, Fishing gear entanglement, Fibropapillomatosis, Hawaiian Islands, Marine reptile mortality, Pacific Ocean

BACKGROUND

Green turtles (*Chelonia mydas*) are the most abundant large marine herbivores found throughout the world and in the Hawaiian Islands. The Hawaiian population of green turtles that was once depleted has increased since its 1974 protection under Hawaiian Law and 1978 protection under the Endangered Species Act (Balazs and Chaloupka 2004). Green turtles migrate long distances during their lifetime, from nesting to foraging

Citation: Dentlinger S, McDermid KJ, Weyenberg G, Jim LMR, Rice MR, Balazs GH. 2024. Four decades of green turtle (*Chelonia mydas*) strandings on Hawai'i Island (1983–2022): causes and trends. Zool Stud **63:**16. doi:10.6620/ZS.2024.63-16.

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 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 females 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 a herpesvirus 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 O'ahu, 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).

Although Chaloupka et al. (2008) mentioned that 6% of statewide strandings occurred on Hawai'i Island from 1982-2003, long-term stranding data specifically from Hawai'i Island have not been thoroughly analyzed previous to this study. Hawai'i Island merits additional scientific scrutiny of its green turtle stranding patterns with the most up-to-date, inclusive data available because of the island's large size (over half of total Hawaiian land area), southernmost location in the archipelago, lowest human population density, and important turtle foraging and resting areas-recently proposed as critical habitat by the US Fish and Wildlife Service and the National Oceanic and Atmospheric Administration (Endangered and Threatened Wildlife and Plants: Designation of Critical Habitat for Green Sea Turtle 2023; Endangered and Threatened Wildlife and Plants: Proposed Rule To Designate Marine Critical Habitat for Six Distinct Population Segments of Green Sea Turtles 2023).

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 Hawai'i Island green turtle strandings is presented to (1) identify the causes of strandings affecting green turtles around Hawai'i Island, (2) assess trends in strandings, and (3) identify differences and similarities between strandings in west and east Hawai'i Island.

MATERIALS AND METHODS

Data Collection

Data were collected on turtles stranded on Hawai'i Island (19.6°N, 155.5°W, land area 10,430 km² with coastal circumference of 428 km) from 1983–2022 by members of the Pacific Islands Fisheries Science Center under the US National Marine Fisheries Service, the University of Hawai'i at Hilo Sea Turtle Stranding Response Team, and the Hawai'i Preparatory Academy Sea Turtle Research Program. The database used in this study was compiled from records available at https:// georgehbalazs.com/wp-content/uploads/2023/10/19822018-Hawaii-Stranding-Data.pdf. The west and east coasts of Hawai'i 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 Hawai'i included locations from Miloli'i north to Kawaihae, and east Hawai'i included locations from South Point north to Hawi (Fig. 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: SCL = 1.245 + 0.913 CCL (Chaloupka et al. 2008). Determination of size classes of turtles followed Balazs (1980): juvenile-post hatchling to 65 cm SCL; subadult-rom 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). Humantake (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).

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



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.

sex of stranded turtles for all of Hawai'i Island. When comparing west and east Hawai'i, 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 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.

RESULTS

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

Of the 754 stranded turtles in the records, slightly over half had no discernable 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. 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).

Temporal trends

The number of strandings on Hawai'i Island has fluctuated over the years but shows an overall increase over time (Fig. 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 low overall, the number of FP-caused strandings was higher after 2000 (Fig. 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 Tohoku tsunami, while in east Hawai'i FP is the second leading cause (Table 1, Fig. 3).

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 three categories: Human-caused (hook-and-line, boat impact, human

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

	E	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	

take, and net); predation, disease and weather (shark attack, FP, and Misc.); and the original unknown category. The 2011 Tohoku 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 the date of stranding provides significant information about the relative rates of stranding among the three consolidated cause categories.

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 Hawai'i ($\mu \pm SE = 58.7 \pm 1$ cm SCL, n = 227) were significantly larger (*t*-test, $t_{378} = 6.29$, $p = 9 \times 10^{-10}$) than those in west Hawai'i ($\mu \pm SE = 51.3 \pm 0.6$ 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, and 455 gender undetermined cases, also with marginally different distributions between sides of the island (Chi-square, $X_2 = 6.4$, p = 0.042).

FP tumor presence/absence

As shown in table 3, 460 records indicated the absence of FP tumors, 150 records noted the 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 with side of the island, with turtles stranding in east Hawai'i more likely to have



Fig. 2. Number of strandings from 1983–2022 for Hawai'i 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 Hawai'i 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



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.



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.

tumors than those in west Hawai'i (Chi-square test, $X_2 = 197$, $p < 10^{-10}$).

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 of 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 Hawai'i had 146 turtles strand alive and 221 strand dead, while east Hawai'i had 213 turtles strand alive and 160 strand dead.

DISCUSSION

Seven hundred and fifty-four green turtles were recorded stranded on Hawai'i 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 independently of the variables observed



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

Table 3.	Fibropapillomatosis tumor presence	in
stranded tu	rtles by side of Hawai'i island	

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

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

in these records.

Strandings on Hawai'i 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 Hawai'i under Regulation 36 and their 1978 protection under the Endangered Species Act (Balazs and Chaloupka 2004; Bennett and Keuper-Bennett 2008). The increase in turtle 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 Hawai'i 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 (Fig. 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). In a turtle carcass drifter experiment along the shores of the Mississippi, public reporting of stranded carcasses was unexpectedly low: on popular mainland beaches, only 50% of the stranded turtles were reported; on accessible, but more remote barrier islands, only 11.1% of stranded carcasses were reported by citizens, and 0% of turtle carcasses that drifted into marshes were reported (Cook et al. 2021). These results send a strong message that remoteness of and public accessibility to stranding

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

areas greatly influence the discovery of turtles, and that even structured stranding networks with established reporting mechanisms" may be overestimating the rate of reporting by the public, which influences the conclusions that can be drawn from citizen-derived data.

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 Tohoku earthquake off the coast of Japan and the subsequent tsunami, large waves, and hazardous currents that it caused around Hawai'i 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 Hawai'i 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, Hawai'i County and State beach parks were closed for recreational use by executive decree (County of Hawai'i, Office of the Mayor 2020; State of Hawai'i, 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 Hawai'i Island coasts, and subsequent to decreased 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 O'ahu 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). Peak sea turtle stranding months during 2010-2019 in the Gulf of Mexico were also in the spring to summer (March to August) (Cook et al. 2021; Howell et al. 2021). Strandings on Hawai'i 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 O'ahu showed a similar secondary peak of strandings in September (Chaloupka et al. 2008). Although the major Hawaiian green turtle nesting season is mid-April to September/October in the Northwestern Hawaiian Islands (Niethammer et al. 1997), no seasonal variation in green turtle abundance within localized coastal Hawaiian foraging grounds has been documented (Balazs unpublished). The higher spring/summer stranding patterns seen on Hawai'i Island may reflect seasonal differences in water temperature which affects carcass decomposition rates (Cook et al. 2021), periodic shifts in shoreline human activity and stranding reporting, or cyclical changes in surf, currents, and winds that can push carcasses to shore. In the Hawaiian Islands, northeasterly trade winds are the most common weather pattern, especially in the summer; however, other weather patterns could influence turtle carcass drift. Migratory mid-latitude low pressure systems are common October to April with about nine fronts passing over Hawai'i Island in a season, during which winds shift from southwesterly to northerly. Kona Storms or cold-core lows, November to April, although rare with unpredictable paths, can cause waterspouts, torrential rain, and high surf; and tropical cyclones from June to mid- November, can bring high surf, storm surge, and strong onshore winds to Hawai'i Island (Longman et al. 2021b; Nullet 2023). In addition, El Niño Southern Oscillation events sporadically impact the Hawaiian Islands and can cause weakened trade winds, less rainfall, and warmer ocean temperatures (El Niño phase) between November to April or stronger trade winds, greater rainfall, and cooler ocean temperatures (La Niña phase) (Longman et al. 2021a).

Hook-and-line fishing gear was the most common known cause of stranding of green turtles on Hawai'i Island as a whole. Fishing gear strandings show a similar qualitative pattern to the overall time series (Fig. 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 O'ahu, 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).

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), New Caledonia (Read et al. 2023), and Greece (Panagopoulos et al. 2003). However, unlike the line/ hook entanglements on Hawai'i Island, in Taiwan, pond nets were the most common fishing gear causing turtle strandings over 23 years (Cheng et al. 2019). In contrast, at Samandağ Beach on the eastern Mediterranean coast of southern Türkiye (Turkey), from 2002–2017, fishing activities caused only 7% of the green turtle standings, while marine pollution accounted for 56% of strandings (Sönmez 2018). Fibropapillomatosis was the second most common cause of stranding on Hawai'i Island, whereas Chaloupka et al. (2008) found FP to be the main cause of stranding in green turtles in O'ahu, 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. Although slightly over half of the stranded green turtles in this study were listed with "unknown" cause of mortality, these turtles still provide valuable temporal, geographic, and biological data. We share this predicament of unknown cause with others studying sea turtle strandings. For example, 50% of strandings in New Caledonia were unknown, defined as "no necropsies were done and no apparent cause of death by external examination" (Read et al. 2023). Chaloupka et al. (2008) also had high rates of strandings with unknown causes. In our study and others, given the circumstances of discovery (time, weather patterns, location, retrieval), condition of the animal (undetermined health and behavior prior to stranding, unspecified time of death, decomposition, or scavenging), and limited resources for extensive diagnostic procedures (necropsies, histopathology, toxicology, and microbiology), many stranded turtles remain forever in the category of unknown causes of mortality. However, the goal should be to increase reporting of strandings by the public, to encourage detailed observations at time of discovery, and develop

systematic survey programs by scientists to detect stranded turtles even in areas not frequented by the public, because robust understanding of stranding patterns and causes of mortality is key to the survival of green turtles in Hawai'i.

In this study, the record collection process kept eight categories of stranding cause, however, for modelling purposes we reduced these to three 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 (Fig. 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 Hawai'i Island had different distributions of stranding cause. West Hawai'i Island had a higher proportion of shark attack and boat impact strandings, while east Hawai'i had more FP and human take strandings. Increased shark attack strandings on west Hawai'i 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 Hawai'i 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 Hawai'i 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 Hawai'i 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). However, in Türkiye and Taiwan, most green turtle strandings involved sub-adult and juvenile turtles (Sönmez 2018; Cheng et al. 2019). The high proportion of juveniles stranding may be a result of increased nesting populations at French Frigate Shoals in the Northwestern Hawaiian Islands 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 Hawai'i Island than on west Hawai'i, 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 an event. A spatial trend in size-classes was also reported by Chaloupka et al. (2008): larger turtles stranded on Maui and Kauai than on O'ahu.

There was no gender-bias of stranded green turtles on Hawai'i 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 Hawai'i Island had no tumors indicative of FP. No cases of internal FP tumors have been reported without the presence of external tumors (Work et al. 2004). A decline in FP prevalence has been documented previously in Hawaiian green turtles. Twenty-one of 66 turtles observed with tumors in one summer on Maui were seen later with no tumors (Bennett et al. 2000), indicating regression of the FP. The low number of stranded turtles with FP on Hawai'i 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 Hawai'i, whereas FP was very rare on green turtles that stranded on west Hawai'i. The west (Kona) coast of Hawai'i 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 Hawai'i 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 Hawai'i Island, FP was more often found in O'ahu 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 Hawai'i 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 Hawai'i 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 Hawai'i, 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 other research on O'ahu, Maui, and Kauai where approximately 75% of green turtles stranded dead (Chaloupka et al. 2008) and on Taiwan where 80% of stranded turtles were deceased (Cheng et al. 2019). 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'i and 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.

CONCLUSIONS

Despite the large percentage of unknown causes of stranding, this long-term data set provides important information on Hawai'i Island green turtle strandings. The considerable contribution of hook-and-line fishing gear to strandings emphasizes the need for additional mitigation efforts, such as barbless hooks and effective line removal techniques (https://dlnr.hawaii.gov/dobor/ marineanimalhotline/). In Hawai'i, the public has a high level of awareness of sea turtles, but we have an imperative to increase the availability of information on what a person should do if a hooked, entangled, injured or stranded turtle is found. Continued monitoring of turtle strandings and careful data collection on stranded individuals are critical to the conservation of green turtles.

Acknowledgments: We would like to thank the following individuals, agencies, and organizations that contributed to data collection, data availability, and/or mentorship over the last four decades: Summer Martin, Brittany Clemans, Shandell Brunson (deceased), Shawn Murakawa, Irene Kelly, Jen Sims, Megan Lamson,

Rebecca Ostertag, John Coney, Leon Hallacher, Walter Dudley, Jason Turner, NOAA Marine Turtle Biology & Assessment Program, NOAA Pacific Islands Fisheries Science Center, NOAA Pacific Islands Regional Office, University of Hawai'i at Hilo Marine Option Program Sea Turtle Stranding Response Team, Hawai'i Preparatory Academy Sea Turtle Research Program, and the State of Hawai'i Department of Land and Natural Resources, Division of Aquatic Resouces.

Authors' contributions: Study conception and design by Skylar Dentlinger, George Balazs, and Karla J. McDermid. Data compilation, initial analysis and first draft prepared by Skylar Dentlinger. Follow-up analyses, modeling, and final manuscript and code preparation by Grady Weyenberg. All authors made significant contributions to editing and revision of the manuscript, provided important intellectual content, and have read and approved the finalized version.

Competing interests: The authors declare that no funds, grants, or other support were received to assist in the preparation of this manuscript. The authors have no relevant financial or non-financial interests to disclose.

Availability of data and materials: All data analyzed during this study are included in this published article and its supplementary material (Table S1).

Consent for publication: All authors agree and consent for this research to be published.

Ethics approval consent to participate: This is an observational study compiled from publicly available records. No ethical approval is required.

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Supplementary Materials

Table S1. Hawai'i Island Stranding Data for *Chelonia mydas*: List of dates, locations, causes, sex, size, and status. (download)