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ORIGINAL PAPER

Dynamics of foraging interactions between cookiecutter sharks (*Isistius spp.*) and short-finned pilot whales (*Globicephala macrorhynchus*) in Hawai‘i

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Abstract

Cookiecutter sharks (*Isistius spp.*) are small pelagic squaloid sharks found throughout tropical and sub-tropical waters that are known to feed opportunistically on a range of prey, including animals much larger than themselves. Short-finned pilot whales (*Globicephala macrorhynchus*) are resident to Hawai‘i Island and are often observed with fresh and healed cookiecutter shark bites. In this study, cookiecutter bites were used to infer the spatiotemporal patterns of the foraging behaviour of sharks on pilot whales off the Hawaiian Islands (21°N, 158°W to 18.5°N, 154.5°W). A photo-identification catalogue of 399 resident short-finned pilot whales (representing 5,859 identifications of known individuals from 365 encounters from 2003 to 2012), were used to infer the prevalence and seasonal variation in shark presence. The mean proportion of the pilot whale’s body visible for documenting shark bites was 22.2% (SD ± 10.0). A total of 9,281fresh, healed, and scarred bite marks were documented on 396 of 399 whales (99.2%). Bites were most frequently documented on the head (32.9% of all bites), followed by the lateral sides (29.8%) and peduncle (26.1%), while the dorsal fin had the lowest percentage of bites (11.2%). The presence of fresh bites varied with ordinal date, with peaks in April, July and mid-October and were also negatively correlated with sea surface temperature. There was also a peak in fresh bites in the transition between crescent and quarter lunar phases. These results provide further evidence that cookiecutter sharks in Hawai‘i may perform seasonal migrations or dietary shifts.

Keywords Cookiecutter · Foraging · Hawai‘i · Pilot Whale · Shark

Introduction

Understanding the behaviour, distribution and movement patterns of mesopelagic predators can be a challenging undertaking. This can be especially difficult for smaller predators such as cookiecutter sharks (*Isistius* spp.*)*. Cookiecutter sharks are small cigar shaped, pelagic squaloid sharks typically no more than 50 cm in length with a short snout and large eyes (Jahn and Haedrich 1988). Within the genus there are at least two species, the smalltooth cookiecutter (*I. brasiliensis*) and the largetooth cookiecutter (*I. plutodus*), with the largetooth distinguished via variation in colouration and fin shape (Garrick and Springer 1964; de Figueiredo Petean and de Carvalho 2018). Both share similar distributions being found in tropical waters typically from around 20ºN to 20ºS and depths down to 3,500 m (Strasburg 1963; Jones 1971; Jahn and Haedrich 1988; Nakano and Tabuchi 1990), however *I. plutodus* has only been identified from sporadic identifications, mainly in the Atlantic Ocean (Garrick and Springer 1964; de Figueiredo Petean and de Carvalho 2018). Cookiecutter sharks have an unusual feeding mode that facilitates the removal of a “plug” of flesh from their prey, leaving a characteristic crater wound on the animal if the attack was successful and a

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crescent-shaped wound if the full plug of flesh has not been removed (Jones 1971; Papastamatiou et al. 2010). Cookiecutter shark prey includes the majority of large open-ocean predators including marine mammals, teleosts, and sharks (Papastamatiou et al. 2010; Hoyos-Padilla et al. 2013; Best and Photopoulou 2016; Santos et al. 2024). Wounds from cookiecutter sharks have been described on many marine mammal species including cetaceans, both odontocetes and mysticetes, (Dwyer and Visser 2011; Best and Photopoulou 2016; Grace et al. 2018), and pinnipeds (Le Boeuf et al. 1987). In Hawaiʻi, cookiecutter bites have been observed on a number of species, both island-resident and open-ocean species, including spinner dolphins (*Stenella longirostris*) (Norris and Dohl 1990), goose-beaked (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales (McSweeney et al. 2007), and Hawaiian monk seals (*Neomonachus schauinslandi*) (Hiruki et al. 1993). Due to the limited known distribution of *I. plutodus* we presume all bites on Hawaiian cetaceans are from *I. brasiliensis.*

Despite their ability to feed on prey much larger than themselves, stomach contents and chemical tracer analysis reveal that the majority of the cookiecutters' diet in the central Pacific around Hawaiʻi still consist of smaller micronekton prey such as squid (Carlisle et al. 2021). Based on catch data and stable isotopes, it is thought that cookiecutter sharks are diel vertical migrators remaining in deeper water during the day and swimming to the surface at night (Jahn and Haedrich 1988; Nakano and Tabuchi 1990; Papastamatiou et al. 2010). These studies have also provided evidence that cookiecutter sharks are present in Hawaiian waters year-round, but may display seasonal migrations or shifts in diet, being more abundant during the summer and fall months (Papastamatiou et al. 2010; Carlisle et al. 2021).

Short-finned pilot whales (*Globicephala macrorhynchus*), hereafter referred to as pilot whales, are the most frequently encountered cetacean species in and around the main Hawaiian Islands (Baird et al. 2013, 2024). An abundance estimate in 2017 for the Exclusive Economic Zone (EEZ) surrounding the Hawaiian archipelago was approximately 8,000 individuals (Bradford et al. 2021), however this estimate does not distinguish between insular or island-associated and pelagic populations (Baird 2016). Data from extensive satellite tagging and association analyses based on photo-identification has shown that the pilot whale population around the main Hawaiian Islands is divided into three insular communities showing a propensity for slope areas with depths less than 3,000 m (Mahaffy et al. 2015; Baird 2016; Van Cise et al. 2017; Kratofil et al. 2023). A long-term photo-identification study focused on the eastern community demonstrated that pilot whales off the island of Hawaiʻi have a hierarchical social structure where individuals travel in stable, mixed-sex social units composed of related individuals and that multiple units preferentially associate to form social clusters (Mahaffy et al. 2015; Van Cise et al. 2017). Some pilot whale groups show year-round residency to the area while others termed "visitors" only use the area occasionally (Mahaffy et al. 2015). Dive behaviour from depth-transmitting satellite tags in Hawaiʻi revealed that pilot whales dive deepest during the day (31% of dives; mean = 666.1 ± 16.7 m) but more frequently at night (58% of dives, mean = 415.5 ± 14.8 m) (Owen et al. 2019), possibly following vertical prey migrations of Histioteuthid and Onychoteuthid squid (Young 1975). Lunar phase has also been observed to influence dive behaviour as has season, with animals diving deeper, longer, and farther from shore during a full moon compared to a new moon. Seasonal diving behaviour also shows that dives during the winter months (February – April) are deeper, longer, and further from shore than in summer or autumn (Owen et al. 2019).

When studying cryptic and difficult to observe species, the use of a proxy can be employed to gather data. In this study, the cookiecutter shark bite wounds and scars observed on another species are used as a proxy to provide unique insights into the foraging dynamics of the sharks. Here we use cookiecutter shark bites on pilot whales to assess changes in shark foraging ecology. As our study population of pilot whales are largely resident to Hawaiʻi Island, we remove confounding factors from previous studies using landed pelagic fish at a fish auction as a proxy (e.g., where location of capture is unknown, Papastamatiou et al. 2010). Since previous studies have suggested seasonal movements of cookiecutter sharks in Hawaiian waters (Papastamatiou et al. 2010), we predict that the probability of pilot whales being bitten will be highest in the summer. Furthermore, as noted, pilot whale space use and diving behaviour varies with lunar phase (Owen et al. 2019). During the full moon, pilot whales are farther offshore and diving deeper, thus we would expect more overlap with cookiecutter sharks during full moons versus the new moon.

Materials and methods

Study location and photographic data

The study was conducted off the leeward (western) side of Hawaiʻi Island over an area of approximately 2,500 km^2, with depths ranging from shallow coastal water to approximately 5,000 m (Fig. 1). Pilot whale photos were collected during 15 field trips off Hawaiʻi Island from 2003 to 2012 as part of a long-term, multi-species assessment of cetaceans in Hawaiʻi (see Baird et al. 2013) as well as from the Pacific Islands Fishery Science Center and opportunistic sightings by the Wild Whale Research Foundation. Directed research

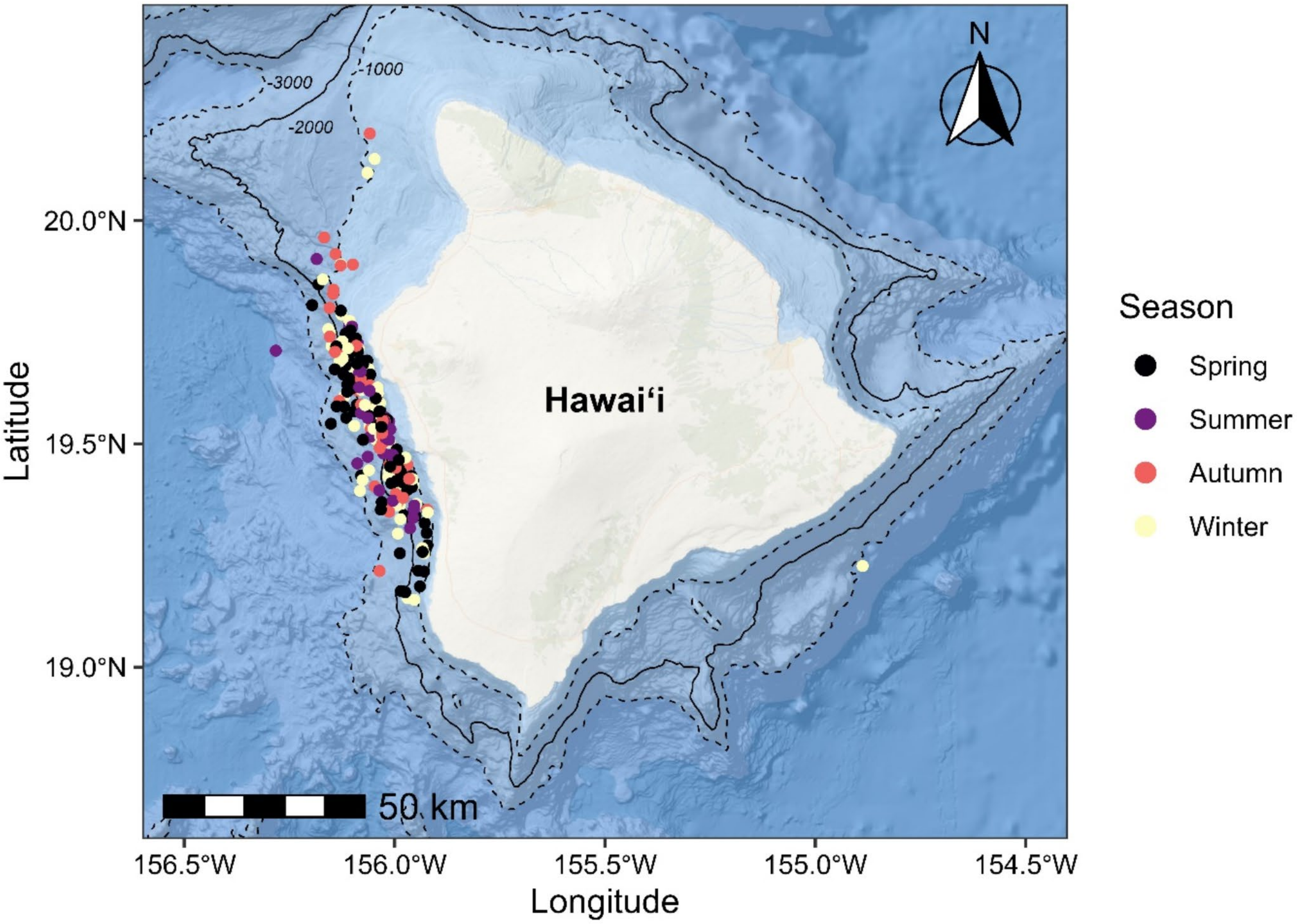


Fig. 1 Map showing locations of short-finned pilot whale sightings used in this study, color-coded by oceanographic season. While the primary study area is off the west side of Hawai‘i Island, the one group off the east side of the island was matched to a known island-resident group

surveys ranged in length from one to six weeks and used vessels ranging from 5.5 to 18 m in length (although vessels 5.5 to 8.4 m were used in most surveys) with two to six observers on board scanning 360 degrees around the boat. The size of the study area precluded surveying the entire area in a day; instead, daily tracks were driven by sea conditions (attempting to remain Beaufort 3 or less with less swell) while minimizing overlap with tracklines from the previous day. Pilot whale groups were approached for species confirmation, to take photos (from the surface) for individual identification and to collect sighting data, including date, GPS location (latitude / longitude), and group size (min, max, best) (Baird et al. 2013, 2024). Attempts were made to photograph the right and left sides of every individual in the group regardless of size or distinctiveness level, although this was not always possible due to field limitations such as time of day, Beaufort sea conditions, fuel constraints, and typical animal surfacing behaviour. A sighting or group was defined using a 1,000 m chain-rule where all individuals within 1,000 m of other individuals are assumed to be associated (Mahaffy et al. 2015). Methodology used to process photos for photo-identification is discussed in detail in Mahaffy et al. (2015). Briefly, photos from each sighting were sorted by individual using unique natural markings on the dorsal fin and were then visually compared to the photo identification catalogue; if a match was found, the individual was added to the catalogue under the existing identification (ID) number (e.g., HIGm0001) and if no match was found the individual was assigned a new ID. The best photo from each sighting of an individual was assigned a photo quality rating (1 = poor, 2 = fair, 3 = good, 4 = excellent) and the individual was also rated for distinctiveness (1 = not distinctive, 2 = slightly distinctive, 3 = distinctive, 4 = very distinctive) when it was added to the catalogue (Mahaffy et al. 2015). In order to record as many cookiecutter shark bites and scars as possible, analyses were not restricted by distinctiveness or photo quality. While the lack of restrictions increases the chances of missed matches, it also ensures all documented scars and bite wounds are included. Individual sighting histories in the photo-identification catalogue were used to determine the degree of residency to the island of Hawai‘i; only pilot whales resident to the island (those recorded in five or more sightings over three or more years, Mahaffy et al. 2015) were included in the study, and individuals used in the study were not seen off any other island. Analyses of cookiecutter shark bites were restricted to sightings where bites were visible on at least one individual in the group.

Cookiecutter shark bite analysis

Within each sighting of an individual, all relevant photos were used, allowing for the assessment of a larger proportion of the body than was visible in a single photograph. Photos were examined to determine cookiecutter shark bite presence, number, and location on the body (Fig. 2a). Each side of the body was divided vertically into four areas (head, lateral, dorsal fin, and peduncle; Fig. 2b) in order to quantify the location of bites and scars, and also separately divided into five sections of roughly equal size (each comprising ~ 10% of the to the total body length) in order to calculate the percentage of the body seen in each identification (see section below on Statistical analysis and modelling). For modelling purposes, we assumed that approximately 50% of the animal was below the water line during typical surfacing behaviour (Fig. 2b). For each sighting of an individual (which may be comprised of multiple photographs), we recorded which of the total five sections above the waterline were visible for each side, to determine the proportion of the body that was available for analysis.

Cookiecutter shark bites were distinguished from similarly-sized wounds and scars (such as those caused by conspecifics) by their slightly ovoid shape and uniform depth (Fig. 3). All bites were classified as fresh, healing or scarred and reviewed using criteria adapted from Dwyer and Visser (2011) to describe wound colouration, bite depth, and degree of colonisation by cyamids (Table 1). Cookiecutter shark bites on cetaceans in Hawai‘i are often observed with whale lice (*Cyamidae; Amphipoda*); cyamids are epibiont ectoparasites that feed on host skin and scar tissue and collect

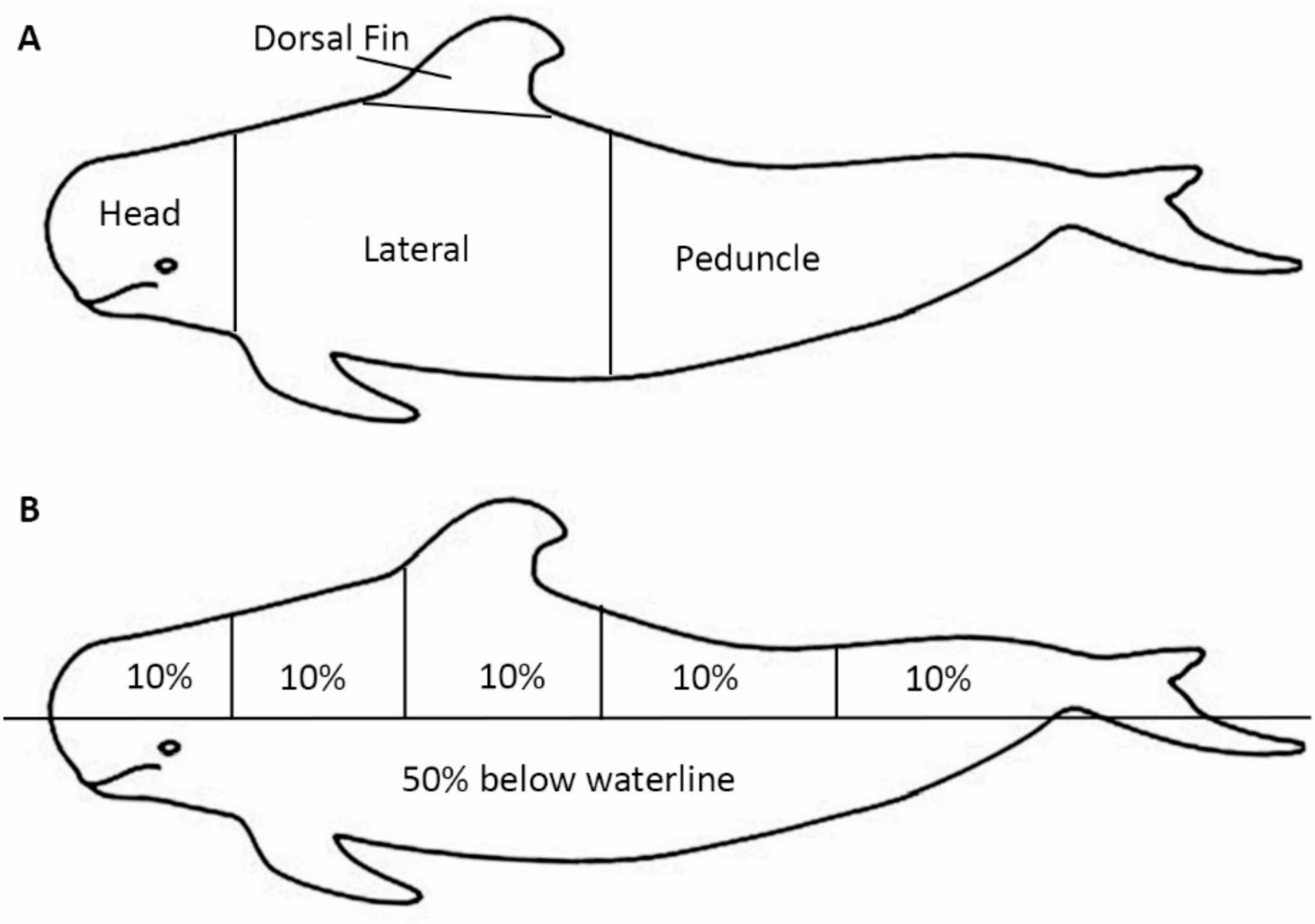


Fig. 2 Areas on short-finned pilot whale body where cookiecutter shark bites were recorded. (**A**) Location on body (**B**) division of body used to approximate percentage sections of the pilot whale's body that were observed during each sighting. The maximum total body area observed was typically only 50% as the ventral region was often below the waterline during normal surfacing behaviour

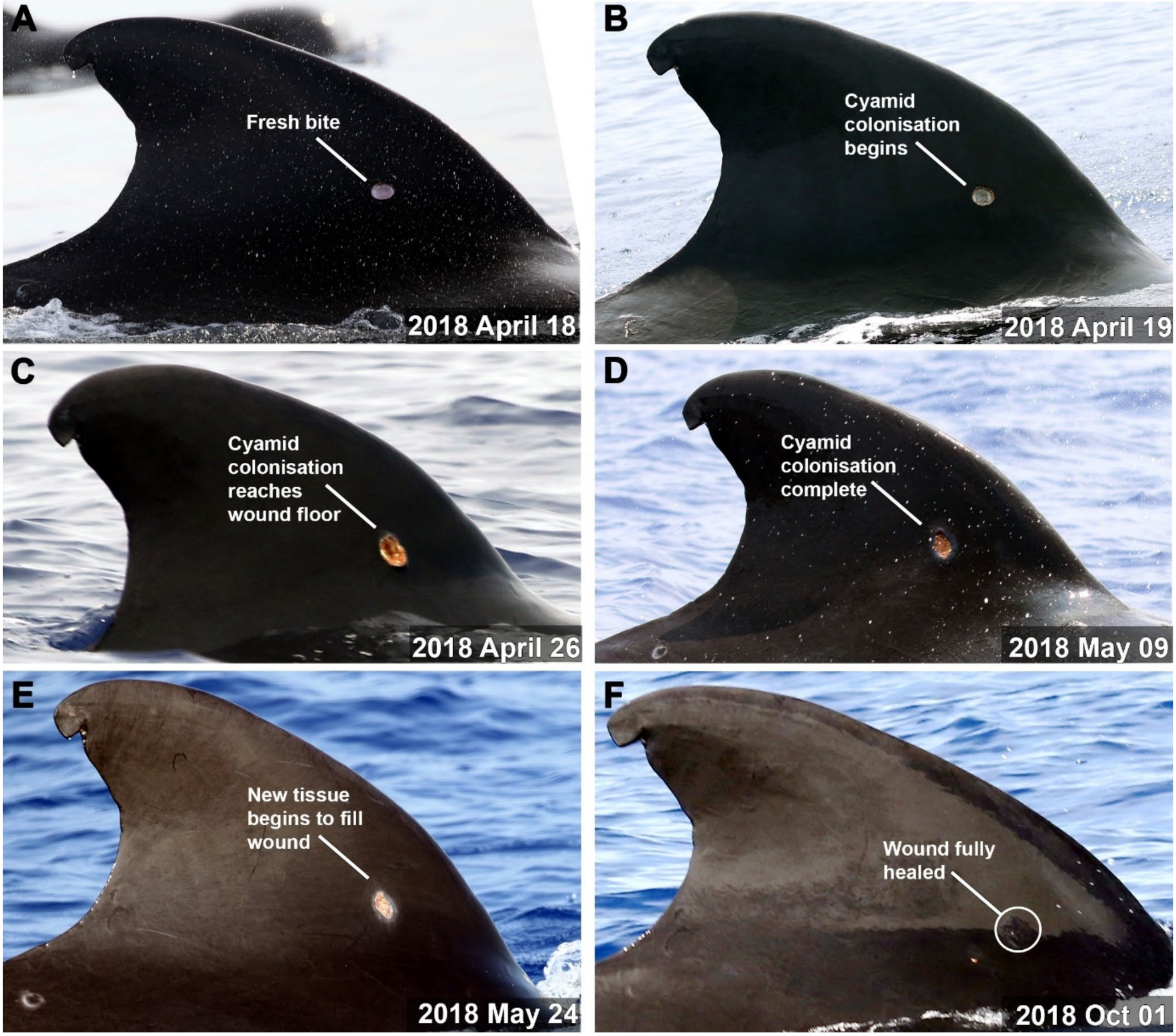


Fig. 3 Wound progression on individual HIGm0784 taken within the study area between April-October 2018. (**A**) Wound is fresh, bright pink crater with minimal cyamid presence. (**B**) Wound colouration is more muted with cyamid colonisation beginning around edges. (**C**) Cyamid colonisation has progressed reaching the bottom of the wound crater, some yellow colouration on the perimeter. (**D**) Wound entirely filled with cyamids. (**E**) New tissue is filling wound crater, some inflammation still present. (**F**) Wound is entirely healed with faint outline of scar present. Photo credits: **A**, **B** (Annie B. Douglas/Cascadia Research), **C** (Jordan K. Lerma/Cascadia Research), **D-F** (Colin J. Cornforth)

Table 1 Qualifying states of cookiecutter shark bites observed on short-finned pilot whales

Bite classification	Colouration	Depth	Cyamid colonisation
Fresh	Red/Pink	Crater, later filled with inflamed tissue	No/Few cyamids
Healing	Orange	Depression	Full colonisation
Scarred	Re-pigmented	Smooth	No cyamids

in protected areas of the body (e.g., corners of the mouth, blowhole, genital slit) and in "lesions with thickened edges" in fast-swimming odontocetes, and require direct physical contact for transmission between host individuals (Seger and Rowntree 2018; Lehnert et al. 2021). The time needed for wound colonisation to begin is dependent on several factors, including whether cyamids were already present on the injured animal or must be acquired through contact with a conspecific and the overall health of the injured animal, as slower swimming speeds reduce drag and may impact colonization rate (reviewed in Ten et al. (2022).

Fresh bites were observed as pink or red crater-shaped depressions often filled with inflamed tissue. This early immune response was most commonly visible as tissue swelling (Fig. 3a, Suppl. Figure 2a). All bites classified as fresh were yet to be colonised by cyamids, or had minimal cyamid presence, and are suspected to be less than one week old. We based this on observations where cyamid colonisation was recorded approximately five to eight days after the bite occurred (Suppl. Figure 1, 2). Additionally, photographs of a partial bite and complete bite, estimated to be no more than three and five days old respectively, further demonstrate the progression of healing (Suppl. Figure 1, 2).

Healing bites were observed as depressions in the tissue that were typically orange in colour due to the presence of cyamids. Healed bites (e.g., scars) were generally observed as tissue that had filled in, with surfaces that were either smooth or slightly uneven compared with surrounding skin. Healed tissue was often partially or fully re-pigmented and lacked cyamids (Fig. 3f). While estimating the time from bite to initial cyamid colonisation for all individuals is beyond the scope of this study, we provide an example of wound healing from a cookiecutter shark bite from 2018 on HIGm0784, a member of the Hawai‘i Island resident community, to illustrate the process (Fig. 3). Although this example falls outside the study period, this individual was seen 12 times during the study period and provides the best photographic example of wound healing for illustrative purposes.

Once the first cyamids appeared on the fresh bite (Fig. 3a), the rate of colonisation was rapid, with a noticeable increase in cyamids after one day and a high degree of colonisation within the three weeks that follow, (Fig. 3b, c, d). As healing progressed, the wound became shallower with a less concave appearance, and new tissue growth was observed from the bottom and/or sides of the crater (Fig. 3e). When healing reached the scarring stage, the wound was filled with new tissue and the skin had re-pigmented, leaving a slightly lighter-coloured halo around the original wound and the skin had an uneven appearance around the border (Fig. 3f). At this stage cyamids are absent as conditions for attachment become unsuitable, and they typically move back to their usual areas around the mouth and other crevasses in the skin. In general, scar shapes were similar to those observed by Dwyer and Visser (2011), typically forming a round or ovoid shape, sometimes with an uneven surface (Fig. 3f). Observed scars that had healed in a crescent shape were likely the result of an unsuccessful cookiecutter attack which did not result in the full removal of the typical plug of flesh (Suppl. Figure 2) (Dwyer and Visser 2011).

Statistical analysis and modelling

To explain spatiotemporal patterns in the presence and absence of bite marks, a combination of abiotic data (date, year, sea surface temperature (SST), lunar phase, lunar illumination (LI), and data on social clusters were included in the statistical analysis. Weekly average sea surface temperatures were obtained from National Oceanic and Atmospheric Administration (NOAA) using AVHRR Pathfinder Sea-Surface Temperature v5 and v5.1 for the study area (Suppl. Figure 3). The area used for SST was from 19^{o}N to 20.25^{o}N and from 156^{o}W to 158^{o}W. Lunar phase and lunar illumination were obtained using the *lunar* package in R (Lazaridis 2015) for each survey date. Phases were combined into five groups combining similar illumination: waxing crescent and waning crescent were combined, as were waxing gibbous and waning gibbous, as per Owen et al. (2019). Seasons were grouped into Autumn (November to January), Winter (February to April), Spring (May to July), and Summer (August to October) as per Flament et al. (1996). As individuals within the same social cluster may potentially experience similar exposure to cookiecutter sharks, social cluster (from Mahaffy et al. (2015) was included in subsequent analyses. In order to investigate the distribution of fresh bites across a pilot whale's body, a comparison of the observed versus expected number of bites was conducted based on the location on the body and area seen (Fig. 2). Fresh bite proportions for each location were calculated and adjusted for whether one or both sides of the body were seen. A chi-squared test was performed using R Statistical Software (v4.2.2; (R Core Team 2022) to compare observed and expected, assessing deviations from the expected distribution based on the body area seen.

Presence or absence of fresh bites for each animal in each sighting were modelled in R Statistical Software (v4.2.2; R Core Team 2022) using generalised additive binomial mixed models (GAMM) with a complementary log-log link due to zero inflated data. GAMMs were applied using *Gamm4* (Wood and Scheipl 2020). Modelling was undertaken with temperature, lunar phase, lunar illumination, and ordinal date being used as explanatory variables, with pilot whale social cluster included as a random effect to account for potential grouping of data. A likelihood ratio test was conducted to assess effectiveness of the inclusion of the random effect, and Spearman's rank correlations were used to test for collinearity. The best fitting model was selected using a forward stepwise model selection (Zuur et al. 2009), based on Akaike information criterion (AIC) scores of the underlying generalised linear model of the GAMM (ESM Table 1). The percentage of the pilot whale visible had an exponential relationship with the percentage of animals observed with fresh bites, therefore this was added to the

Table 2 Breakdown of total cookiecutter bites on short-finned pilot whales by status of bite and month of year

Month	Total Individuals	Total Identifications	Total Fresh bites	Total Healing Bites	Total Scarred bites
January	122	185	4	8	87
February	48	48	1	2	37
March	155	233	8	32	160
April	314	1,336	39	139	1,811
May	261	587	17	87	1,280
June	35	35	2	2	21
July	354	1,115	27	102	1,730
August	283	621	17	73	1,248
September	125	247	0	20	204
October	155	378	22	21	551
November	127	523	8	40	675
December	157	551	16	47	734
Total	2,136	5,859	161	573	8,538

model as an offset. Model accuracy was tested using K-fold cross validation using the *caret* package in R (Kuhn 2008), graphical outputs were plotted using the *ggplot2* package (Wickham 2016).

Results

Photos from 399 individual pilot whales from 12 social clusters, obtained from a total of 5,859 identifications (i.e., repeated encounters of individuals), were included in analyses. Identifications were distributed roughly similarly across lunar phases (ranging from 282 to 382 individuals). There were similar numbers of individuals available from the Hawaiian winter (517), spring (650), and summer (563), but fewer (406) available from the Hawaiian autumn (Table 2). Bites of various stages were observed on 396 of the 399 individuals (99.2%). A total of 169 fresh bites were recorded on 115 individuals, representing 161 identifications. Of the 115 individuals with fresh bites, most (108) had only a single fresh bite, five had two fresh bites, and one had three fresh bites. Individuals with fresh bites were sighted a median of 22 days before the fresh bite was recorded (range 1–1,057 days) and were not seen off any other island. This large range between re-sightings likely reflects the size of the study area (and thus the inability to document all groups present) and the nature of field projects (e.g., short periods of focused effort spread out over several years) rather than the residency of individuals. There were 573 healing bites recorded on 209 individuals, representing 488 identifications. Some whales had occurrences of more than one healing bite, but it could not be determined if the bites occurred relatively close in time (e.g., during the same day or week). Of the 209 individuals with healing bites most (167) had a single healing bite, 28 had two healing bites, 12 had three healing bites, one had four healing bites, and one had six healing bites. A total of 8,538 scars were recorded on 386 individuals, representing 2,774 identifications. Scarring was the most common bite state observed: 31 individuals carried one scar, 44 had two scars, 37 had three scars, 53 had four scars, 39 had five scars, 41 had six scars, 38 had seven scars, 24 had eight scars, 19 had nine scars, and 12 had ten scars, 48 had more than ten scars; one individual carried 37 scars. Individuals with fresh bites were re-sighted a combined 698 times with a fresh, healing or healed bite visible. Re-sightings of individuals after recording of a fresh bite had a mean number of re-sightings of 10.3 (SE ± 0.87) (ESM Table 2), 39.88% of these re-sightings observed the same side of the body, and 31.20% of re-sightings observed the same location on the body. Not all re-sightings were able to observe the same side of the animal or the same location on the animal body subject to local conditions and behaviour. Many individuals had multiple bites in varying states of healing/re-pigmentation. Healing bites and scars were observed in every month of the year, and fresh bites were observed in all months except September (Table 2).

Table 3 Location of fresh cookiecutter shark bites on short-finned pilot whales. Comparisons of observed versus expected fresh bites by location

	% of bites by location	*n* Observed	*n* Expected
Dorsal Fin	11.2	18	16
Head	32.9	53	33
Lateral	29.8	48	48
Peduncle	26.1	42	64

Pearson's Chi-sq = 9.3348, df = 3, p value = 0.02515

The mean proportion of the body seen during each sighting was 22.2% (SD ± 10.0), therefore more bites were likely present but unobservable due to being below the waterline (Fig. 2b). Most fresh bites recorded were located on the head (32.9%), lateral sides of the body (29.8%) and peduncle area (26.1 %) while the dorsal fin had the lowest percentage of fresh bites (just over 11%) (Table 3).

When taking the area of each section of the body into account and whether one or both sides were photographed during a sighting, there was a greater than expected number of bites on the head ($X^2=9.33$, $p=0.025$) (Table 3), and a lower than expected number of bites on the peduncle.

The GAMM showed that the predicted binomial presence/absence was influenced by surface temperatures, ordinal date and lunar illumination as smooth terms, including an offset of the percentage of the body viewed in each sighting plus the social cluster of the animal in question as a random effect (Table 4). There was a decreased likelihood of fresh bites at higher temperatures (Fig. 4a). Ordinal date also influenced the likelihood of fresh bites with three main peaks centred around the 110th, 206th and 288th days of the

Table 4 Results of model of best fit for effects of abiotic variables on the prevalence of fresh cookiecutter bites on short-finned pilot whales. Coefficients and diagnostics (Chi-sq and *p*-values) indicate the effect of each parameter level

		X^2	df	*p*-value
RMSE: 0.52	*Parametric Response Variable*			
SD: 0.008	Sea surface temperature	68.07	1	<0.0001
	Non-parametric Response			
	Lunar illumination	515.9	8.849	<0.0001
	Ordinal Date	260.8	8.951	<0.0001

Fig. 4 Generalised additive mixed model predicted response of the influences of fixed abiotic variables on the presence of fresh cookiecutter bites on pilot whales. (A) sea surface temperature, (B) ordinal date, and (C) lunar illumination on the probability of fresh bite presence (left hand axis), and the observed presence/absence of fresh bites (right hand axis). Grey shaded areas represent the 95% CI, red dashed lines indicate ranges of lunar illumination for each moon phase using the *lunar* package (Lazaridis 2015)

year approximately corresponding to late April, mid-July, and mid-October (Fig. 4b). The first peak in bite probability at day 110 had a probability of fresh bite occurrence of 0.06 (SE ± 0.011). The next peak at day 206 was 0.08 (SE ± 0.015), and the last peak of 0.09 (SE ± 0.02) occurred on day 288. Lunar illumination also showed a significant influence with increases in the probability of fresh bites just before the new moon to crescent phases, and during the transition between crescent moon and quarter (Fig. 4c). Year was also tested as a random effect, but the value was too close to zero to be effective as a random effect.

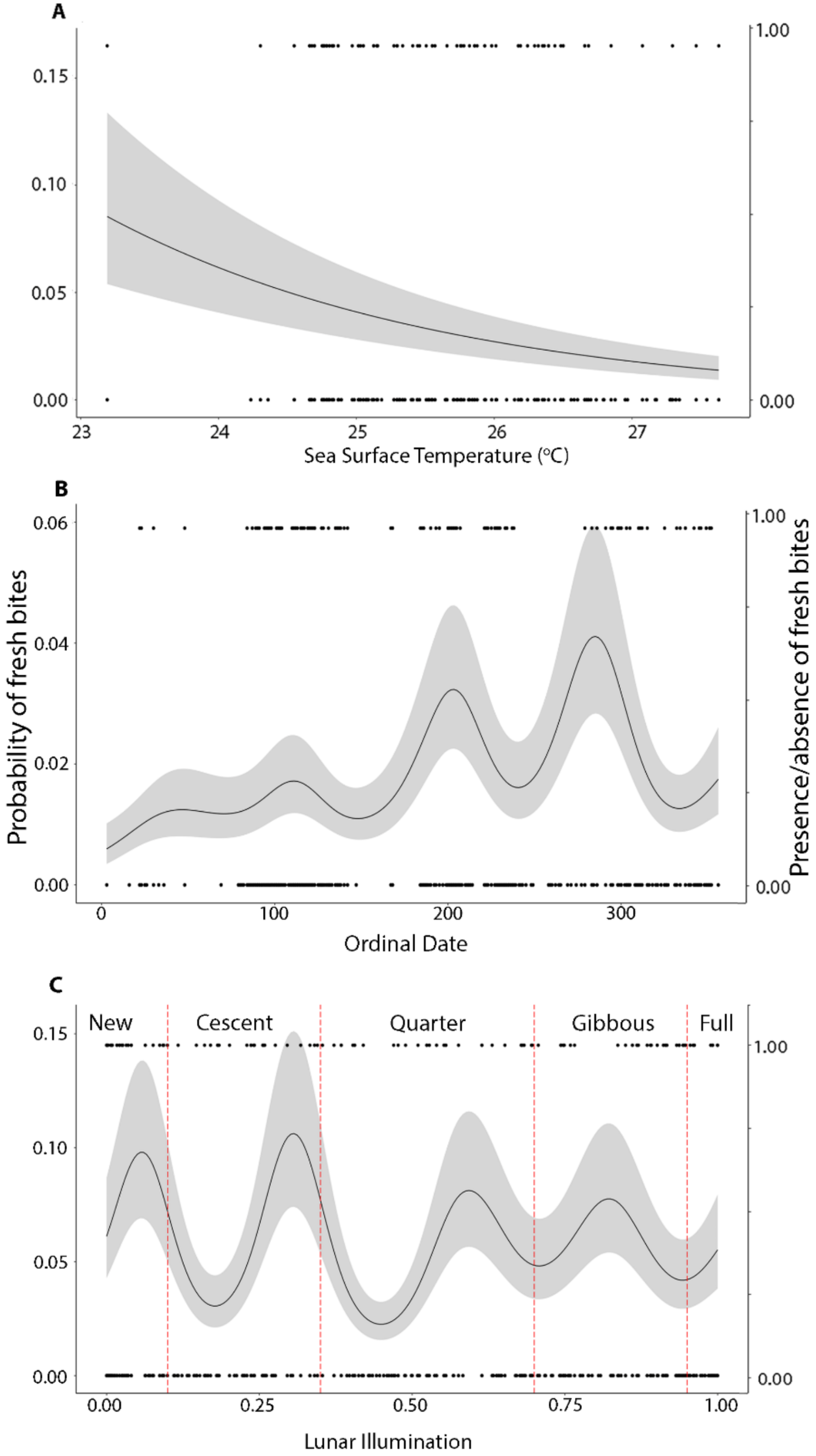
The inclusion of pilot whale social cluster in the model significantly improved model accuracy ($X^2 = 75.8$, $p < 0.0001$), indicating the presence of cluster-specific effects. However, the variance component for the random effect (cluster) was estimated to be 0.355 (SD ± 0.59), indicating high variability among clusters in the latent scale of the complementary log-log model. The intraclass correlation coefficient (ICC) was approximately 0.097, suggesting that around 9.7% of the variability in the presence or absence of fresh bites could be attributed to differences between clusters.

Discussion

Our results show that probability of cookiecutter bites on resident pilot whales varies by season, lunar phase, and water temperature. In this study we obtain additional understanding of cookiecutter shark foraging ecology (and their interaction with a marine mammal prey species) by using bite wounds on free-swimming pilot whales. We estimate that fresh bites observed on pilot whales likely occurred within one week of the individual being photographed as evidenced by the observed timeline of wound progression (Fig. 3, Suppl. Figure 1, 2), and therefore interactions almost certainly took place in waters off the west side of Hawai‘i Island. The vast majority of pilot whale encounters used in our study are within a high-density foraging area for short-finned pilot whales (Abecassis et al. 2015; Kratofil et al. 2023), reflecting that they typically spend extensive time in this area. Satellite-tag deployments on 43 individuals from this population have shown that they remain strongly associated with the island over periods of weeks to months (Baird, unpublished, see Baird 2016; Kratofil et al. 2023). By concentrating on a resident cetacean population, we could determine how the probability of fresh bites varied based on both abiotic conditions and season.

We observed a general seasonal pattern in the presence of fresh bites. While there was an overall increase in bite probability from late April through mid-October, the number of bites were not consistent (Table 2). Cookiecutter shark bite probability peaked in October (Ordinal date 290) but was lowest during the winter months (Fig. 4b). There were troughs between the peaks where pilot whales were seen, but virtually no fresh bites were observed. For example, no fresh bites were recorded during September despite 247 observations of 125 individuals (Table 2). Stable isotope analyses of the liver and muscle tissues of cookiecutter sharks off Hawai‘i suggest that they exhibit seasonal shifts in diet, or in the location where they forage (Carlisle et al. 2021). The probability of fresh cookiecutter bites on bigeye tuna (*Thunnus obesus*), the majority of which were caught within the Hawai‘i EEZ and sold at the Honolulu fish auction, similarly peaked from October-December (Papastamatiou et al. 2010). Landed swordfish (*Xiphias gladius*) on the other hand, are primarily caught outside the Hawaiian EEZ and showed a peak in fresh bites from March-May (Papastamatiou et al. 2010). Combined, these results suggest either that cookiecutter sharks show seasonal shifts in their diet, habitat (e.g., moving away from the islands in the winter) or display seasonal changes in interactions with pilot whales. Interestingly, while seasonal shifts in bite probability were observed, the distribution of pilot whale sightings along the west coast of Hawai‘i remained spatially consistent across seasons (Fig. 1). This indicates that the likelihood of encounters with cookiecutters may be influenced more by cookiecutter shark movements or environmental factors rather than spatial movements of pilot whales.

The diet of cookiecutter sharks in Hawai‘i includes squid (Carlisle et al. 2021), which are also prey for pilot whales, suggesting the potential for competitive interactions between sharks and pilot whales (Seagars and Henderson 1985; Sinclair 1992). A high biomass of vertical diel migrating micronekton, including squid, occurs off the west coast of Hawai‘i Island, which migrate horizontally and vertically (Benoit-Bird et al. 2001). All whale observations in this


A
0.15
0.10
0.05
0.00
1.00
0.00
23
24
25
26
27
Sea Surface Temperature (°C)
B
0.06
0.04
0.02
0.00
1.00
0.00
0
100
200
300
Ordinal Date
Probability of fresh bites
Presence/absence of fresh bites
C
New
Cescent
Quarter
Gibbous
Full
0.15
0.10
0.05
0.00
1.00
0.00
0.00
0.25
0.50
0.75
1.00
Lunar Illumination

study were recorded during daylight hours, so it was not possible to ascertain whether bites had occurred during diurnal or nocturnal periods. Pilot whales in Hawaiʻi dive deeper during the day (mean = 666 m) than at night (mean = 415 m), although they perform more dives at night (Baird 2016). Our data shows an increase in shark bite probability peaking before the transition from new to crescent moon, and before the crescent to quarter moon (Fig. 4c). Micronekton in the mesopelagic boundary community increase their depth and move farther offshore during periods of high lunar illumination (Benoit-Bird et al. 2009; Abecassis et al. 2015; Prihartato et al. 2016; Comfort et al. 2017). Finally, pilot whales dive shallower and for shorter durations during the Quarter and Crescent lunar phases (Owen et al. 2019), which may cause them to spend more time in near-surface waters and could increase susceptibility to cookiecutter shark bites. Although the primary micronekton layer moves deeper during high lunar illumination, residual prey near the surface and opportunistic foraging by cookiecutters may increase near-surface-water predation on pilot whales. Increased surface illumination may also impact cookiecutter shark ability to hunt in surface waters or attract prey (Widder 1998).

Sea surface temperature showed a significant effect on the probability of pilot whales being bitten, with bite probability decreasing as SSTs increased. Based on trawl data from the north Pacific, cookiecutter sharks were caught at temperatures ranging from 18 °C to 26 °C (Nakano and Tabuchi 1990). We recorded no fresh bites on pilot whales in September, the month with the highest average temperatures (27 ± 0.35 °C (Suppl. Figure 3), despite 125 individuals being photographed from nine different sightings. Water temperatures off Hawaiʻi are relatively stable but these results further suggest that cookiecutter sharks may avoid surface waters > 26–27 °C, possibly retreating to cooler, deeper waters. This interpretation assumes that cookiecutter sharks are predating whales at the surface, and it could reflect a broader thermal preference within the sharks' habitat range.

Pilot whale social structure may influence the dynamics of how pilot whales and cookiecutter sharks interact, although model predictions had a high standard deviation, suggesting that there is substantial variation in the effect across social cluster. Pilot whales in Hawaiʻi are known to have a social structure characterized by strong, long-term associations (Alves et al. 2013; Mahaffy et al. 2015), suggesting individuals from the same social groups are exposed to cookiecutter sharks at similar rates and may therefore have similar numbers or types (e.g., fresh, healed) of bites. As the spatial distribution of pilot whales throughout the year appeared relatively homogenous, any variation in bite rates between social clusters is more likely influenced by changes in cookiecutter distribution patterns or environmental factors.

Cookiecutter sharks appeared to show some selection for biting the head and dorsal areas of pilot whales, with fewer bites observed on the lateral and peduncle areas (Table 3). Previous work involving both odontocetes and mysticetes found that there were higher numbers of cookiecutter bites on the peduncle of mysticetes in comparison to odontocetes (Best and Photopoulou 2016). The prevalence of cookiecutter bites around the head and dorsal region may be due to several factors such as differences in body composition, behaviour and locomotion patterns, and predator-prey interactions. Blubber composition in short-finned pilot whales varies with body location, with areas between the pectoral and dorsal fin being the most metabolically active and those surrounding the peduncle as relatively inert (Noren et al. 2021). This could lead to selection of specific body areas during predation. In other species, such as rough-toothed dolphins (*Steno bredanensis*), examination of the ventral side was facilitated through their aerial behaviour and this area was often covered in cookiecutter scars (Baird 2016). Unfortunately, pilot whales rarely leap out of the water and examination of the ventral side was therefore not possible during this study, although some records of underwater sightings were obtained. Given the low number of sightings, the ventral side was not evaluated for bite presence hence, our estimates of bite probabilities on short-finned pilot whales are conservative. While cookiecutter shark bites on pilot whales may not be fatal (although some small dolphins may die from bites that penetrate into the abdominal cavity (Baird 2016), they may still reduce pilot whale fitness.

We provide new insight into the foraging dynamics of cookiecutter sharks, an incredibly versatile pelagic predator whose bites are ubiquitous on pelagic predators in tropical waters. Cookiecutter shark bite probability on short-finned pilot whales appears to be influenced by season, lunar phase, and sea surface temperature. Bite probability appears to peak in alignment with lunar-driven shifts in the micronektonic layer and pilot whale dive patterns, indicating increased vulnerability at certain depths. However, within this study we were unable to ascertain which point in this interaction presented the highest risk to pilot whales. Given the influence that sea surface temperature has on cookiecutter sharks' predation, further research into the relationship between cookiecutter shark thermal tolerance and vertical distribution would help clarify whether temperature directly impacts their surface activity and bite behaviour. Our findings reveal new insights into predator-prey dynamics between cookiecutter sharks and marine mammals, highlighting the intricate foraging patterns and ecological interactions within pelagic ecosystems.

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Author contributions All authors contributed to the study conception and design. Data collection and preparation were conducted by S.D. Mahaffy and R.W. Baird, project supervision was conducted by Y.P. Papastamatiou, and data analysis was conducted by N.L. Walker-Milne. The first draft of the manuscript was written by N.L. Walker-Milne, and all authors commented on the previous versions of the manuscript. All authors reviewed and approved the final version of the manuscript

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Data availability The datasets generated during and/or analysed during the current study are available in the Zenodo repository, [https://doi.org/10.5281/zenodo.14721710]. The code used for analysis is available on GitHub, [https://github.com/NWMilne/Cookiecutters]. These resources are accessible and comply with the repository's data policies.

Declarations

Conflict of interest The authors have no conflict of interest.

Ethics approval Data were collected under NOAA Fisheries Scientific Research Permits 731–1509, 731–1774, and 15330 issued to RWB, and research methodologies were approved by the Cascadia Research Collective Institutional Animal Care and Use Committee.

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