Inter-Research Science Publisher
Marine Ecology Progress Series
Volume 775:119–135
Published December 11, 2025
https://doi.org/10.3354/meps14977

OPEN ACCESS

Relative role of operational patterns and environmental conditions on cookie cutter shark damage in the Hawaiʻi longline fishery

Justin J. Suca[1,*], Donald R. Kobayashi[2], Hing Ling Chan[2], J. Hauʻoli Lorenzo-Elarco[3,4]

[1]Department of Oceanography, University of Hawaiʻi at Mānoa, Honolulu, HI 96822, USA
[2]Pacific Islands Fisheries Science Center, 1845 Wasp Blvd. Honolulu, HI 96818, USA
[3]Honolulu Community College, 874 Dillingham Blvd. Honolulu, HI 96817, USA
[4]Ka Haka 'Ula o Ke'elikōlani, College of Hawaiian Language, University of Hawaiʻi at Hilo, Hilo, HI 96720, USA

ABSTRACT: Cookie cutter sharks *Isistius* spp. (nahunaiki) are a small shark species that act as a micropredator for large pelagic organisms. Little is known about these sharks due to their cryptic behavior, resulting in most inferences about their distribution coming from patterns in the wounds they leave on prey. Here, we used documentation of these cookie cutter shark bites on fish caught in the Hawaiʻi longline fishery, coupled with catch location and timing, to better understand how fisher behavior and environmental conditions are associated with cookie cutter shark bites. Specifically, we analyzed patterns in cookie cutter shark bites for the nighttime shallow-set sector targeting swordfish *Xiphias gladius* (aʻu kū) and the daytime deep-set sector targeting bigeye tuna *Thunnus obesus* (ʻahi poʻonui). Our results indicated that cookie cutter shark bites primarily occurred on hooked fish when operations extended longer into nightfall, during low lunar illumination, and along the edges of the North Pacific subtropical gyre. Bites were more common on average in the shallow-set fishery than the deep-set fishery, likely due to the nearly full nighttime operational window. The frequency of cookie cutter shark bites on fish caught in the deep-set sector has increased over time due to fishing extending further into nighttime hours. Our findings provide insight into the ecology of cookie cutter sharks, context for the increasing frequency of cookie cutter shark bites in the deep-set Hawaiʻi longline fishery, and important information for fishers regarding the potential costs of increased effort leading to fish damaged by cookie cutter shark bites.

HŌʻULUʻULU MANAʻO: He manō liʻiliʻi ka nahunaiki (cookie cutter shark; *Isistius* spp.), a he poʻiiʻa liʻiliʻi ia o nā mea ola o ka moana nui ākea. Kākaʻikahi loa ka ʻike e pili ana i ia manō o ka ʻike kākaʻikahi ʻia, a kuhi ʻia kahi o ia manō e noho ana ma nā pōaleale nahuna i waiho ʻia ma ona mau luapoʻi. Ma kēia pepa nei, ua kālailai ʻia ka ʻike i loaʻa mai no nā pōaleale nahuna a ia poʻe nahunaiki ma luna o nā iʻa mai ka ʻoihana lawaiʻa aho loa o Hawaiʻi me ke kālailai pū ʻia o kahi a me ka wā i lawaiʻa ai i mea e hoʻomaopopo ʻia mai ai ka pilina o ka ʻoihana lawaiʻa, ke ʻano kaiapuni, a me nā nahuna o ka manō nahunaiki. Ua kālailai ʻia nō nā lauana nahuna a ka poʻe manō nahunaiki ma ka māhele lawaiʻa aho loa kau pili ʻilikai o ka pō no ka iʻa aʻu kū (swordfish; *Xiphias gladius*), a me ka māhele lawaiʻa aho loa kau hohonu o ke ao no ka iʻa ʻahi poʻonui (bigeye tuna; *Thunnus obesus*). Ma ia kālailai ʻana, ua ʻike ʻia ka nui o nā nahuna ma luna o nā iʻa i ka lawaiʻa ʻana ma nā ahiahi a aumoe paha, ka wā hoʻi i ʻemi loa mai ai ka māʻamaʻama ʻana o ka malama, a ma kaʻe hoʻi o ke au lalo kopikala o ka Pākīpika ʻĀkau. Ua ʻoi aʻe ka maʻamau o nā nahuna i ʻike ʻia ma ka māhele lawaiʻa aho loa kau pili ʻilikai ma mua o ka māhele lawaiʻa aho loa kau hohonu, a pēlā nō paha no ka lawaiʻa ʻana ma ke au pouli loa o ka pō, a ua ʻoi aʻe nō ka nui o ka manawa i ʻike ʻia ai nā nahuna ma nā iʻa i lawaiʻa ʻia i ka lawaiʻa aho loa kau hohonu ma ke au ʻana o ka manawa i loko o nā hola ahiahi a aumoe paha. He waiwai loa kēia ʻano noiʻina no ka ʻike kaiaola o ka poʻe manō nahunaiki, ka pōʻaiapili o ka nui o ka manawa o nā nahuna a ka poʻe manō nahunaiki i ka ʻoihana lawaiʻa aho loa kau hohonu o Hawaiʻi, a me ka ʻike nui a koʻikoʻi no ka poʻe lawaiʻa e pili ana i nā kumu lilo o ka lawaiʻa ʻana i nā iʻa i pōaleale i nā nahuna o ka poʻe manō nahunaiki o ka pō.

KEY WORDS: Cookie cutter shark · Mesopelagic · Longline · Distributions

*Corresponding author: jsuca@hawaii.edu

Publisher: Inter-Research · www.int-res.com

Muku ka malama, nanahu ka nahunaiki[2] o ka pō. [1]

When the new moon arises, the cookie cutter shark bites.

[1]Summary of a key finding as told through an ʻōlelo noʻeau, a new proverbial saying from an indigenous Hawaiian worldview.

[2]Etymology: There are no known traditional Hawaiian names or Polynesian cognates for the cookie cutter shark (*Isistius* spp.), nor are there any surviving stories that recorded historical observations of the shark by the Native Hawaiian people. Due to its elusiveness, the authors theorize that Native Hawaiians rarely or never encountered cookie cutter sharks. However, it was likely that this ocean nation saw the characteristic bites of these sharks on the bodies of some of their seafood catches. 'Nahuna' meaning 'bite,' and 'iki' meaning 'little, small' are combined to form 'nahunaiki,' the new name offered to describe the cookie cutter shark in the Hawaiian language. The authors advocate that Indigenous Ecological Knowledge is not stagnant and fixed in the past. Rather, this new Hawaiian name, as well as the new proverbial saying offered in this paper — 'muku ka malama, nanahu ka nahunaiki o ka pō' — represents a living, breathing, and thriving Hawaiian language and culture, that when paired in a complementary manner with Western science, becomes a true representation of meaningful engagement and collaboration.

1. INTRODUCTION

Cookie cutter sharks *Isistius* spp. (nahunaiki) are a small (<1 m) circumtropical and subtropical mesopelagic to bathypelagic shark species. The most notable feature and behavior of this shark is its feeding mode as a micropredator of many large marine taxa (Benz & Bullard 2004). These small sharks remove nearly circular sections of flesh from species ranging from large pelagic fishes (Papastamatiou et al. 2010) to cetaceans (Best & Photopoulou 2016, Feunteun et al. 2018), and even humans (Honebrink et al. 2011, Minaglia & Liegl 2024). Although cookie cutter sharks also consume micronekton directly (Jahn & Haedrich 1988, Carlisle et al. 2021), it is the damage left by their bites on larger creatures that has inspired numerous studies on these species.

The cookie cutter shark comprises 2 species: the common cookie cutter shark *Isistius brasiliensis* and the bigtooth cookie cutter shark *I. plutodus*. Most work and interactions are presumed to originate from common cookie cutter sharks, as bigtooth cookie cutter sharks have only been recorded in a dozen instances around the globe (Stehmann & Kukuev 2015). Cookie cutter sharks are thought to be vertical migrators, as human interactions with these sharks only occur at night, and fresh bites occur near the surface at night on captured fishes, with little to no direct observations of cookie cutter sharks during daylight hours (Papastamatiou et al. 2010, Minaglia & Liegl 2024). As a largely mesopelagic to bathypelagic species, the cookie cutter shark is thought to have evolved a unique method of attracting prey — a lure generated from the lack of bioluminescence around their gills. The bioluminescence on their ventral side is used for countershading, but one small section lacks this coloration, and this gap may look like a prey item to larger taxa (although this is hypothesized and yet to be confirmed *in situ*; Widder 1998). Cookie cutter sharks are then presumed to attack the predatory animal they have attracted.

The distribution of cookie cutter sharks largely remains undescribed. This lack of data is in large part due to their ability to avoid most net gear when towed at depth and the rarity of the species being caught by hook and line gear. Distributional patterns of cookie cutter sharks have been inferred based on the bite marks on large organisms such as cetaceans and large pelagic fish catches (Papastamatiou et al. 2010, Best & Photopoulou 2016, Feunteun et al. 2018). In and around Hawaiʻi, the distribution of cookie cutter sharks has not been assessed, but patterns in the species they prey on have been documented in fishery-dependent data from the Honolulu fish auction (Papastamatiou et al. 2010). This study found that certain species, such as swordfish and opah *Lampris* spp., are more often preyed upon by cookie cutter sharks than are epipelagic predators, such as blue marlin *Makaira nigricans* (aʻu). These species may provide insight into the relative distribution of cookie cutter sharks (e.g. the habitat of cookie cutter sharks may overlap more with swordfish than with blue marlin).

The Hawaiʻi longline fishery is the highest-value fishery in Hawaiʻi, generating over $110 million in 2024 (WPRFMC 2025). The fishery is divided into 2 sectors: the Hawaiʻi deep-set longline fishery (DSLL), targeting bigeye tuna *Thunnus obesus* (ʻahi poʻonui), and the shallow-set longline fishery (SSLL), targeting swordfish *Xiphias gladius* (aʻu kū; He et al. 1997, Gilman et al. 2012). The Hawaiʻi SSLL is the largest swordfish fishery in the USA in terms of landings and revenue, primarily targeting swordfish near the North Pacific Transition Zone with hook depths of ~50 m (Fig. 1) (He et al. 1997, Sculley & Brodziak 2020). The market for this SSLL fishery is driven by demand in the continental USA. This fishery primarily fishes in the winter months, with typically 15–20 boats participating in the winter each year and 0–5 boats operating in the summer (Sculley & Brodziak 2020). The SSLL is heavily monitored due to a history of sea turtle interactions in the fishery, resulting in 100% observer coverage for SSLL trips (Howell et al. 2008, 2015, Ito & Childers 2014). In the early 2000s, the SSLL was closed by court order due to sea turtle interactions and reopened with the required use of fish bait (as opposed to squid) and large circle hooks to mitigate sea turtle interactions (Chan & Pan 2016). The SSLL is also restricted to setting after dark to mitigate seabird interactions, typically fishes 4–6 hooks per float, and fishes ~1000 hooks per set (Ito & Childers 2014).

The DSLL targets bigeye tuna, with maximum hook depths from 200–400 m, fishing closer to the Hawaiian archipelago (Hawaiʻi Pae ʻĀina), both to the north and south, than the SSLL throughout the year (He et al. 1997, Gilman et al. 2012). However, the 2010s saw an increase in effort by the DSLL to the north and east (Chan 2023). The fishery typically has ~125 active boats and operates year-round (Ito & Childers 2014, Woodworth-Jefcoats et al. 2018). Due to lower rates of interaction with protected species (e.g. sea turtles and marine mammals) compared to the SSLL, the DSLL has historically maintained approximately 20% observer coverage (Ito & Childers 2014). Time of setting is not regulated for this fishery; a set typically has 20–35 hooks float^{-1}, and often has 2500–3500 hooks set^{-1} (Ito & Childers 2014).

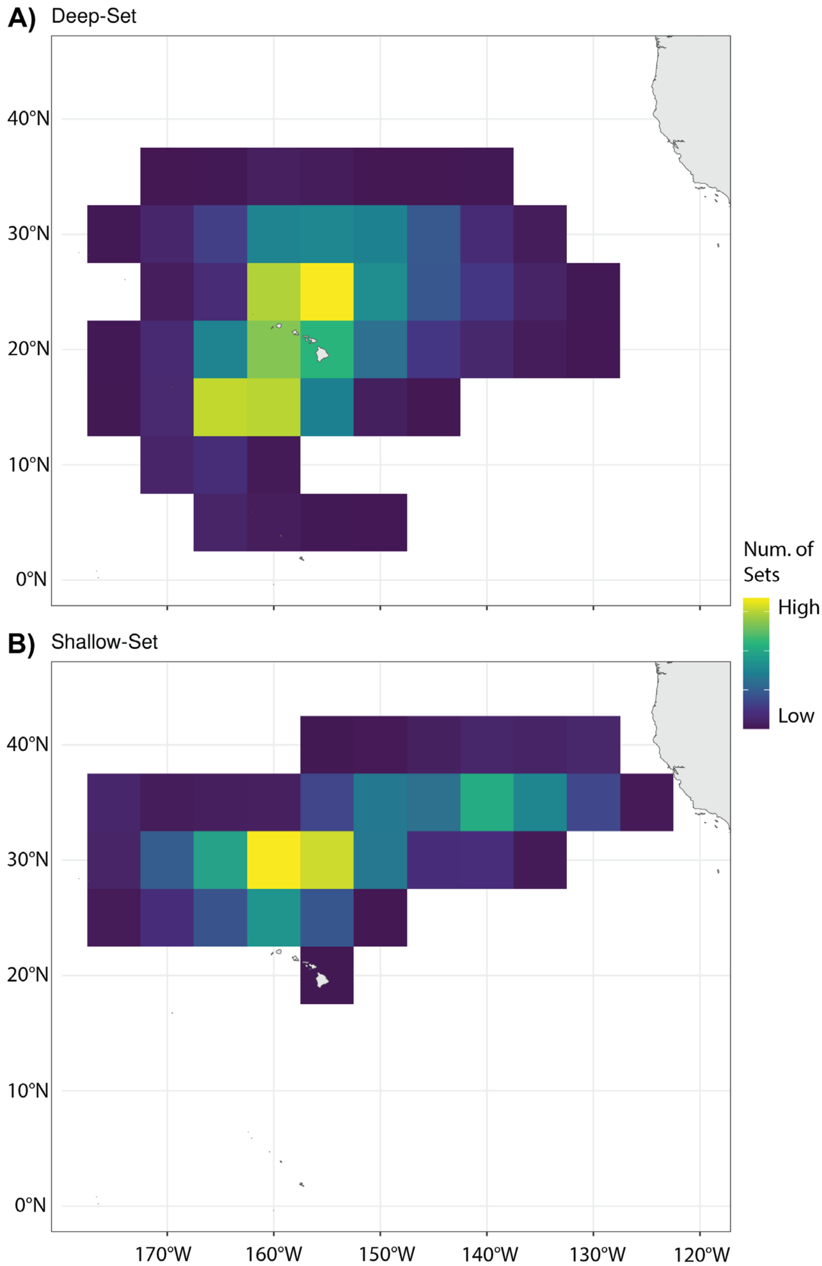

Fig. 1. Relative fishing effort by sets from 2005–2022 for the Hawaiʻi (A) deep-set longline fishery and (B) shallow-set longline fishery. Data are from the Pacific Islands Region Observer Program. Exact number of sets not displayed to maximize confidentiality

The DSLL is a low-volume, high-value fishery in which individual fish are auctioned daily in Honolulu, with many of these fish sold for local consumption. The nature of this process leads to the price of individual fish being sensitive to appearance, which can be hurt by cookie cutter shark bites (Papastamatiou et al. 2010, Chan et al. 2025). Indeed, the auction records whether an individual fish has a cookie cutter shark bite (1–3 bites) or cookie cutter shark damage (4+ bites) on the individual tags to let buyers know of the damage (M. Goto pers. comm.). This leads to a deleterious economic impact of cookie cutter sharks for both fisheries, but it is more pronounced for the DSLL due to the selling process involving individual fish (Papastamatiou et al. 2010) rather than pallets of individuals grouped together (common for swordfish from the shallow-set). Cookie cutter shark bites on longline-caught fish have become more prevalent, with nearly 25% of fish on the auction having a cookie cutter shark bite or damage in recent years, including exceptional cases in which >50% of fish sold had a cookie cutter bite (Chan et al. 2025) (Fig. 2). The increasing trend in cookie cutter shark damage in this fishery has led to

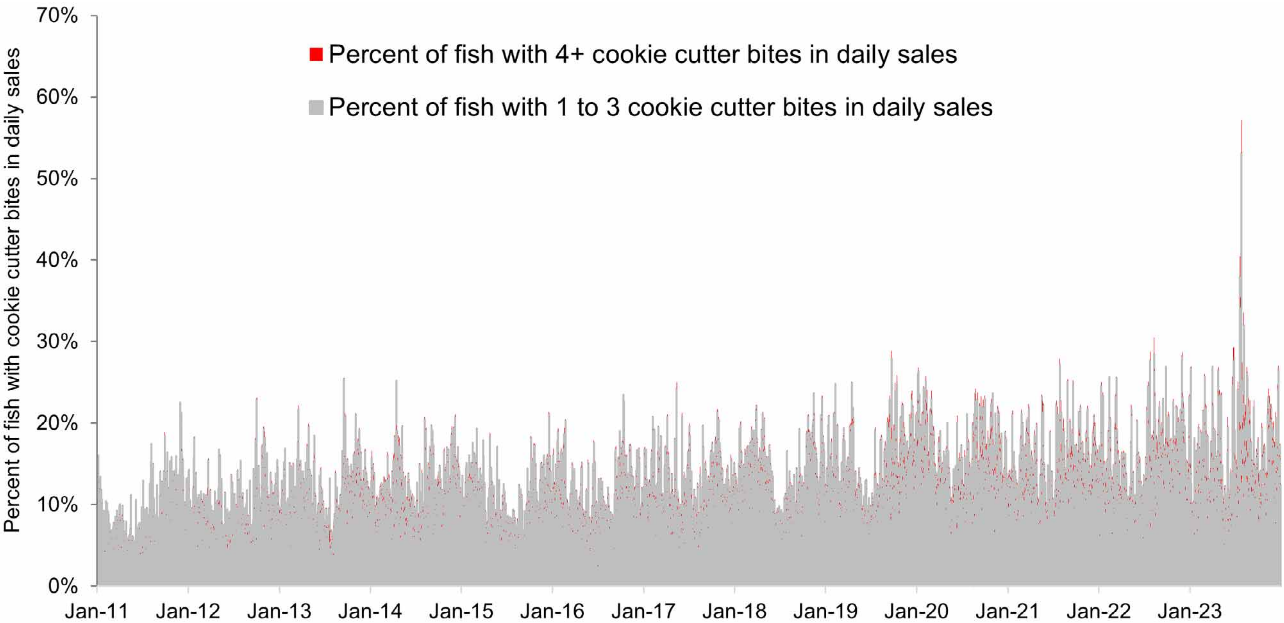

Fig. 2. Daily incidences of cookie cutter shark bites recorded in daily sales at the United Fishing Agency in Honolulu, the largest fish auction in Hawaiʻi, for fish with minor damage (1–3 bites) and more serious damage (⩾4 bites) between 2011 and 2023. Data from Chan et al. (2025)

concerns and questions about why this may be happening.

Here, we used information collected by fishery observers on both the SSLL and DSLL sectors of the Hawaiʻi longline fishery to better understand the environmental and operational (fishing gear and fisher behavior) associations of cookie cutter bites on fishes caught in these fisheries. Specifically, we aim to answer the questions of how cookie cutter damage on fish varies between fishery sectors, how it varies throughout space and time, and how gear configuration and fishing duration relate to the probability of a fish on a given set being bitten by a cookie cutter shark. This will allow us to better understand whether the recent spatial changes in fishing effort and increases in fishing duration — particularly for the DSLL — have contributed to the increased incidence of cookie cutter shark damage on fishes caught in this longline fishery.

2. MATERIALS AND METHODS

2.1. Cookie cutter bite data

Cookie cutter shark bite information came from the Pacific Islands Regional Observer Program. This program records information at the species level for each set (a single full deployment of a longline from setting of gear through haulback) on a given Hawaiʻi longline trip, with coverage based on the set type of the trip. SSLL trips (hook depth of 20–50 m) have 100% observer coverage, while DSLL trips (hook depth of 200–400 m) have approximately 20% observer coverage. Since 2004, whether a trip is SSLL or DSLL must be declared before making the trip. In addition to species-level catch data for each set, the observer program records the number of hooks, branchline length, floatline length, mainline lengths, light devices used (for SSLL trips), number of floats per set, bait type, set positions, and set and haul times (Table 1). Until 2015, the presence of fresh cookie cutter shark bites was also recorded at the individual fish level. However, due to some inconsistencies in the format of recording (e.g. using a specified column per fish or commenting in the notes), we were unable to confidently trace back all bites to individual fish. This means that a total count of bites per set could not be identified reliably. We thus used information at the set level for our analyses, focusing on whether any fish caught on a given set had a bite or not (presence–absence at the set level). Consistent recording of cookie cutter shark bites at the set level by observers ended in 2016. Due to the restart of the SSLL fishery in the mid-2000s after a bycatch-induced closure, we decided to use the observer program data between 2005 and 2015 for modeling analysis. Note that observer data exists after 2015; it is only the recording of cookie cutter shark bites that ceased.

Table 1. Variables used in boosted regression tree models to assess the patterns in cookie cutter (CC) shark bite occurrence on fish caught in the Hawai'i longline fishery. SSLL: shallow-set longline fishery; PIROP: Pacific Islands Regional Observer Program; GLORYS: Global Ocean Physics Reanalysis; ESA OC-CCI: European Space Agency Ocean Color—Climate Change Initiative; JMA: Japanese Meteorological Agency; NOAA: National Oceanic and Atmospheric Administration

Variable type	Variable	Units	Hypothesis	Source
Operational	Floatline length	m	Depth of fishing gear	PIROP
	Branchline length	m	Depth of fishing gear	PIROP
	Hooks per float	Count	Depth of fishing gear	PIROP
	Light devices per hook (SSLL only)	Count	Effectiveness of fishing and potential attraction of CC sharks	PIROP
	Night hours	h	Longer soak times at night could lead to higher interactions with CC sharks	PIROP
	Day hours	h	Longer soak times generally could lead to higher interactions with CC sharks	PIROP
Temporal	Year	yr	Interannual variability not attributable to other variables	PIROP
	Day	Day of year	Seasonality	PIROP
	Lunar cycle	Radians	Vertical migration and visibility of CC sharks at night	'lunar' package in R (Lazaridis 2022)
Environment—Ocean state	Sea surface temperature (SST)	°C	Thermal preference	GLORYS
	Spatial standard deviation in sea surface temperature (SST SD)	°C	Anomalous warm or cold waters in a region leading to patterns departing from typical spatial pattern	GLORYS
	Sea surface height (SSH)	m	Indicator of divergence and convergence at gyre scales	GLORYS
	Spatial standard deviation of sea surface height (SSH SD)	m	Indicator of boundaries between gyres and indicator of eddy activity	GLORYS
	Sea surface salinity (SSS)	None	Indicator of water masses	GLORYS
	Spatial standard deviation in sea surface salinity (SSS SD)	None	Indicator water mass boundaries	GLORYS
	Current speed	m s^{-1}	Preference for strength of current regimes	GLORYS
	Mixed layer depth (MLD)	m	Depth of thermocline affecting vertical migrating behavior of CC sharks	GLORYS
	Chlorophyll concentration	mg m^{-3}	Productivity-driven aggregation of prey or CC sharks	ESA OC-CCI
Atmosphere—Ocean Indices	Meridional El Niño—Southern Oscillation Index		Broader-scale phenomena that may change SST, MLD, and productivity on longer time scales	JMA
	Pacific Decadal Oscillation		Broader-scale phenomena that may change SST on longer time scales	NOAA
	North Pacific Gyre Oscillation		Broader-scale phenomena that may change SSH and MLD on longer time scales	NOAA

2.2. Environmental data and other predictors

Environmental data were paired to the center of each set at daily resolution (sea surface temperature, sea surface height, sea surface salinity, current speed, mixed layer depth, and chlorophyll *a* [chl *a*] concentration). Except for chl *a*, all environmental predictors were paired using the Global Ocean Physics Reanalysis model as part of the Copernicus Marine Environment Modeling system (Jean-Michel et al. 2021) (our Table 1). We chose to use this model output due to its accurate representation of ocean state variables (Jean-Michel et al. 2021, Amaya et al. 2023) and for consistency in variable sourcing, mitigating issues that occur from using multiple data sources that measure properties through different methods. Spatial standard deviations of sea surface temperature, sea surface height, and sea surface salinity were calculated approximately within one degree latitude and longitude of the center of the set as a proxy for thermal fronts, pressure gradients, and water mass variability, respectively (Abrahms et al. 2019, Becker et al. 2020). Atmosphere–ocean–climate patterns were also added as predictors in the model to determine whether large-scale processes influence variability in cookie cutter shark interactions that are not explained by other environmental covariates in the model, including multivariate El Niño–Southern Oscillation Index, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation (Table 1). We included the lunar phase as a predictor using the 'lunar' package (Lazaridis 2022) in R v.4.2.2 (R Core Team 2022). We represented the lunar cycle using radians (0–2π) to allow for maximum flexibility in identifying which aspect of the lunar phase may correspond to bite probability, as lunar illumination alone prevents discrimination between waning and waxing phases. We also included the number of day hours (hours from sunrise to sunset) and night hours (sunset to sunrise) that occurred over the full course of a set. If a set lasted multiple days, these day and night hours were summed across those days to generate a cumulative number of day and night hours across the full set. Sunrise and sunset times were gathered using the position of the set and the date using the 'suncalc' package in R (Thieurmel & Elmarhraoui 2019).

2.3. Model formation and fitting

We modeled the occurrence of a cookie cutter shark bite event on any fish on a given set using ensemble boosted regression trees (BRTs) with the 'dismo' (Elith et al. 2008) and 'gbm' packages in R (Ridgeway et al. 2022). BRTs are a machine learning approach formed from many decision trees and have the advantage of dealing with missing predictor variables, a moderate amount of predictor collinearity (although we do not include environmental variables with >0.7 correlation coefficients; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m775p119_supp.pdf), and can be used to model complex non-linear relationships and predictor interactions (Elith et al. 2008). However, machine learning approaches are susceptible to overfitting, which can lead to unstable response curve shapes and attribute variable importance to noise. We attempt to reduce overfitting using a hybrid cross-validation ensemble approach whereby the data set was iteratively split into 50 different training sets comprising 75% of the data, with model skill performance assessed on the remaining 25% of the data for each iteration (test sets; cross-validation). All 50 individual models are retained to develop estimates of relationships between cookie cutter bite probabilities and predictor variables, resulting in smoothed response curves for each relationship (ensemble). The number of trees was selected using the 'gbm.step' function within the 'gbm' package. The tree complexity was set as a maximum of 5 (to allow for fish count [number of fish caught on a given set]), day of year, and operational timing to interact with environmental variables), a learning rate of 0.005, and a bag fraction of 0.75. Learning rate was set to 0.005 as the slowest learning rate possible that did not result in greater than 10 000 trees (Elith et al. 2008). A bag fraction of 0.75 was selected following Hazen et al. (2021), although it falls on the upper end of the range used in a number of studies (Elith et al. 2008, Scales et al. 2017, Welch et al. 2023).

We modeled the occurrence of cookie cutter shark bites for the SSLL and DSLL fisheries independently. Variable importance was calculated to identify the most influential predictors for each fishery. Variable importance measures the frequency at which a variable is used for tree splitting and is weighted by how much this variable improves model fit. Note that latitude and longitude were not included as predictors to avoid artificial stickiness to the models, allowing cookie cutter interaction rates to be connected to environmental conditions rather than forcing a spatial structure on the pattern. A normally distributed random number was included as a variable for each fishery sector model (SSLL and DSLL), and an ensemble of 25 models was initially constructed to obtain an estimate of mean variable importance for the random variable. Any variable with a mean importance less than that of the random variable was removed from consideration for that fishery sector before generating the 50-model ensemble for the fishery sector. The random variable was also removed before fitting the 50-model ensembles.

Model skill for each sector was measured using the area under the curve (AUC) of the receiver operating curve for the 25% test set (Huang & Ling 2005). This metric represents an aggregate measure of classification model performance across all possible classification thresholds, integrating true positive rate and false positive rate (ranging from 0 to 1, with 0.5 being equivalent to random). We also assessed model skill through the true skill statistics (TSS), a separate measure of classification model performance that is less sensitive to low occurrences, representing the difference between the true positive rate and false positive rate (ranging from −1 to 1, with 0 being equivalent to random; Allouche et al. 2006). We present the mean AUC and TSS across the 50-model ensembles for each sector.

Estimates of the occurrence of cookie cutter bite events were made at the set level, and then set-level estimates were binned at the monthly level or spatial level (1° × 1°). Estimates were calculated using all available sets from the observer program data. Each of the 50 individual models was used to generate a prediction for each set, and the average of these probabilities was used as the point estimate. For each month or spatial bin of BRT-modeled probability of cookie cutter bites on a set, correlations (R^2) were calculated by relating the proportion of sets that had a fish with cookie cutter shark damage (observations) to the mean modeled probability of cookie cutter shark damage on each set within that month or spatial bin. We recognize that these metrics are not measuring the same quantity, but they are similar enough to be relatable and thus provide a sense of model performance. We further recalculated bite probabilities, fixing a specific set of predictors based on those to which the models were sensitive. Specifically, due to the importance of night hours, fish count, and seasonal cycle for the DSLL, we made model estimates of cookie cutter damage probabilities over each set from the observer program from 2005–2022 with (1) fish count per set held constant at the mean (53.5 fish set^{-1}) and fishing day set as the mode of day of operation (Day 292; i.e. night hours allowed to vary), (2) fish count per set held constant at the mean (53.5 fish set^{-1}) and night hours held constant at the mean (10.1 h; i.e. day-of-the-year of fishing allowed to vary), and (3) night hours held constant at the mean (10.1 h), and fishing day set as the mode of day of operation (Day 292; i.e. fish count allowed to vary). These parameters were held constant in simulations to evaluate (1) the impact of overnight operations, (2) the degree to which the seasonal cycle influences bite probability, and (3) the influence of catch rate shifts on the probability of a cookie cutter shark bite on a set.

3. RESULTS

3.1. Model fit and trends in DSLL

The DSLL had a moderate bite incidence per set (69.2% of sets). Model skill for cookie cutter shark damage on a fish at the set level for the DSLL was passable, although not strong (AUC = 0.76, TSS = 0.39). Retrospective fit at the spatial level was also moderate for the DSLL sector (R^2 = 0.54). Modeled bite probability and proportion of sets with a bite were highest to the east in the DSLL (Fig. 3A,B), with an additional hotspot west of the main Hawaiian Islands. Monthly fit was stronger than spatial fit, with R^2 = 0.93. Both the observed and modeled cookie cutter shark bite probability showed evidence of a seasonal cycle in the DSLL (Fig. 4A). Model estimates of cookie cutter bite probabilities between 2016 and 2022 (after cookie cutter damage was no longer reported by the observer program) showed a continued seasonal cycle and a slight decline in the probability of bite in recent years in the DSLL.

3.2. Model fit and trends for SSLL

Overall bite incidence was highest on a per set basis in the SSLL (81.5% of sets). Model skill for cookie cutter damage on a fish at the set level for the SSLL was also passable (AUC = 0.78, TSS = 0.42). Retrospective fit at the spatial level was strong for the SSLL (R^2 = 0.75). Modeled bite probability and proportion of sets with a bite were high throughout the SSLL fishing domain except for the eastern portion of effort near the California Current (i.e. east of 130° W; Fig. 3C,D). Monthly fit was also strong for the SSLL (R^2 = 0.89; Fig. 4B). Model estimates of cookie cutter bite probabilities between 2016 and 2022 showed little pattern as the high bite probability remained consistent during the winter months when the fishery is most active.

3.3. Variable importance and partial dependence plots

Variable importance metrics indicated the relative role of the numerous drivers contributing to cookie cutter bite incidence by fishery sector (Fig. S2). Fish count was important for both fisheries, although much more so for the DSLL (Fig. S3). For the DSLL, night hours, day of year, sea surface temperature, lunar cycle, and sea surface height were the next 5 most important predictors (Fig. 5). Partial dependence plots for the DSLL indicate that probability of cookie cutter damage on a given set is highest after 10 night hours, during the winter, at sea surface temperatures less than 22°C, during the new moon (near 0 and 2π), and in higher sea surface heights (>0.4 m) (Fig. 5).

Outside of fish count for the SSLL, sea surface salinity, lunar cycle, sea surface height, sea surface temperature, and day of year were the 5 most important predictors (fish count was second most important

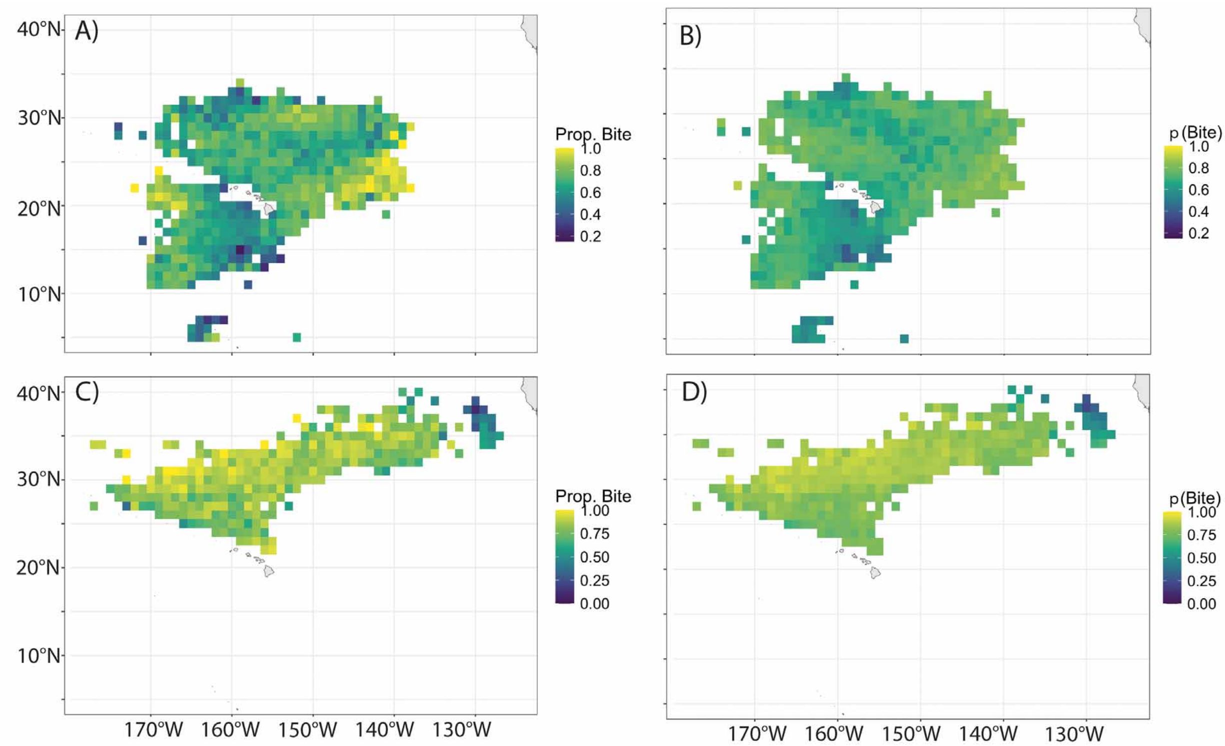

Fig. 3. Proportion of sets in 1° × 1° spatial bins from 2005–2015 with a fish that had an observed cookie cutter shark bite for the (A) deep-set longline fishery (DSLL) and (C) shallow-set longline fishery (SSLL), along with modeled estimates of the probability of cookie cutter shark bites for the (B) DSLL fishery and (D) SSLL fishery

after sea surface salinity; Fig. 6). Partial dependence plots for the SSLL indicate that the probability of cookie cutter damage on a given set is highest at sea surface salinity values higher than 33.5, peaks during the darkest phases of the lunar cycle, at elevated sea surface heights (>0.4 m), above 17°C sea surface temperature, and is highest during the winter and spring (Fig. 6).

The time series of the predictions over the DSLL data set with fish count and day of year held constant (i.e. night hours left to vary) resulted in an asymptotic increase in probability of a fish being bit on a set (Fig. 7A). Predictions over the DSLL data set with fish count and night hours held constant (i.e. day of year allowed to vary) resulted in a notable seasonal oscillation in the probability of a bite on a set, with increases in the winter months (November–April) and decreased in the summer (Fig. 7B). Predictions over the DSLL data set with night hours and day of year held constant (i.e. allowing fish count to vary) resulted in high frequency oscillations in bite probability with a peak in the mid-2010s and a subsequent decline in recent years (Fig. 7C).

Average number of night hours operated per set for the DSLL indicated a continued increase from 2005–2022 with a persistent seasonal cycle (Fig. 8A). The increase in night hours per set appears to be linked to an increase in the number of hooks per set (Fig. 8B). The mean night hours per set in the DSLL increased from ~8 h in 2005 to ~11 h in 2022 (Fig. 8A). This also corresponds to an increase in the number of hooks per set in the DSLL, rising from ~2000 in 2005 to ~3000 in 2022, with an average increase of about 50 hooks set^{-1} yr^{-1} (Fig. 8B). The monthly mean number of hooks per set and the monthly mean number of night hours were highly correlated (Pearson correlation coefficient = 0.80, $t = 19.227$, df = 214, $p < 0.001$; Fig. 8C). Positive residuals (i.e. greater than expected night hours per number of hooks) in this relationship occurred primarily in the winter (1 November–31 March), while negative residuals primarily occurred in the summer (1 April–31 October; Fig. 8C).

4. DISCUSSION

4.1. Darkness and cookie cutter shark damage

Our model results indicated that the occurrence of cookie cutter shark damage on fish in the Hawaiʻi longline fishery is tightly linked to the duration of darkness during operation (e.g. higher probability of bites during longer night operations, new moon, and during winter months). Notably increasing trends in

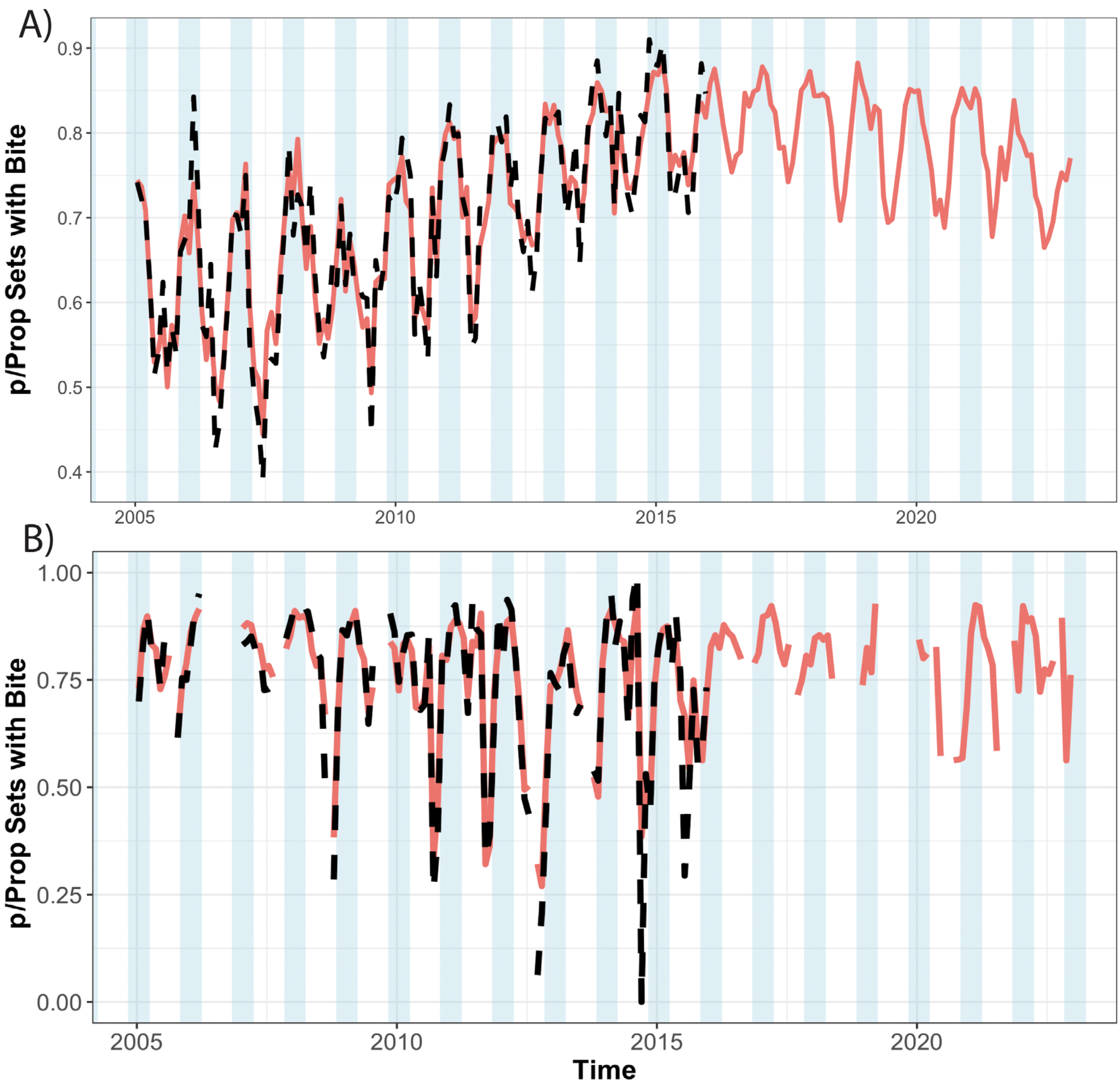

Fig. 4. Observed proportion of cookie cutter shark bites on sets in a month (black dashed lines) and mean modeled estimates of the probability of the cookie cutter shark bites on sets in a given month (red solid lines) for the (A) deep-set longline fishery and (B) shallow-set longline fishery. Blue shading indicates winter months (November–March)

cookie cutter damage seen in the fish sold at the Honolulu fish auction appear to be primarily linked to operational patterns in the DSLL fishery, namely increased duration of sets leading to increased number of night hours for a given set, as this was the only parameter that resulted in an increase in predicted bite probability on its own. The already high frequency of cookie cutter shark damage on a given set in SSLL (~81 %) and restriction to only set during night hours means damage in this fishery has much less potential to increase in the coming years. The DSLL fishery, however, is not restricted by hour of the day, allowing the fishery to operate throughout the night. Limits are likely to occur in the coming years, however, as the mean operational time of a single set has neared a full day, even exceeding one day at times, limiting the amount of time a set could increase without further compromising catch quality.

The pattern of increased bites during winter is consistent across studies of cookie cutter shark bite interactions with their prey species (Papastamatiou et al. 2010, Best & Photopoulou 2016, Feunteun et al. 2018).

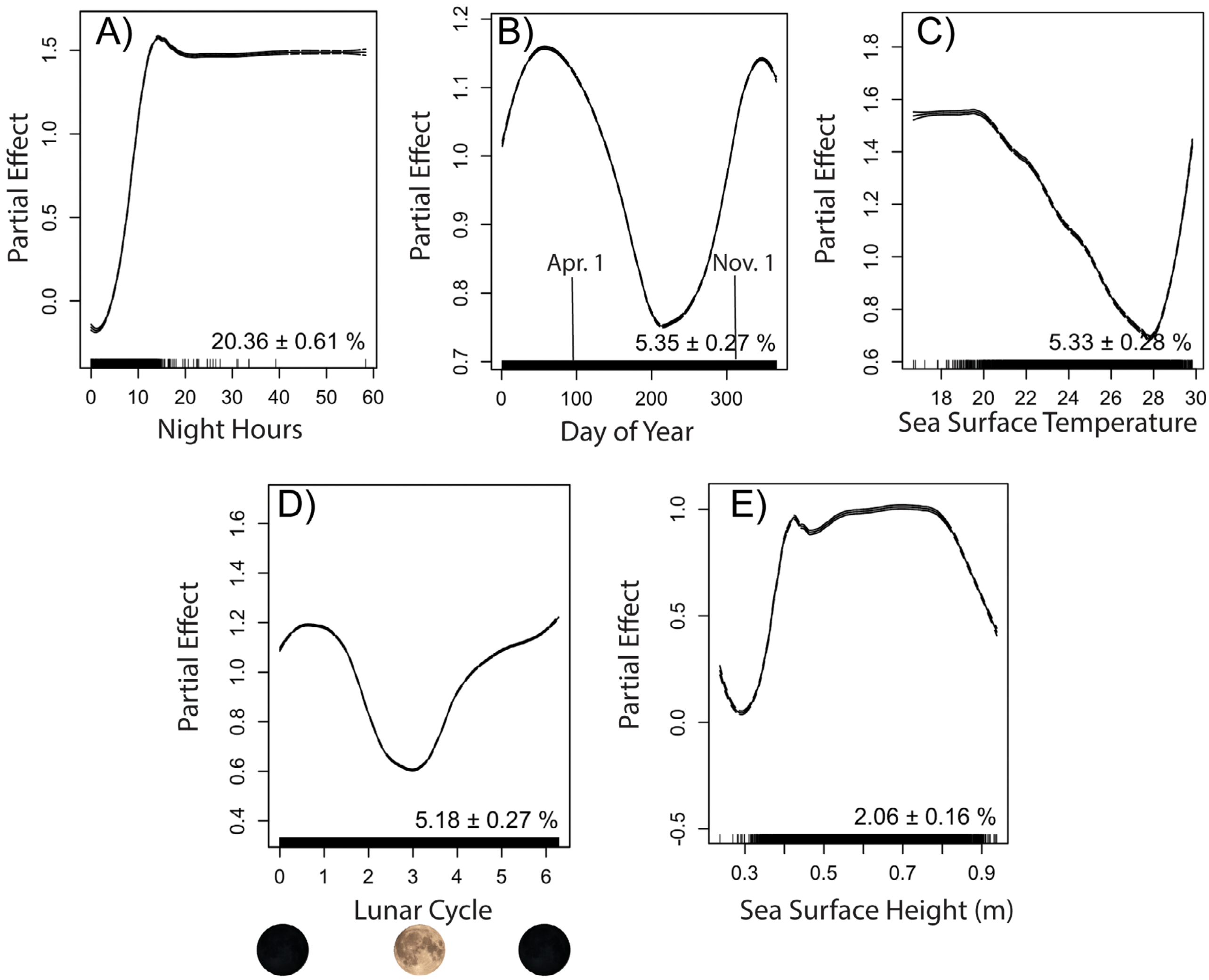

Fig. 5. Partial dependence plots for the 5 most important predictors (outside of permit number and fish count) (A) night hours, (B) day of year, (C) sea surface temperature, (D), lunar cycle, and (E) sea surface height for models of the occurrence of cookie cutter shark bites on fishes caught on a set in the Hawaiʻi deep-set longline fishery. Numbers in the lower right corner indicate variable importance and the standard deviation of variable importance across the model ensemble. Dashed lines: bounds of 95% confidence interval within the ensemble (note not equivalent to standard statistical 95% confidence interval). Hash marks above horizontal axis of each plot: density of observations for the given parameter. Vertical axes are on a logit scale. Night hours: the number of hours of fishing during a set that occurred between sunset and sunrise. High values indicate sets that lasted for exceptionally long durations due to issues such as gear damage or loss. For day of year, 1 April and 1 November are noted, with line segments to orient readers to time of year. New moon (black circle) and full moon (moon icon) noted on the lunar cycle partial dependence plot

Papastamatiou et al. (2010) found that bites on swordfish occurred less in the summer than in the winter months. While they did not clarify why, our study indicates this may simply be due to the longer nights during this period. Another study in Martinique found that cookie cutter shark bites on cetaceans were more common during winter (Feunteun et al. 2018). This indicates that the pattern is not unique to the Pacific Ocean or to species caught in the Hawaiʻi longline fishery. It is noteworthy that the cookie cutter bite probability by day of year did not correspond directly with day length. Specifically, higher bite probabilities were observed in late fall and early winter (i.e. October–December, day of year >300) compared to January–March, despite similar day lengths. The fall peak relative to late winter has been noted for the DSLL using auction observations (Papastamatiou et al. 2010) and bites from pilot whales in west Hawaiʻi (Walker-Milne et al. 2025). This may be linked to a combination of the movement of cookie cutter sharks, as hypothesized by Walker-Milne et al. (2025), or the movement of the fishers relative to the

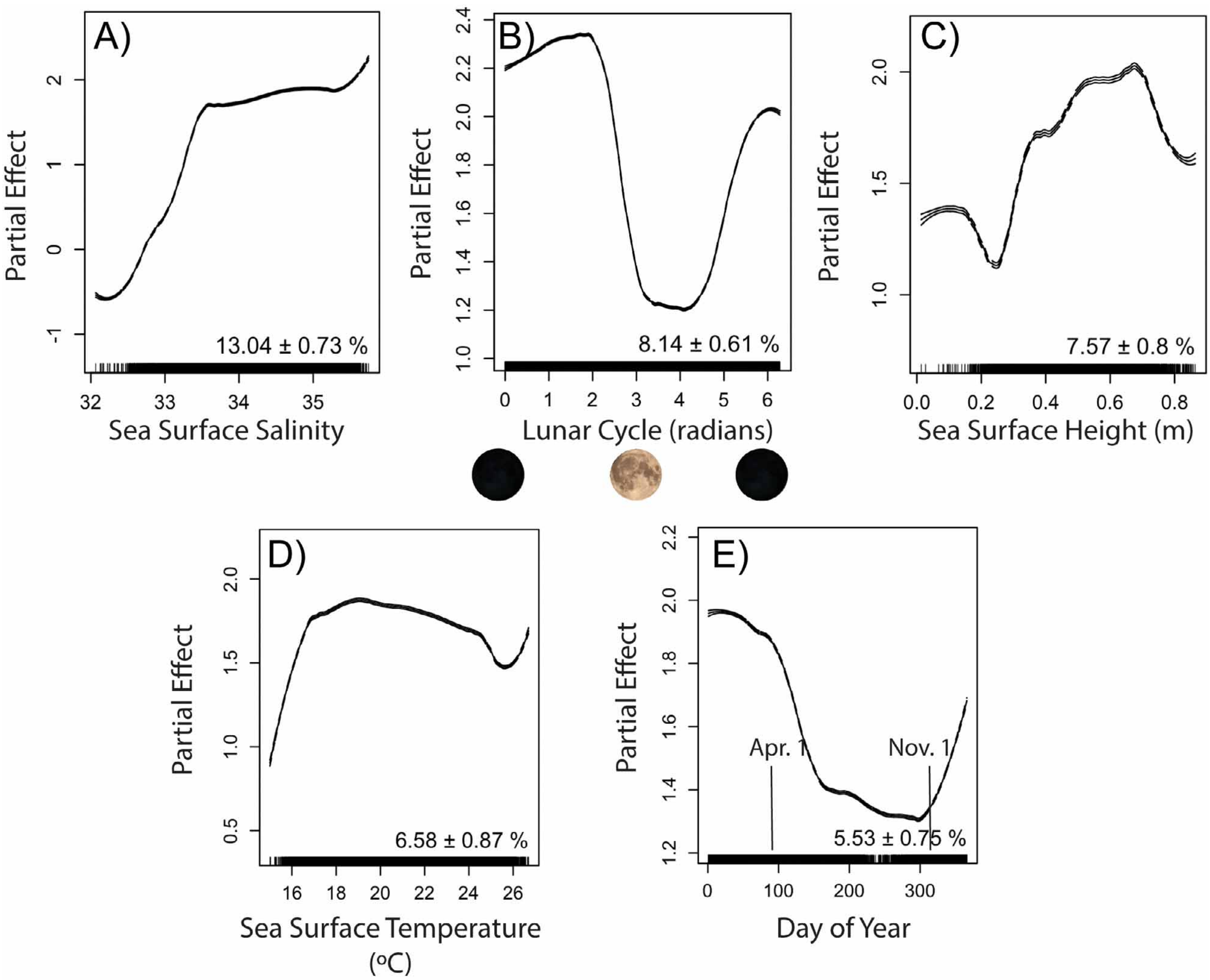

Fig. 6. Partial dependence plots for the 5 most important predictors (outside of permit number and fish count) (A) sea surface salinity, (B) lunar cycle, (C) sea surface height, (D) sea surface temperature (SST), and (E) day of year for models of the occurrence of cookie cutter shark bites on fishes caught on a set in the Hawai'i shallow-set longline fishery. See Fig. 5 for further details

movement of cookie cutter sharks. Two reasons to support the latter hypothesis are (1) seasonal movement of fishers in the DSLL (Woodworth-Jefcoats et al. 2018) and (2) the observation that bite probability was highest in the spring for the SSLL (which operates north of Hawai'i), as observed both in this study and Papastamatiou et al. (2010). Thus, seasonal movement or feeding behavior changes in cookie cutter sharks seem probable, as suggested by Carlisle et al. (2021), but this likely interacts with fishery movements in complex ways.

In the domain of the Hawai'i longline fishing grounds, particularly for the SSLL, the areas where fishing occurs in cold (<17°C) and relatively low salinity (<33.5) surface conditions are connected to the subpolar gyre, and in the case of salinity, the upwelling shadow of the California Current Ecosystem (although note that this salinity can vary due to source water variability; Gomez-Valdes & Jeronimo 2009, Bograd et al. 2015, Ren & Rudnick 2021). These cold and fresh waters provide an important constraint, indicating that cookie cutter interactions are limited to tropical and subtropical water masses, as suggested in previous work (Nakano & Tabuchi 1990, Menezes et al. 2022, Santos et al. 2024). Indeed, cookie cutter bite probabilities peaked at elevated sea surface height values for both fisheries, an indication that bites occurred in subtropical gyre waters rather than the subpolar gyre, eastern Pacific upwelling zone, or near equatorial waters (sea surface temperature, sea surface height, and sea surface salinity are all moderately correlated; Fig. S1). However, the peak bite probability at temperatures just above 17°C may have as much to do with prolonged nights at

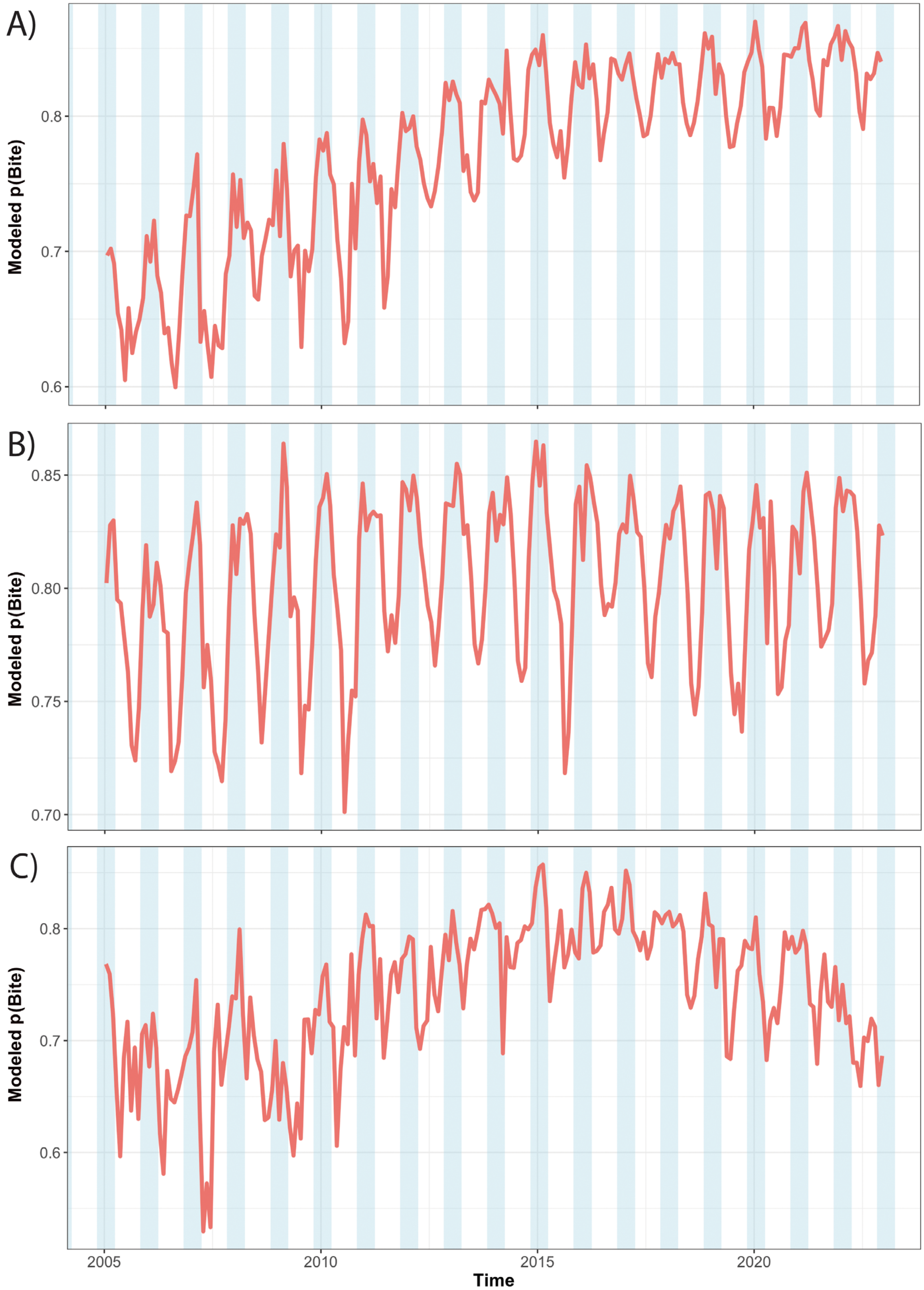

Fig. 7. Predicted probability of occurrence of cookie cutter shark bites on fish in a given set in the deep-set longline fishery by month if (A) fish count per set is held constant at the mean (53.5 fish set^{-1}) and fishing day set as the mode of days of operation (Day 292; i.e. night hours allowed to vary), (B) fish count per set is held constant at the mean (53.5 fish set^{-1}) and night hours are held constant at the mean (14.6 h; i.e. day-of-year of fishing allowed to vary), (C) night hours are held constant at the mean (14.6 h) and fishing day set as the mode of days of operation (Day 292; i.e. fish count allowed to vary). Blue shading indicates winter months (November–March)

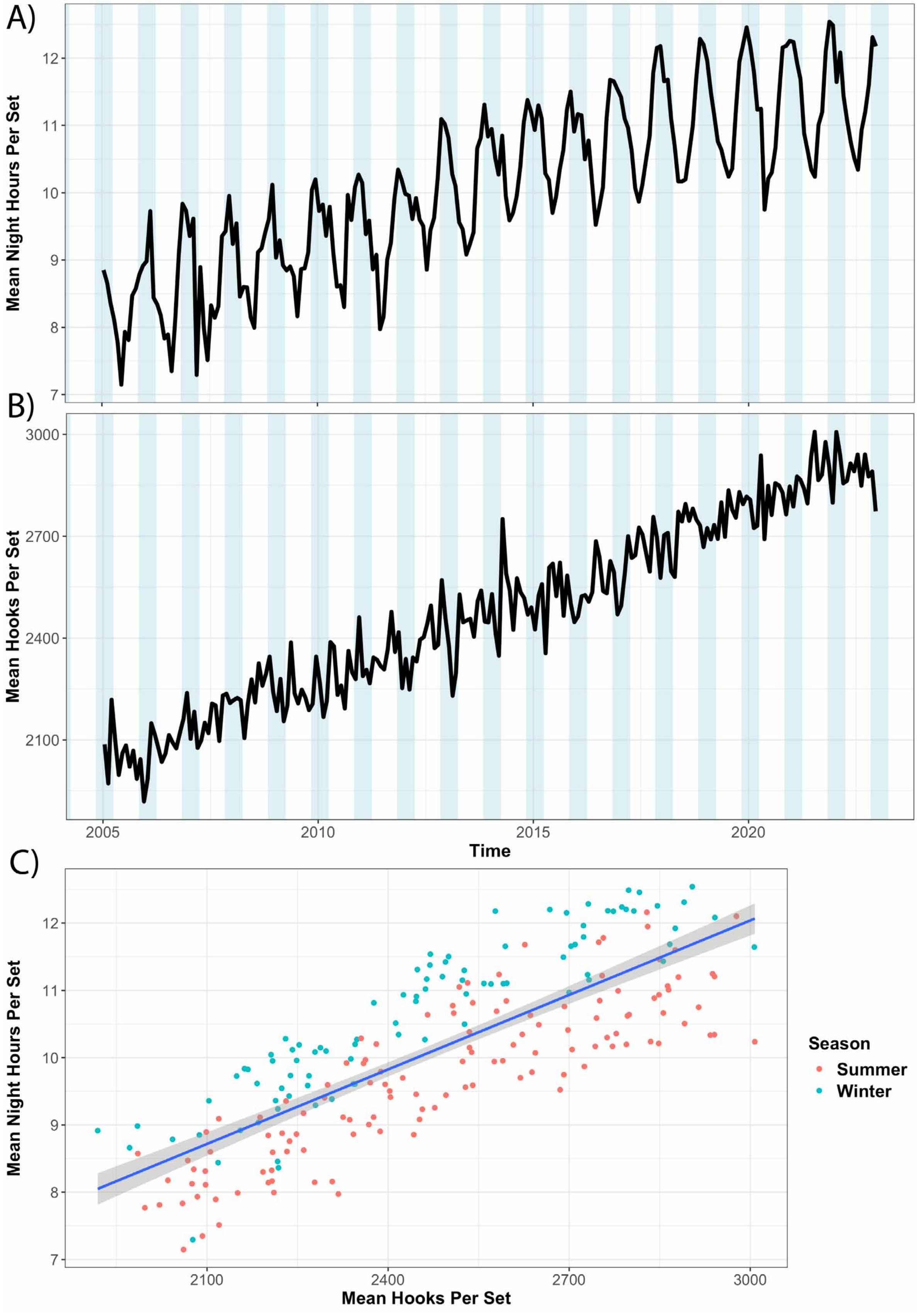

Fig. 8. From 2005–2022 for the Hawai'i deep-set longline fishery, (A) monthly mean night hours per set, (B) monthly mean number of hooks per set, and (C) the relationship between monthly mean hooks per set and monthly mean night hours per set. Points are colored according to season (red: summer; blue: winter; Pearson correlation coefficient = 0.88). Blue shading indicates winter months (November–March). In (C), the blue line represents linear model fit between mean hooks per set and mean night hours per set, and gray band the 95% confidence interval

these high latitudes in addition to true thermal preference at these temperatures for cookie cutter sharks (although note these are not strongly correlated throughout the data set; Fig. S1). The increased interactions in areas of moderate temperatures may be a product of their high productivity and large prey biomass. Cookie cutter sharks are known to not only eat chunks of large animals, but also directly consume mesopelagic micronekton (Carlisle et al. 2021). The boundaries of the subtropical gyre are known to have elevated biomasses of these prey items in waters that may remain warm enough for cookie cutter shark thermal habitat (Wetherall 1991, Brodeur et al. 1999).

Increased interactions in the small pocket of DSLL fishing at high temperatures and low latitudes complicate the relationship between bite probability and moderate sea surface temperatures. These areas, roughly ~5° N, are much warmer than other areas of high cookie cutter shark interactions. This area corresponds to the Intertropical Convergence Zone (ITCZ), an area where the trade winds from the Northern and Southern hemispheres meet, leading to enhanced cloud cover. It is plausible that the enhanced cloud cover of the region could dim lunar illumination, leading to relatively darker conditions that are prime for cookie cutter shark interactions with longline-caught fish. Indeed, cloud cover has been shown to modulate the vertical migration of mesopelagic organisms in other systems (Omand et al. 2021). Further assessment of how the ITCZ influences these interactions and vertically migrating species is warranted. However, there is a notable dip in the probability of cookie cutter shark bites around warm water outside of these few sets near the ITCZ. Decreased bite probability at temperatures >27°C was apparent in our results, as well as those of Nakano & Tabuchi (1990) and Walker-Milne et al. (2025). Collectively, this suggests that cookie cutter sharks may have an upper thermal limit in their distribution. However, occasional interactions with cookie cutter sharks may occur in warm surface temperatures during times of pronounced darkness.

4.2. Potential future of cookie cutter damage in the DSLL and SSLL

Trends and the probability of the future of cookie cutter shark interactions are likely to vary notably by fishery sector in the Hawaiʻi longline fleet. The SSLL fishery is capped in terms of time-of-day operations, and thus its ability to extend sets is limited by regulations imposed to mitigate seabird and turtle interactions. The only mechanism by which rates of cookie cutter shark interactions on a per set basis would increase is through changes in the timing of seasonal operations and catch composition. The fishery primarily operates in the fall and winter, with minimal operations occurring in the late spring and summer. Thus, fishing primarily occurs during the time of year with the highest probability of cookie cutter shark interactions. However, in the early years of the fishery, more fishing did occur in the summer months, when there was larger fleet involvement (McCracken 2018). This likely would have resulted in a lower interaction rate per set due to the shorter amount of darkness. The SSLL also primarily operates during the full moon, as this corresponds with the lowest likelihood of cookie cutter shark interactions. The fishery has become increasingly focused on the full moon for efficiency, with the mean proportion of sets conducted during the full moon (between the first and third quarter) increasing from ~55% in 2005–2007 to ~70% in 2020–2022 (Fig. S4), likely leading to a relative decrease in the interactions compensating for the slightly increased night hours. If fishing operations were to extend to larger windows again or if fishing becomes less targeted on the full moon, bites may increase, but this is generally unlikely. The DSLL does not typically target a specific lunar phase, with ~50% of sets occurring between the first and third quarter moon (what one would expect if fishing on the lunar cycle is random). Therefore, lunar phase is unlikely to have major implications for the future of this fishery.

For the DSLL, operational characteristics have much more of an opportunity to change moving forward, as this fishery is not constrained by the same time of day and light limitations as the SSLL. Hooks per set have increased nearly 50 hooks set^{-1} yr^{-1}, and operational times have increased ~10 min yr^{-1} set^{-1} to about 2900 hooks set^{-1} currently. Other fisheries, such as the Japanese longline fleet, started exceeding 3000 hooks set^{-1} in the 1990s, suggesting there remains an opportunity for growth (Tuck et al. 2003). It is worth noting that there may initially be a relatively small increase in the likelihood of bites from increased operation times moving forward. The mean set times from start to finish encompass more than 20 h, often occupying the entirety of a night. This suggests that extended soak times may initially lead to increased soak during the day, given that a full night is already being occupied.

Catch composition may play a role in the likelihood of cookie cutter shark bites on a set, given noted differences in bite probability by species (Papastamatiou et al. 2010). The SSLL focuses on a single species, with relatively consistent bycatch patterns in the wintertime during their highest effort. The primary catch, swordfish, is also a species that has been recorded to have the highest rates of cookie cutter bites of all species documented in the fish Honolulu auction (Papastamatiou et al. 2010). This high bite rate is likely linked to the diel vertical migration patterns of swordfish following those of cookie cutter sharks, resulting in high overlap throughout the diel cycle (Carlisle et al. 2021, Santos et al. 2024). The DSLL, however, tends to have more variable catch composition, with the relative portion of yellowfin to bigeye tuna shifting in space, in addition to highly variable catch of mesopelagic taxa (e.g. lancetfish *Alepisaurus ferox*, monchong *Taractichthys steindachneri*, and opah *Lampris* spp.) and epipelagic catch (e.g. mahimahi *Coryphaena hippurus*, ono/wahoo *Acanthocybium solandri*, aku/skipjack tuna *Katsuwonus pelamis*, and aʻu/blue marlin *Makaira nigricans*). Past work has indicated that cookie cutter shark bites are much more common on swordfish, opah, and bigeye tuna than on epipelagic species such as marlin, yellowfin tuna, and skipjack tuna (Papastamatiou et al. 2010).

Thus, changes in the relative composition of these taxa will lead to variability in the likelihood that fish on a given set will be bitten by a cookie cutter shark. Indeed, the spatial pattern of the relative proportion of vertically migrating bigeye tuna compared to yellowfin tuna on a given set indicates that the areas to the north and east, where cookie cutter bites are most prevalent, are also where bigeye dominate the relative tuna catch composition (Fig. S5). If the DSLL fishery increases its fishing effort in the north and east of the main Hawaiian Islands, the incidence of cookie cutter bites is likely to increase.

4.3. Future considerations

Our study was able to accurately replicate cookie cutter interactions on longline sets for both sectors of the Hawaiʻi longline fishery, but we did not specifically answer how total bites per set varied through time or how bites vary by hooked species (i.e. target vs. bycatch), leaving opportunity for future research on this topic. Future studies could look specifically into a subset of high-quality data (i.e. remove a substantial number of observations that lacked fish-level information) to identify patterns in the bite rates among target species. Auction data could also be analyzed to incorporate relative damage to individuals and compare this to past research (Papastamatiou et al. 2010). The Honolulu fish auction keeps records of the cookie cutter bites on individual fish sold, including those that have a high number of bites (≥4). This information could be linked back to trip number to identify environmental and operational conditions in scenarios where many sold fish from that trip are highly damaged. However, it is worth noting that the signal will need to be strong and, ideally, the trip will need to have sets closely collocated, as set-level information on bites is not available to pair with these data.

In addition to inquiry using existing data streams, future work could examine how other fisheries interact with cookie cutter sharks. Specifically, in Hawaiʻi, several small boats target bigeye and yellowfin tuna using ʻika shibiʻ and ʻpalu ahiʻ fishing, a form of handline fishing targeting tuna at depth (~50–150 m). Ika shibi fishing occurs at night, which may lead to cookie cutter shark interactions if patterns in this fishery are consistent with our observations from the DSLL and SSLL fisheries. Shortline fisheries targeting bigeye and swordfish near Hawaiʻi Island and Cross Seamount are also likely to interact with cookie cutter sharks due to the nature of the fishery having partial nighttime operations and longer soak times than handline fisheries. Collaborating with fishers across fishery sectors will be beneficial to better understand the timing of bites, species that are typically bitten, and whether interactions with cookie cutter sharks vary by fishery for reasons beyond the effort at night.

Finally, an important consideration for cookie cutter shark interactions is how shifting environmental conditions due to climate change may affect the distribution of cookie cutter sharks and, thus, interactions with target species. Our models do include a suite of environmental variables that could be used in climate change projections. However, more research is needed to better understand whether the associations identified in this work are truly tied to those environmental parameters or whether they are proxies for other factors, such as catch composition, night hours fished, or lunar phase. Once mechanistic environmental relationships are determined, a modeling effort comparing how target species distributions are likely to shift relative to cookie cutter sharks is warranted.

Data availability. Due to the sensitivity of the information on fishing locations, we cannot share raw data used for this study. Code is available at https://github.com/jsuca18/Cookie_Cutter_Damage.

Acknowledgements. We thank Eric Kingma of the Hawaiʻi Longline Association and Michael Goto of United Fishing

Agency for their interest and feedback on the results of our study. We thank Ryan Rykaczewski for providing comments on an earlier version of the manuscript. Funding was provided by the Pacific Islands Fisheries Science Center.

LITERATURE CITED

Abrahms B, Welch H, Brodie S, Jacox MG and others (2019) Dynamic ensemble models to predict distributions and anthropogenic risk exposure for highly mobile species. Divers Distrib 25:1182–1193

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43: 1223–1232

Amaya DJ, Alexander MA, Scott JD, Jacox MG (2023) An evaluation of high-resolution ocean reanalyses in the California current system. Prog Oceanogr 210:102951

Becker EA, Carretta JV, Forney KA, Barlow J and others (2020) Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. Ecol Evol 10:5759–5784

Benz GW, Bullard SA (2004) Metazoan parasites and associates of chondrichthyans with emphasis on taxa harmful to captive hosts. In: Smith M, Warmolts D, Thoney D, Hueter R (eds) The elasmobranch husbandry manual: captive care of sharks, rays, and their relatives. Ohio Biological Survey, Columbus, OH, p 325–416

Best PB, Photopoulou T (2016) Identifying the 'demon whale-biter': patterns of scarring on large whales attributed to a cookie-cutter shark *Isistius* sp. PLOS ONE 11: e0152643

Bograd SJ, Buil MP, Lorenzo ED, Castro CG and others (2015) Changes in source waters to the Southern California Bight. Deep Sea Res II 112:42–52

Brodeur R, McKinnell S, Nagasawa K, Pearcy W, Radchenko V, Takagi S (1999) Epipelagic nekton of the North Pacific subarctic and transition zones. Prog Oceanogr 43:365–397

Carlisle AB, Allan EA, Kim SL, Meyer L, Port J, Scherrer S, O'Sullivan J (2021) Integrating multiple chemical tracers to elucidate the diet and habitat of cookiecutter sharks. Sci Rep 11:11809

Chan HL (2023) How climate change and climate variability affected trip distance of a commercial fishery. PLOS Clim 2:e0000143

Chan HL, Pan M (2016) Spillover effects of environmental regulation for sea turtle protection in the Hawaii longline swordfish fishery. Mar Resour Econ 31:259–279

Chan HL, Kobayashi D, Suca J (2025) Hedonic price model of Hawaiʻi ʻAhi tuna (*Thunnus obesus* and *Thunnus albacares*) market: implications of climate change and shark depredation. PLOS Clim 4:e0000595

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Feunteun A, de Schrevel C, Verhaegen M, Chevallier D, Duchemin M, Ziani N, de Montgolfier B (2018) First evaluation of the cookie-cutter sharks (*Isistius* sp.) predation pattern on different cetacean species in Martinique. Environ Biol Fishes 101:749–759

Gilman E, Chaloupka M, Read A, Dalzell P, Holetschek J, Curtice C (2012) Hawaii longline tuna fishery temporal trends in standardized catch rates and length distributions and effects on pelagic and seamount ecosystems. Aquat Conserv 22:446–488

Gomez-Valdes J, Jeronimo G (2009) Upper mixed layer temperature and salinity variability in the tropical boundary of the California Current, 1997–2007. J Geophys Res Oceans 114:2008JC004793

Hazen EL, Abrahms B, Brodie S, Carroll G, Welch H, Bograd SJ (2021) Where did they not go? Considerations for generating pseudo-absences for telemetry-based habitat models. Mov Ecol 9:5

He X, Bigelow KA, Boggs CH (1997) Cluster analysis of longline sets and fishing strategies within the Hawaii-based fishery. Fish Res 31:147–158

Honebrink R, Buch R, Galpin P, Burgess GH (2011) First documented attack on a live human by a cookiecutter shark (Squaliformes, Dalatiidae: *Isistius* sp.). Pac Sci 65:365–374

Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. Endang Species Res 5: 267–278

Howell EA, Hoover A, Benson SR, Bailey H, Polovina JJ, Seminoff JA, Dutton PH (2015) Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. Fish Oceanogr 24:57–68

Huang J, Ling CX (2005) Using AUC and accuracy in evaluating learning algorithms. IEEE Trans Knowl Data Eng 17:299–310

Ito RY, Childers J (2014) US swordfish fisheries in the North Pacific Ocean. ISC/14/SWO-WG/06; PIFSC Work Pap WP-14-001. Pacific Islands Fisheries Science Center (PIFSC), National Marine Fisheries Service (NMFS)

Jahn AE, Haedrich RL (1988) Notes on the pelagic squaloid shark *Isistius brasiliensis*. Biol Oceanogr 5:297–309

Jean-Michel L, Eric G, Romain BB, Gilles G and others (2021) The Copernicus global 1/12° oceanic and sea ice GLORYS12 reanalysis. Front Earth Sci 9:698876

Lazaridis E (2022) lunar: calculate lunar phase & distance, seasons and related environmental factors. R package version 0.2-1. https://CRAN.R-project.org/web/packages/lunar/index.html

McCracken ML (2018) Hawaii permitted shallow-set longline fishery estimated anticipated take level for Endangered Species Act listed species. PIFSC Data Tech Rep No. DR-18-014

Menezes R, Marinho JPD, De Mesquita GC, Da Silva GB (2022) Cookiecutter shark (*Isistius* spp.) bite patterns on pelagic fishes in aggregated schools in the western equatorial Atlantic Ocean. Environ Biol Fishes 105:519–530

Minaglia S, Liegl M (2024) Moonless night sky increases *Isistius* species (cookiecutter shark) and live human contact. PLOS ONE 19:e0291852

Nakano H, Tabuchi M (1990) Occurrence of the cookiecutter shark *Isistius brasiliensis* in surface waters of the North Pacific Ocean. Jpn J Ichthyol 37:60–63

Omand MM, Steinberg DK, Stamieszkin K (2021) Cloud shadows drive vertical migrations of deep-dwelling marine life. Proc Natl Acad Sci USA 118:e2022977118

Papastamatiou YP, Wetherbee BM, O'Sullivan J, Goodmanlowe GD, Lowe CG (2010) Foraging ecology of cookiecutter sharks (*Isistius brasiliensis*) on pelagic fishes in Hawaii, inferred from prey bite wounds. Environ Biol Fishes 88:361–368

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ren AS, Rudnick DL (2021) Temperature and salinity extremes from 2014–2019 in the California Current System and its source waters. Commun Earth Environ 2:62
Ridgeway G, McCaffrey DF, Morral AR, Cefalu M, Burgette LF, Pane JD, Griffin BA (2022) Toolkit for weighting and analysis of nonequivalent groups: a tutorial for the R TWANG package. Rand Corporation, Santa Monica, CA
Santos L, Veloso JV, Santos TB, Bezerra NPA, Oliveira P, Hazin FHV (2024) An equatorial mid-Atlantic Ocean archipelago as nursery area for the cookiecutter shark: investigating foraging strategies of neonates through bite mark inferences. J Fish Biol 104:1290–1298
Scales KL, Hazen EL, Jacox MG, Edwards CA, Boustany AM, Oliver MJ, Bograd SJ (2017) Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography 40:210–220
Sculley ML, Brodziak J (2020) Quantifying the distribution of swordfish (*Xiphias gladius*) density in the Hawaii-based longline fishery. Fish Res 230:105638
Stehmann MFW, Kukuev EI (2015) Two southeastern Atlantic records of the rare largetooth cookie-cutter shark, *Isistius plutodus* (Selachii, Squaliformes, Dalatiidae). Cybium 39:73–77
Thieurmel B, Elmarhraoui A (2019) suncalc: compute sun position, sunlight phases, moon position and lunar phase. R package version 0.5. https://CRAN.R-project.org/web/packages/suncalc/index.html
Tuck GN, Polacheck T, Bulman CM (2003) Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. Biol Conserv 114: 1–27
Walker-Milne NL, Papastamatiou YP, Mahaffy SD, Baird RW (2025) Dynamics of foraging interactions between cookiecutter sharks (*Isistius* spp.) and short-finned pilot whales (*Globicephala macrorhynchus*) in Hawaiʻi. Mar Biol 172:63
Welch H, Savoca MS, Brodie S, Jacox MG and others (2023) Impacts of marine heatwaves on top predator distributions are variable but predictable. Nat Commun 14:5188
Wetherall JA (ed) (1991) Biology, oceanography, and fisheries of the North Pacific transition zone and subarctic frontal zone. NOAA Tech Rep NMFS 105
Widder EA (1998) A predatory use of counterillumination by the squaloid shark, *Isistius brasiliensis*. Environ Biol Fish 53:267–273
Woodworth-Jefcoats PA, Polovina JJ, Drazen JC (2018) Synergy among oceanographic variability, fishery expansion, and longline catch composition in the central North Pacific Ocean. Fish Bull 116:228–239
WPRFMC (Western Pacific Regional Fishery Management Council) (2025) Annual SAFE Report for the Pacific Pelagic Fisheries Fishery Ecosystem Plan 2024. WPRFMC, Honolulu

Editorial responsibility: Reniel Cabral, Townsville, Queensland, Australia
Reviewed by: Y. P. Papastamatiou and 2 anonymous referees
Submitted: February 14, 2025; Accepted: August 11, 2025
Proofs received from author(s): November 27, 2025