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**Hawaii Pelagic Longline Demonstrates the Need to Consider Multispecies Impacts
In Bluewater Tine-Area Closures**

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Hawai'i's pelagic longline fishery demonstrates the need to consider multispecies impacts in bluewater time-area closures

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Abstract

Cap-based time-area closures can reduce the incidental capture of specific non-target species in fisheries by temporarily closing fishing areas when bycatch exceeds a threshold. The displacement of fishing effort can result in bycatch tradeoffs by increasing interactions with other species or even negate the intended effect of the closure. Here, we assessed the change in bycatch risk for a suite of species of concern resulting from the Southern Exclusion Zone (SEZ), a 343 796 km² bycatch cap-based time-area closure designed to protect false killer whales from mortality and serious injury in the Hawai'i deep-set longline fishery. The SEZ was enacted twice between 2018 and 2020. We found that during the SEZ closures, fishing effort increased along the eastern and southern SEZ border, where species like oceanic whitetip sharks, giant manta rays, and olive ridley sea turtles showed the most concentrated risk, indicating high susceptibility to overlap with displaced effort. Scalloped hammerhead sharks and green and leatherback sea turtles faced moderate risk near heavy fishing, while loggerhead turtles and false killer whales showed diffuse risk. These results highlight that while cap-based closures aim to protect a single species, effective Ecosystem-Based Fisheries Management should consider the entire species portfolio in conservation strategies.

Keywords: bycatch mitigation; fisheries management; marine protected area; protected species

Introduction

A common method to reduce bycatch of long-lived species in commercial fisheries is to temporarily, partially, or completely halt fishing operations (Murray et al. 2000). Static marine protected areas (MPAs) are typically long-term, e.g. permanent or over multiple years, no-take or limited-take zones established in specific locations. In coastal, shallow-water zones static MPAs are a common strategy to protect critical habitats and species (Friedlander et al. 2019, Gilman et al. 2019a). Large-scale static MPAs are increasingly being adopted as management solutions in pelagic environments, yet their effectiveness in achieving management goals appears to be context-dependent and variable (White et al. 2010). Static MPAs can be less effective for managing highly mobile species that respond to dynamic ocean conditions, as these species often move in and out of protected areas, reducing the effectiveness of spatial protection (Hyrenbach et al. 2000). Dynamic ocean management (DOM) is a more tailored approach for spatially managing highly mobile species by using near-real-time or real-time data (e.g. oceanography, biology, and socio-economics) to develop management strategies that optimize both ocean conservation and fishery productivity (Hobday et al. 2014, Maxwell et al. 2015). Nascent DOM tools are being incorporated into current ocean management, as a response to legislative or management actions that threaten to diminish or hinder ocean use (Lewison et al. 2015) and demonstrate potential in curtailing bycatch or overharvesting (Maxwell et al. 2015, Pons et al. 2022).

While static MPAs and DOM differ fundamentally in their execution, cap-based closures are an example of a hybrid approach. These strategies, triggered by real-time fishing interactions exceeding a pre-set cap, enact either temporary complete fishery closures or partial closures in the form of static no-take area(s). These bycatch caps have been a common management tool for decades (O'Keefe et al. 2014), particularly for protected species. For example, in California, three confirmed humpback whale, *Megaptera novaeangliae*, entanglements in commercial Dungeness crab, *Metacarcinus magister*, fishing gear leads to a statewide closure of the fishery (CDFW 2020, Free et al. 2023). Prior to 2019, loggerhead sea turtle interactions surpassing the cap set for the Hawai'i shallow-set fishery would trigger a complete closure until the start of the next calendar year (WPRFMC 2024). However, cap-based closures are often structured to minimize interactions for a single species, and unlike the dynamic closures, are not designed to respond to changing ocean conditions. Further, cap-based closures can either curtail fishing effort through cessation of fishing activity or require fishers to redistribute to other fishing grounds. This redistribution may benefit species that co-occur in the closure area or timeframe but also increase the risk of interacting with species outside the closure zone (O'Keefe et al. 2014).

An example of implemented cap-based partial area closures is the Southern Exclusion Zone (SEZ) for the Hawai'i deep-set longline (DSL) fishery. Part of the exclusive economic zone (EEZ) fishing grounds, closes to DSL fishing if a certain

number of false killer whales, *Pseudorca crassidens*, experience mortality or serious injury (MSI) within a year, within the EEZ. The SEZ reopens the following year, or later if more false killer whale MSI occur in the EEZ that year, once the reopening criteria defined in the Take Reduction Plan implementing regulations are met (50 CFR 229.37). The SEZ was designed to mitigate bycatch of both the pelagic and Hawaiian insular false killer whale stocks (75 FR 2853, 19 January 2010; 50 CFR 229.37). It was initially established because the MSI exceeded the Potential Biological Removal level for the pelagic false killer whale stock in 2009 (Carretta *et al.* 2009). This concern was exacerbated by the recognition that the Hawai'i (HI) insular stock, which has overlapping geographic ranges with the pelagic stock and is generally indistinguishable without genetic testing, had fewer than 200 individuals (Oleson *et al.* 2010) and was listed soon after as endangered under the Endangered Species Act (77 FR 70915). Under the Marine Mammal Protection Act (MMPA), a Take Reduction Team was established to reduce such interactions (75 FR 2853, 19 January 2010). The team developed a Take Reduction Plan that was drafted in November 2012 (77 FR 71260, 29 November 2012) and effective 31 December 2012. Take reduction measures included a permanent 282 796 km² LL prohibited area around the Main Hawaiian Islands aimed at minimizing interactions with the HI insular stock, gear requirements, handling and release procedure compliance, and a fleet-wide bycatch cap that would enforce the SEZ. The SEZ was closed twice since its enactment: 24 July–31 December 2018, and 22 February 2019–25 August 2020.

The SEZ is significantly sized at 343 796 km² and makes up 48% of the fishable EEZ around Hawai'i and is a focal area of DSLL fishing effort. Though intended for a single species, the closure of such a large and economically significant area temporarily displaces fishers from the region when the false killer whale cap is triggered. Redistribution of fishing pressure following the SEZ closure, should, at minimum, concentrate fishing effort in the remaining fishing grounds and could increase the bycatch of other species not targeted by the closure if their density in those spaces is higher than in the closed area (Lewison *et al.* 2004, 2014, Gilman *et al.* 2019b). At least seven other protected species that are commonly caught as bycatch co-occur with false killer whales in this region. Take of protected species in the Hawai'i DSLL fishery are managed by a variety of cap-based closures and incidental take statements under the Endangered Species Act (ESA). It is possible that triggering a temporary static closure, such as the SEZ, could inadvertently increase or decrease the risk of meeting or exceeding the allowed take set by other regulations.

The broader impacts of static closures on the bycatch rates of multiple species remain sparsely understood (Lewison *et al.* 2015) but limited examples indicate there are likely considerable multispecies tradeoffs. In the North Atlantic swordfish, *Xiphias gladius*, longline fishery, a three-year area closure aimed at reducing sea turtle bycatch incidentally increased bycatch rates for ten shark species due to fishing effort displacement (Baum *et al.* 2003). Similar outcomes have been observed or simulated in various fisheries across ocean basins (Abbott and Haynie 2012, Gilman *et al.* 2019b, Pons *et al.* 2022). As fisheries management transitions to Ecosystem-Based Fishery Management, decision tradeoffs and their consequences for multiple species should be evaluated. These multi-species tradeoffs complicate both protected species management and

fisheries management and are necessary to assess for informed regulatory decision making (Dunn *et al.* 2011, Grüss *et al.* 2014, Townsend *et al.* 2019).

The potential to displace effort and increase bycatch risk for other species is particularly pertinent for rarely encountered, highly threatened protected species. For these species, relatively few additional fisheries interactions can trigger a suite of management and conservation actions as well as further jeopardize the population (Brownell *et al.* 2019, Dulvy *et al.* 2021). When such fishery interactions do occur, stakes can be higher and more effective, rapid management responses may be warranted. Displacement of fishing effort resulting from area closures could negate their effectiveness and long-term utility of these responsive cap-based static area management strategies. Recent global initiatives aim to protect 30% of the world's land and oceans by 2030, in part through the establishment of oceanic MPAs (Hilborn *et al.* 2022, Blanluet *et al.* 2024). As part of this effort, large-scale static MPAs are increasingly implemented as management solutions in pelagic environments. A comprehensive multi-taxa approach is needed to evaluate the effectiveness of this management strategy, and current cap-based closures provide a window into how oceanic MPAs may operate. Here, we used an Ensemble Random Forest (ERF) modeling approach to evaluate the consequences of the SEZ on the bycatch rates of eight protected megafauna species, including three elasmobranch species, four sea turtle species and a marine mammal. The ERF framework is well-established and is particularly valuable for predicting the presence of rare species (Siders *et al.* 2020). Our models use 17 years of observer data from the DSLL to (i) predict where species interactions are the most probable, (ii) assess the impact of the SEZ closures in 2018 and 2019–2020 on the redistribution of fishing pressure in the Hawai'i DSLL fishery, and (iii) examine the consequences of the SEZ closure on the risk for fishery interactions with a suite of protected species.

Methods

Fishery

The Hawai'i DSLL fishery (~150 participating vessels) operates year-round and primarily targets tuna (*Thunnus* spp.). The fishery operates inside and outside the US EEZ around the Hawaiian Islands. The National Oceanic and Atmospheric Administration (NOAA), until recently, maintained observer coverage around 20% since 2001 to monitor encounters with marine megafauna including the false killer whale. Three stocks of false killer whale occur in this region, including the endangered HI insular stock around the Main Hawaiian Islands, an insular stock associated with the northwestern Hawaiian Islands, and a pelagic stock that moves across a broader area, both within and outside the EEZ (Bradford *et al.* 2020, Oleson *et al.* 2023). The Take Reduction Plan aims to further reduce longline interactions with the HI insular stock and pelagic stock (77 FR 71260). One major challenge for fishing vessels lies in the overlap and therefore differentiation between these stocks. The HI insular stock occurs nearshore and within 140 km from the shoreline of the Main Hawaiian Islands, whereas the pelagic stock inhabits waters 40 km and further out from the shore and beyond the EEZ (McCracken 2010). An existing permanent longline prohibited area that borders the Main Hawaiian Islands seeks to substantially reduce the impact of longline fisheries on the HI insular stock

(77 FR 71260). We therefore assumed that most of the false killer whale interactions observed involve the pelagic stock, and any subsequent references to false killer whales are likely referring to the pelagic stock.

Observed false killer whale MSI in the US EEZ on DSLL trips that meet the established trigger number for a given fishing year results in the closure of the SEZ to DSLL fishing (77 FR 71260). The first closure of the SEZ occurred on 24 July 2018 when two false killer whale interactions resulting in MSI occurred within the EEZ (83 FR 33848) and was closed for the remainder of the year. On 22 February 2019, the SEZ reached the trigger of two false killer whale MSI and was closed (84 FR 5356) until 25 August 2020 when a reopening criterion defined in the Take Reduction Plan regulations was met (85 FR 50959; 50 CFR 229.37).

Protected species

The species we included in our analyses are protected at varying levels under the MMPA and/or ESA and are rarely encountered in the DSLL. These species include: pelagic false killer whale, oceanic whitetip shark (*Carcharhinus longimanus*), scalloped hammerhead shark (*Sphyrna lewini*), giant manta ray (*Mobula birostris*), olive ridley sea turtle (*Lepidochelys olivacea*), green sea turtle (*Chelonia mydas*), leatherback sea turtle (*Dermochelys coriacea*), and loggerhead sea turtle (*Caretta caretta*).

Fishing data

We used set-level data from the 2005–2022 NOAA Pacific Islands Region Observer Program (PIROP; Pacific Islands Regional Office) to develop interaction distribution models for the protected species mentioned above. Until recently, the DSLL fishery targeted ~20% observer coverage, by which an observer is assigned to a vessel using a two-stage sampling process (McCracken 2019). The observers record variables related to fishing operations including the coordinates for each set, catch, and bycatch (McCracken 2019).

To evaluate fleet-wide fishing effort and bycatch risk, we used data from the Hawai'i logbook program from 2016–2022 (Pacific Islands Fisheries Science Center). The logbook data was restricted to 26 August 2016 to 31 December 2022 to assess SEZ closure impacts after the expansion of the Papahānaumokuākea Marine National Monument (PMNM) on 26 August 2016. The total fishing effort was estimated from the logbook data by summing the number of commercial sets that fished within each grid during the open and closed SEZ periods. The difference in fishing effort between periods of the open and closed SEZ was determined by estimating the relative fishing effort within each year/status for each set, averaging across the open or closed timeframes within 100 km² hexagonal grid cells, and subsequently calculating the difference between the two. To ensure the confidentiality of fishing locations, hexagonal grids with <3 vessels were not presented in the plots, but these data were included in the analyses. Risk was assessed using the ERF modeling framework described below.

For analysis and prediction, we extracted 25 environmental variables associated with each fishing set for both the observer and logbook data according to Siders et al. (2020) and Long et al. (2024) (Table S1). These variables occur over different temporal and spatial scales including static (e.g. bathymetry and distance to nearest seamount), temporally dynamic (e.g. lunar

phase), or spatiotemporally dynamic (e.g. sea surface temperature, ocean currents, wind speed, and chlorophyll-a). In cases of highly correlated covariates ($r > 0.7$), one environmental covariate was selected. Spatial proxies (e.g. coordinates, Euclidean distance fields) were not included as predictors in the ERF models. All analyses were conducted in R (version 4.2.1).

ERF bycatch estimation

The ERF modeling framework has been thoroughly documented (see Siders et al. 2020, Text S1 for further details). The full dataset implemented in the ERF here consisted of the bycatch data and the environmental variables for 65 108 observed DSLL sets from 2005 to 2022. Presence and absence data sets for each species of interest (false killer whale, oceanic whitetip shark, scalloped hammerhead shark, giant manta ray, loggerhead sea turtle, leatherback sea turtle, olive ridley sea turtle, and green sea turtle) were constructed. The ERF models identify species-specific factors influencing bycatch and could be used to predict bycatch and its distribution in the DSLL logbook data. In the ERF method, each species dataset was repeatedly sampled with an equal number of presences and absences and partitioned into multiple 90% training and 10% testing subsets. The training sets separately trained 200 random forests with 1000 trees per forest and 5 covariates at each node. The resulting random forest predictions were then assembled into an ensemble model. Model performance metrics [i.e. area under the curve (AUC), root mean squared error (RMSE), and true skill statistic (TSS)] were evaluated for the training and internal test datasets for each species. The probability of presence maps were created for each species averaging the ERF model output across a hexagonal grid (100 km² cell size). To ensure the confidentiality of fishing locations, hexagonal grids with <3 vessels were removed from these maps.

Interaction risk

The trained ERF models were used to predict which unobserved sets (logbook data) had interactions with each species. To ensure that unobserved sets maintain a similar spatial structure to observed sets, we assessed the nearest-neighbor distances using the k -fold nearest neighbor distance matching-based spatial cross-validation (k -fold NNDM LOOCV) (Milà et al. 2022, Linnenbrink et al. 2024) (Fig. S1). To account for variability in the ERF predictions, bootstrapping was performed ($N = 10$), generating resampled predictions for the test dataset. The mean prediction from these bootstraps was used to ensure robust estimates, which were then aggregated to the hexagonal grid by SEZ status and year. To reduce the prediction grid for the models and to facilitate the preservation of confidential information, effort (in sets) was assigned to a grid of 100 km² hexagonal cells based on the centroid of the four coordinates associated with the beginning and end of each longline set and haul. These aggregated ERF-predicted probabilities in each cell, p_i , do not account for prevalence (Manel et al. 2001, Elith et al. 2011, Fukuda and Da Baets 2016), and thus were rescaled to approximate the true probability of interaction. For each year, we accounted for prevalence by multiplying the aggregated probabilities by the ratio of the total estimated interactions reported in the 2023 Pelagic SAFE Report during the analysis period of 26 August 2016 to 31 December 2022 (B_y) (WPRFMC 2024, Table S2) to the sum total of the probabilities in that year. We then effort-weighted these re-scaled probabilities to account for the relative effort

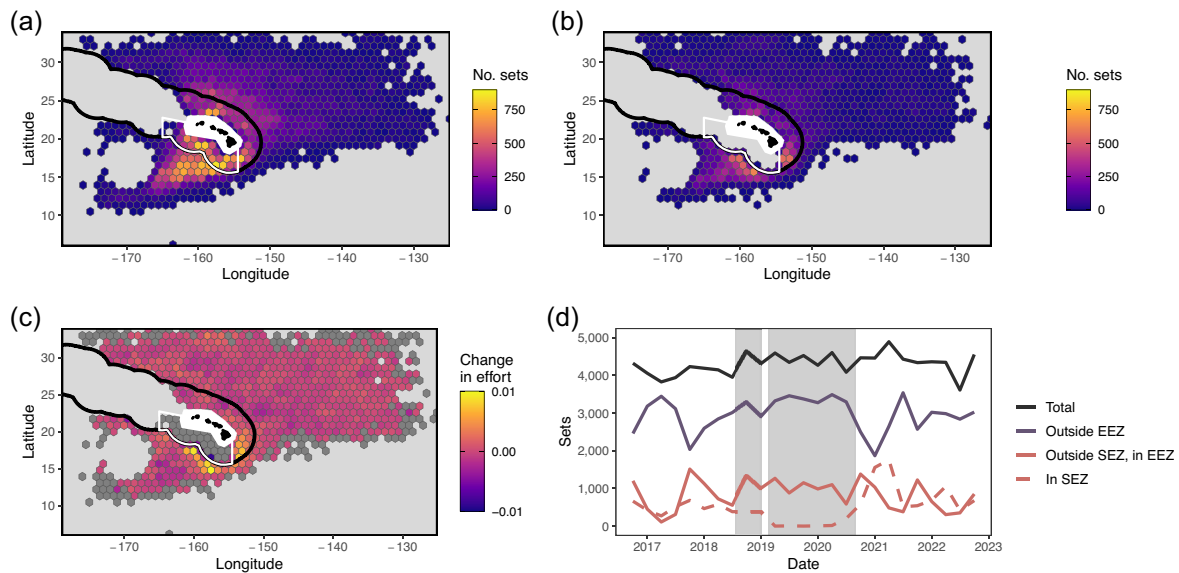


Figure 1. Deep-set longline fishing effort in the central north Pacific Ocean. (a) Fishing effort (by number of sets) when the SEZ is open from 2016 to 2022, (b) fishing effort (by number of sets) when the SEZ is closed in 2018, 2019, and 2020, (c) normalized change in fishing effort between open and closed SEZ. Warm colors indicate (a–b) more fishing effort and (c) a relative increase in effort. (d) Number of Hawai'i-based longline sets by quarter between 1 October 2016–1 October 2022. The gray rectangles indicate the closure of the SEZ (24 July–31 December 2018 and 22 February 2019–25 August 2020). For (a)–(c), the Hawaiian EEZ is outlined in black, SEZ is outlined in white, and longline prohibited area is the solid white filled polygon. Data is from the Hawai'i logbook program (Pacific Islands Fisheries Science Center).

with a given SEZ status block:

$$p_{i,t}^{wt} = p_{i,t} \times \frac{B_y}{\sum_{i=1}^N p_i} \times \frac{E_{i,t}}{\max(E_t)},$$

where $E_{i,t}$ is the total number of sets per cell and scaled relative to the maximum effort in a given SEZ status and year time block. To assess the correlation of bycatch risk between species, the correlation of weekly effort-weighted ERF (by sets) was calculated between each species. The distance of each cell from the SEZ boundary was calculated by taking the Euclidean distance from the centroid of each hexagonal grid cell to the SEZ boundary.

Results

Fishing effort in the Hawai'i longline fishery

Between 26 August 2016 and 12 December 2022, the SEZ was open for 1557 days and a total of 91 086 sets were logged by the Hawai'i DSLL fishery, with the primary fishing effort (no. sets) focused in the SEZ or directly southwest of the SEZ (Fig. 1a). When the SEZ was open, up to 856 sets within a 100 km² hexagonal grid were deployed in the SEZ. The SEZ was closed for a total of 743 days and during that time 41 346 sets were logged. Up to 626 sets within one 100 km² hexagonal grid were deployed outside the SEZ (Fig. 1b). Fishing effort increased on the eastern and southern edges of the SEZ border and slightly north of the Main Hawaiian Islands and remained mostly neutral around the remaining open areas (Fig. 1c).

The total fishing effort (no. sets) in the Hawai'i DSLL fleet increased from 2016 to 2022 (Fig. 1d). Effort tends to peak in the EEZ in the fourth quarter (1 October–31 December), while effort tends to increase outside the EEZ during the second (1 April–30 June) and third (1 July–30 September) quarters. Throughout the SEZ closure, total effort remained relatively high outside the EEZ for 10 consecutive quarters and

deviated from the typical quarterly trend (Fig. 1d). Following the reopening of the SEZ in late 2020, effort increased particularly within the SEZ. During the first quarter of 2021, the SEZ experienced 1761 sets compared to only 484 sets outside the SEZ but within the EEZ (Fig. 1d). At this point, nearly half of the total sets (2245 out of 4894) occurred within the EEZ (Fig. 1d).

Bycatch summary

Interactions with all protected species were rare (interaction rate per set = 0.08–0.0002; Table 1). During observed DSLL sets, oceanic whitetip sharks are most frequently encountered at over an order of magnitude higher than other species, with a total of 5224 interactions over the 18 years in the 65 108 observed sets (Table 1). The available presence data for olive ridley sea turtles (199 interactions) and false killer whales (114 interactions) were relatively similar (Table 1). Meanwhile, there were <50 interactions with giant manta rays or leatherback sea turtles, and fewer than 25 with scalloped hammerhead sharks, green sea turtles, or loggerhead sea turtles out of the 65 108 observed longline sets (Table 1).

ERF model

The models performed with varying success. Threshold-free performance metrics for the various protected species' ERF models demonstrate good model performance. The ensemble AUC was high across all species (0.99–1) (Table 1; Fig. S2). Test performance AUC was greatest for oceanic whitetip sharks (0.84) and giant manta rays (0.80) and lowest for false killer whales (0.53). The test RMSE performed best for the giant manta rays (0.34) and worst for false killer whales and green sea turtles (0.40) (Table 1). Similarly, the test TSS performed best for giant manta rays (0.60) and worst for false killer whales (0.21) (Table 1).

Table 1. Ensemble random forest performance metrics for each protected species.

Species	Ensemble			Test			Interactions	
	AUC	RMSE	TSS	AUC	RMSE	TSS	Interaction rate	Total interactions
Oceanic whitetip shark	1.00	0.33	0.95	0.84	0.37	0.50	.0802	5 224
Olive ridley sea turtle	0.99	0.38	0.95	0.70	0.38	0.38	.0031	199
False killer whale	1.00	0.40	1.00	0.53	0.40	0.21	.0018	114
Giant manta ray	1.00	0.34	0.97	0.80	0.34	0.60	.0007	46
Leatherback sea turtle	1.00	0.39	0.98	0.68	0.39	0.47	.0006	39
Scalloped hammerhead shark	1.00	0.39	0.99	0.67	0.39	0.49	.0004	24
Green sea turtle	1.00	0.40	1.00	0.59	0.40	0.40	.0004	23
Loggerhead sea turtle	1.00	0.39	1.00	0.66	0.39	0.53	.0002	16

Model performance metrics ("Ensemble") measured on the training (observer) dataset and internal performance ("Test") for threshold-free test sets. Metrics include AUC, RMSE, and TSS. The interaction rate indicates how often encounters occurred with each species over the 17 years across the observer data, and the total interactions is the total number of interactions with each species across the 65 108 observed sets.

The most important environmental covariates in predicting species presence often overlapped among species. These covariates included chlorophyll *a* concentration, current conditions (i.e. vorticity or direction), sea surface temperature, and eddy kinetic energy (Fig. S3). The influence of these covariates on the probability of presence for each species varied in both rank and effect (Figs S3–S11). Environmental covariates played a major role in predicting oceanic whitetip shark presence, with all environmental covariates with a mean decrease accuracy >5% (Fig. S3). The other species were also often associated with approximately 5 environmental covariates with a mean decrease accuracy >5%, except for loggerhead sea turtles, which had no important environmental covariates >5% (Fig. S3).

Spatial predictions for protected species

In part, based on differences of importance in environmental covariates and their associations, the ERF predictions resulted in different areas of high probability of presence for each species. Oceanic whitetip sharks, giant manta rays, and olive ridley turtles showed high presence probabilities concentrated south of the Main Hawaiian Islands, with peak concentrations southwest near 5°N 165°W (Fig. 2a, c–d). Similarly, presence probabilities for scalloped hammerhead sharks, and green, and leatherback sea turtles were elevated southwest of the Main Hawaiian Islands, though dispersed across a wider latitudinal band from 5 to 15°N (Fig. 2b, e–f). Loggerhead sea turtles and false killer whale presence probabilities were spatially diffuse, showing no distinct hotspots around the islands (Fig. 2g–h).

Fishery interaction risk during SEZ closures

For all eight species, interaction risk was more widespread when the SEZ was open but became concentrated inside and along the SEZ border when it was closed (Figs 3, 4). During SEZ closures, risk clustered south (16°N 158°W) and east (17°N 153°W) of the SEZ (Fig. 3b, d, f, h, j, l, n, and p). Most species experienced their highest weekly interaction rates during the SEZ closures, ranging from 0.13 (13 per 100 sets) for oceanic whitetip sharks (Figs 3b and 4a) to 0.00004 (4 per 100 000 sets) for scalloped hammerhead sharks (Figs 3d and 4b). The weekly interaction rates for other species during the SEZ closures included 0.00046 for giant manta rays (Figs 3f and 4c), 0.0061 for olive ridley

sea turtles (Figs 3h and 4d), 0.00059 for green sea turtles (Figs 3j and 4e), 0.00089 for leatherback sea turtles (Figs 3l and 4f), and 0.0015 for false killer whales (Figs 3p and 4h). In contrast, loggerhead sea turtle risk was slightly higher when the SEZ was open (0.00037) than closed (0.00032), with hotspots within the SEZ (19°N 159°W) and north of the Main Hawaiian Islands (23°N 158°W) (Fig. 3m–n and 4g).

Interaction risk was higher in both relative magnitude and spatial distribution when the SEZ was open compared to closed for scalloped hammerhead sharks, loggerhead sea turtles, and false killer whales (Fig. 4b, g–h), but lower for oceanic whitetip sharks, giant manta rays, and olive ridley sea turtles (Fig. 4a, c–d). Species correlations may indicate shared risk (Table S3). Oceanic whitetip sharks, hammerhead sharks, manta rays, olive ridley sea turtles, and leatherback sea turtles demonstrate similar spatial risk (correlations ranging from 0.71 to 0.86), likely experiencing concentrated effort near the SEZ (Table S3). False killer whales show a moderately high correlation with most species (strongest correlation with green sea turtles, 0.85). Loggerhead sea turtles show distinct, low correlations with most species (0.1–0.47 with all but green sea turtles, 0.75) (Table S3).

The block assessment for oceanic whitetip sharks demonstrates the interannual variability in interaction risk during the open and closed SEZ (Fig. 5a), with similar patterns in other time blocks and for other protected species (Figs S14–S21). In 24 July–31 December 2017, weekly interaction rate with oceanic whitetip sharks was 0.164 (16.4 per 100 sets) within the SEZ (20°N 163°W) (Fig. 5a). During the 2018 SEZ closure, this risk increased to 0.169 north of the Main Hawaiian Islands (21°N 154°W) and during the 2019 closure, increased to 0.202 in a concentrated area south of the Main Hawaiian Islands (15°N 162°W). Interaction risk remained high but moved within and around the SEZ, to 0.207 in 2020, 0.198 in 2021, and 0.192 in 2022 (Fig. 5a). The eight-month block assessed for interaction risk with olive ridley sea turtles similarly demonstrates the interannual variability in interaction risk when the SEZ was open and closed (Fig. 5b). In the latter part of the second SEZ closure (1 January–25 August 2020), weekly interaction rates were greatest directly east and southwest of the SEZ border, reaching 0.0085 (8.5 per 1 000 sets) at 15°N 158°W (Fig. 5b). When the SEZ reopened, weekly interaction rates were reduced to a maximum of 0.0065 (2021) and more diffused in 2022, with a maxi-

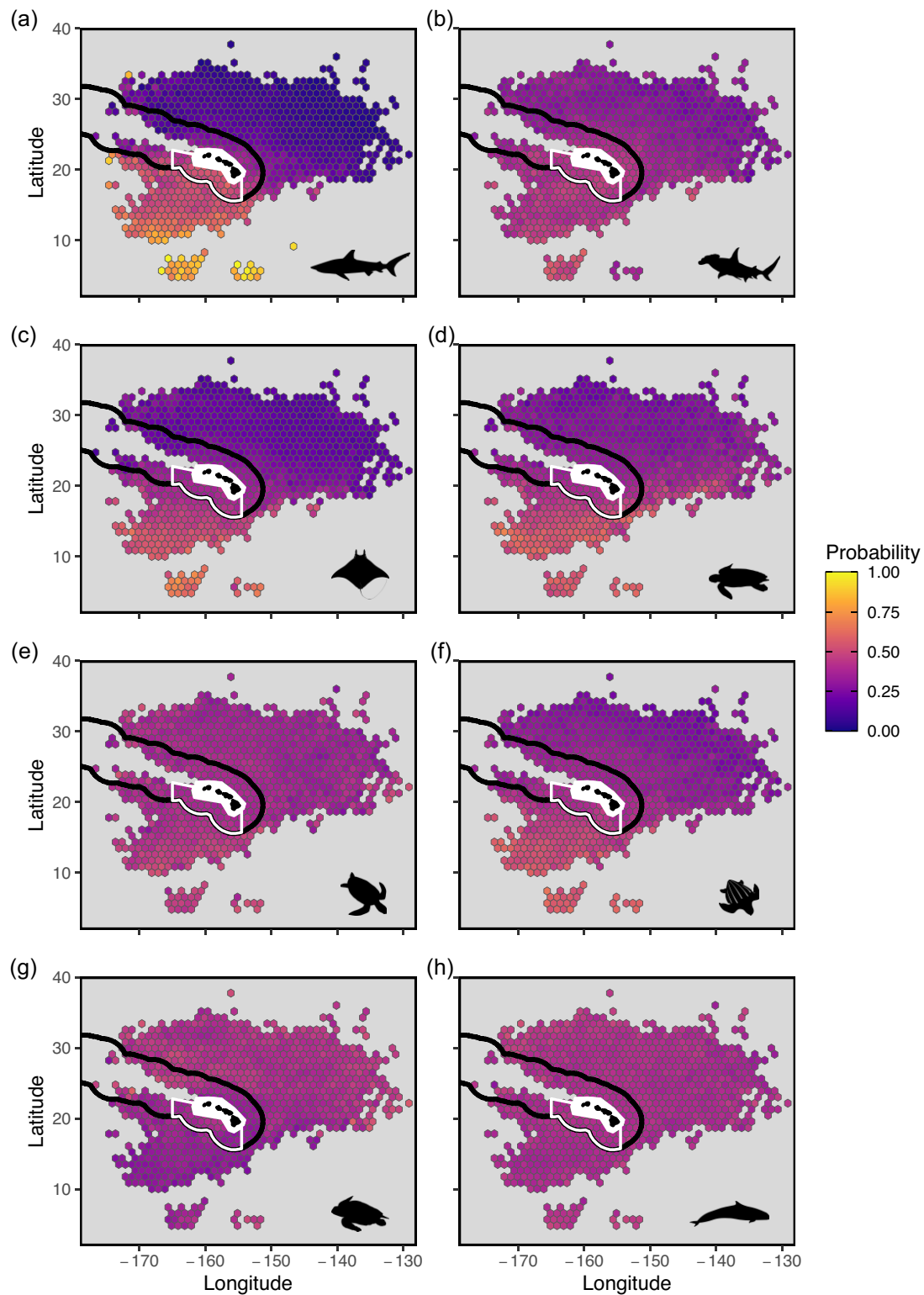


Figure 2. ERF spatial predictions in the central North Pacific Ocean for (a) oceanic whitetip sharks, (b) scalloped hammerhead sharks, (c) giant manta rays, (d) olive ridley sea turtles, (e) green sea turtles, (f) leatherback sea turtles, (g) loggerhead sea turtles, and (h) false killer whales according to ERF models. The scale bar represents the probability of presence, with warm colors indicating a higher probability of presence based on prior fishing interactions. The Hawaiian EEZ is outlined in black, SEZ is outlined in white, and longline prohibited area is the solid white filled polygon.

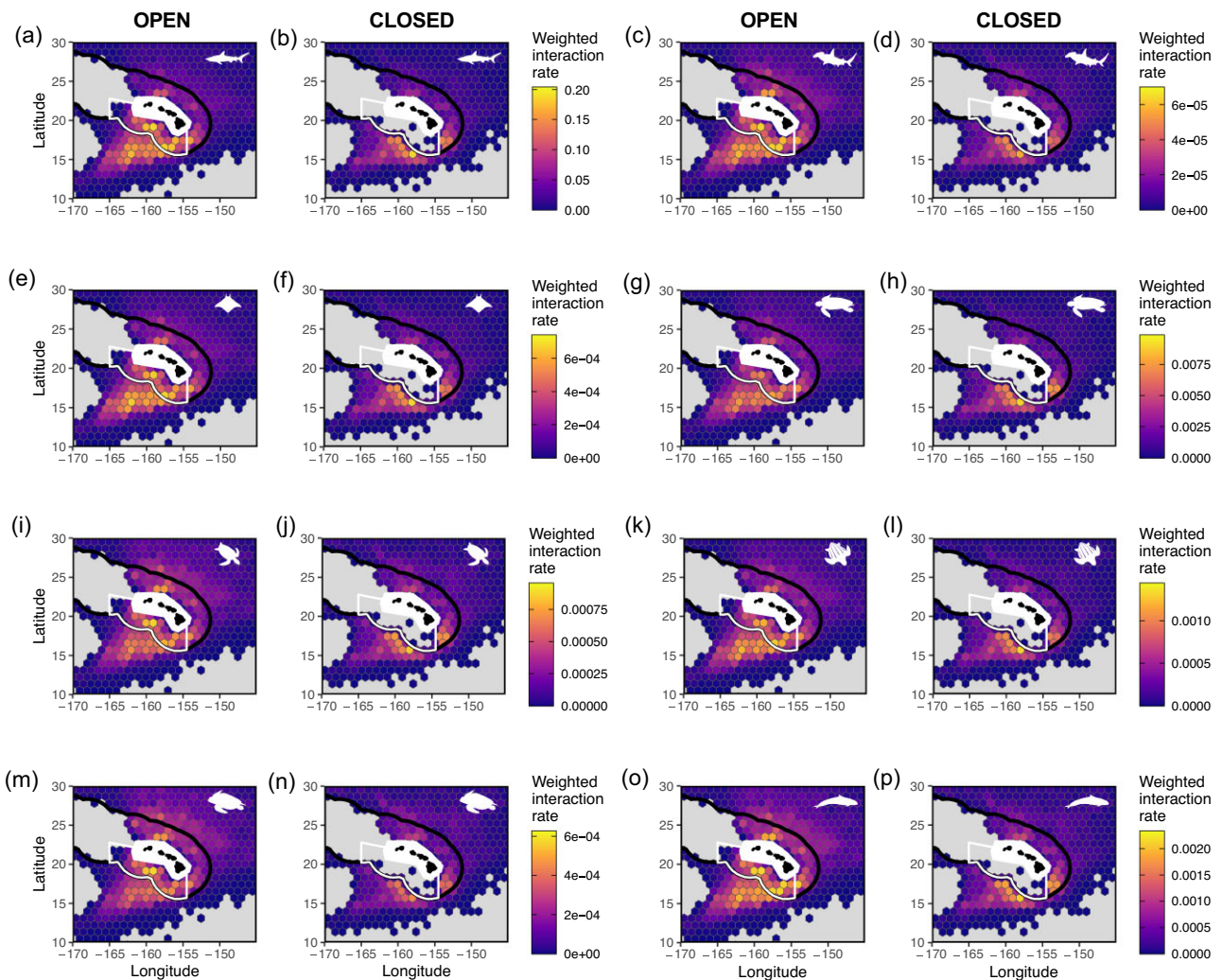


Figure 3. Weighted interaction rates for (a–b) oceanic whitetip sharks, (c–d) scalloped hammerhead sharks, (e–f) giant manta rays, (g–h) olive ridley sea turtles, (i–j) green sea turtles, (k–l) leatherback sea turtles, (m–n) loggerhead sea turtles, and (o–p) false killer whales when the SEZ is open (dates outside of closure between 26 August 2016 and 12 December 2022; columns 1, 3) and closed (24 July–31 December 2018 and 22 February 2019–25 August 2020; columns 2, 4). The Hawaiian EEZ is outlined in black, SEZ is outlined in white, and longline prohibited area is the solid white filled polygon.

mum risk of 0.0086 further outside the SEZ at 14°N 163°W (Fig. 5b).

Discussion

Effort redistribution

Protected species management mandated through the ESA and MMPA are inherently focused on single species but can have broad effects that extend to other protected species. We show the cap-based static area closure (i.e. SEZ) for reducing the risk of false killer whale bycatch within the EEZ around Hawai'i, redistributed pelagic longline deep-set fishing effort to areas on the eastern edges of the closure—similar to “fishing the line” behavior seen around much smaller MPAs (Murawski et al. 2005, Ohayon et al. 2021). This effort redistribution concentrates interaction risk with multiple protected species, including pelagic false killer whales. We conclude that single-species bycatch reduction strategies can inadvertently generate negative outcomes for the target species, other protected species, and the affected fisheries. With many co-occurring single-species bycatch mitigation measures in place,

it may be difficult to untangle which measures act synergistically or antagonistically on the suite of protected species.

Although the SEZ resembles a temporary MPA, its design and implementation highlight a mismatch between traditional MPA strategies—often optimized for benthic habitat and sedentary species—and the conservation needs of mobile pelagic species (Hyrenbach et al. 2000). As global momentum builds toward achieving “30 by 30” ocean protection goals (Hilborn et al. 2022, Blanluet et al. 2024), it is important to recognize that area-based approaches like the SEZ may not provide immediate or long-term benefits for protected species in dynamic, open-ocean systems. The implementation of MPAs can redistribute fishing effort and alter the spatial risk field for interacting with both target and non-target species in the system (Hyrenbach et al. 2000, Hoos et al. 2019, Hilborn et al. 2022). When closures restrict fishing access, effort often shifts to adjacent areas, concentrating fishing activity along closure boundaries (i.e. “fishing the line”) (Cabral et al. 2017). Here, the SEZ closures functioned similarly to a large static MPA (Balmford et al. 2004), restricting access to 48% of the fishable areas within the Hawai'i EEZ for pelagic

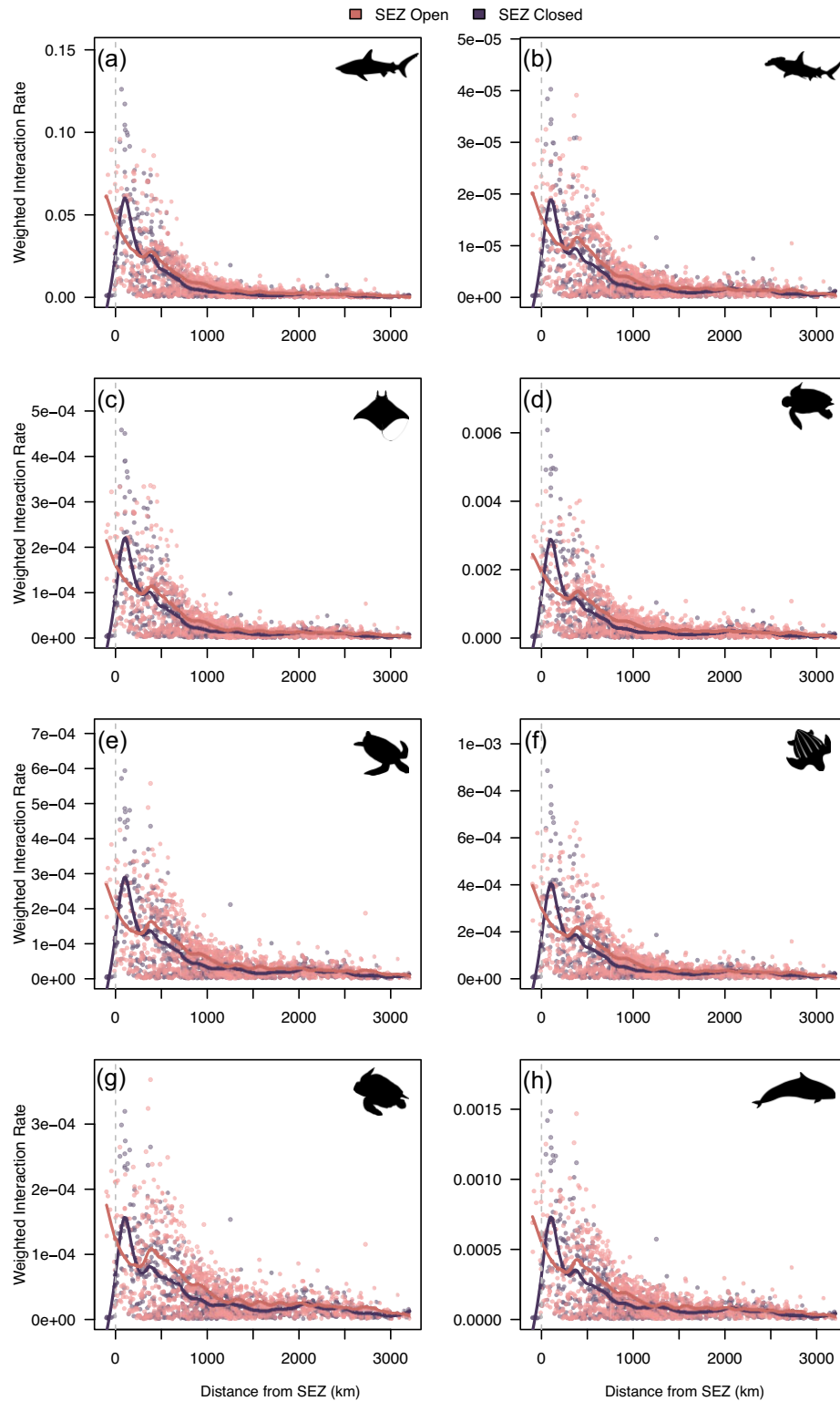


Figure 4. Weighted interaction rates by distance from the SEZ border when the SEZ is open (dates outside of closure between 26 August 2016 and 12 December 2022) or closed (24 July–31 December 2018 and 22 February 2019–25 August 2020) for (a) oceanic whitetip sharks, (b) scalloped hammerhead sharks, (c) giant manta rays, (d) olive ridley sea turtles, (e) green sea turtles, (f) leatherback sea turtles, (g) loggerhead sea turtles, and (h) false killer whales. Each point corresponds to the mean weighted interaction rate for the hexagons corresponding to Fig. 3. Smoothing splines ($spar = 0.6$) are fit according to SEZ status.

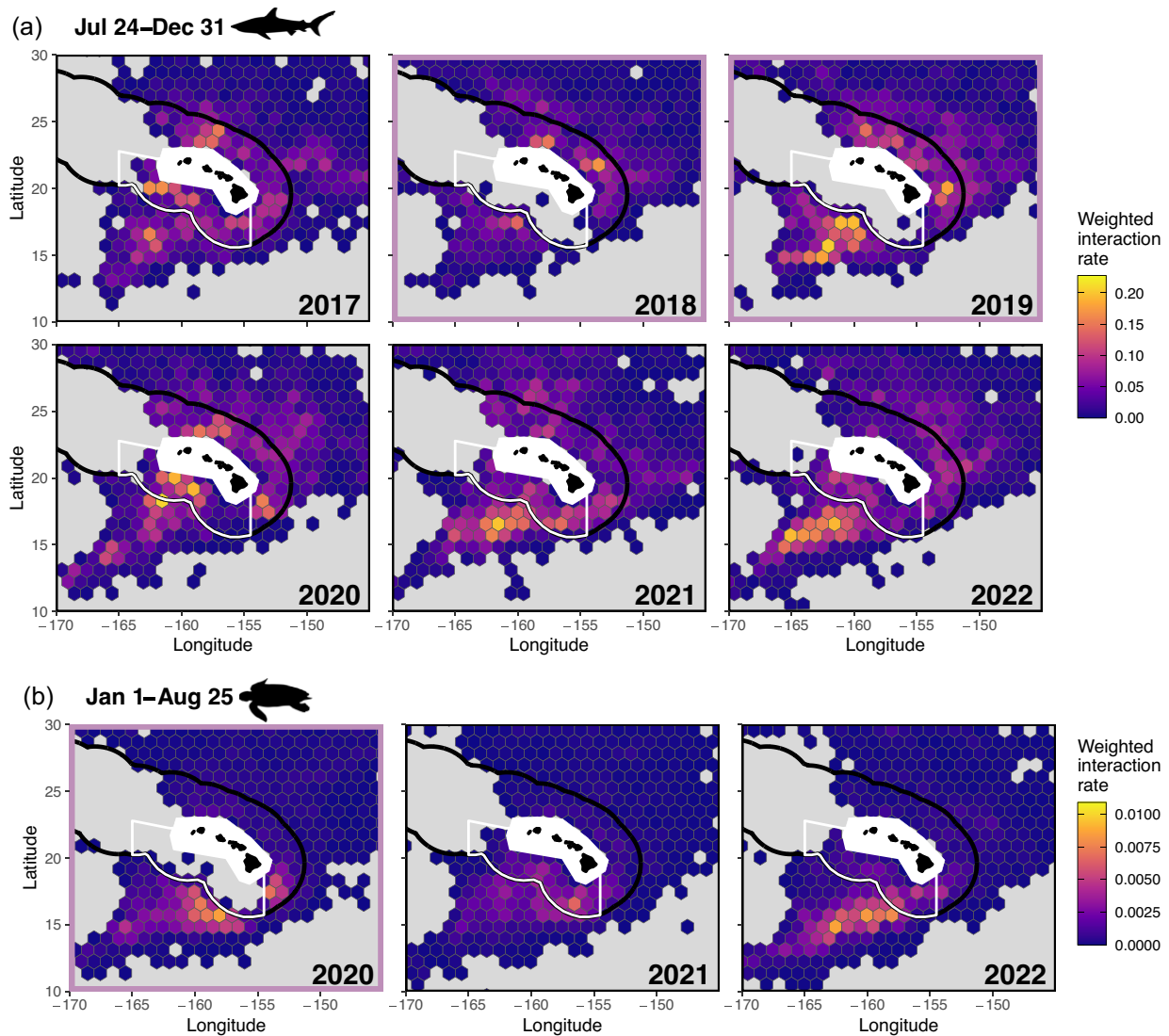


Figure 5. Weighted interaction rates for (a) oceanic whitetip sharks during a closure time block (24 July–31 December) and every year at the corresponding time block, from 2017 to 2022. The time block corresponds with the 2018 SEZ closure (24 July–31 December 2018) and the latter part of the 2019–2020 closure (22 February 2019–25 August 2020). (b) Olive ridley sea turtles during a closure time block (1 January–25 August) and the following years at the corresponding time block, from 2020 to 2022. The time block corresponds with the 2020 SEZ closure (1 January–25 August 2020). Warm colors indicate an increase in interaction rates. Plots outlined in purple are time blocks when the SEZ is closed. The Hawaiian EEZ is outlined in black, SEZ is outlined in white, and longline prohibited area is the solid white filled polygon. Each cell is calculated as relative effort (sets during the time block each year). See [Figs S14–S21](#) for full panels for all 8 species.

longline fishing. However, rather than reducing interactions, these closures primarily displaced effort beyond the EEZ, particularly north of the Main Hawaiian Islands and south and east of the SEZ boundary. Our findings suggest that the SEZ does not, nor was it designed to, reduce fisheries interaction risk for a full suite of protected species, and the fishery's spatial displacement may further exacerbate bycatch risk for these protected species.

Impact on false killer whale bycatch

In the Hawai'i DSL, interaction risk for false killer whales is spatially diffuse and primarily a function of effort. Over the last two decades, the fishery has expanded five-fold in effort and space outside the EEZ (Woodworth-Jefcoats et al. 2018). Spatial shifts in fishing effort have coincided with in-

creased MSI in high-sea areas, possibly because pelagic false killer whales occur in greater densities outside the EEZ (Bradford et al. 2020, Oleson et al. 2023). The mean estimated annual take outside the EEZ increased from an average of 10.0 (2008–2012) to 28.8 takes per year (2015–2019) (Oleson et al. 2020, Fader et al. 2021). Our study showed that the SEZ closures pushed fishing effort outside the EEZ, away from the HI insular stock range (McCracken 2010), but into new areas where the pelagic false killer whales are abundant (Oleson et al. 2023). The risk of false killer whale interactions was particularly high near the SEZ boundary, suggesting that excluding fishing from the SEZ may increase interactions with the pelagic false killer whales.

Assessing the effectiveness of the SEZ in reducing false killer whale bycatch is challenged by the inability of existing models to detect clear ecological drivers of fishery interactions

with false killer whales. Pelagic false killer whales are highly mobile and cue on bait and catch rather than environmental features (Gilman *et al.* 2006a, Hamer *et al.* 2012). As a result, interaction patterns are spatially diffuse and not strongly linked to oceanographic conditions. This weakens the predictive pattern of random forest models, which require strong spatial clustering of presence data to extract meaningful patterns (Siders *et al.* 2020, Long *et al.* 2024, Milà *et al.* 2024). Additionally, the dynamic oceanic and atmospheric conditions around the Main Hawaiian Islands (Friedrich *et al.* 2024) further hinder the model's ability to detect clear ecological patterns (Forney *et al.* 2011), particularly for species with inconsistent environmental associations. These challenges limit the feasibility of DOM, which is more effective when species distribution responds predictably to shifting environmental features (Pons *et al.* 2022, Siders *et al.* 2024).

Impact on non-target protected species

Management strategies for bycatch mitigation introduce tradeoffs that can inadvertently increase or decrease bycatch risk for non-target species (Pons *et al.* 2022, Crespo *et al.* 2024). Strictly speaking, the False Killer Whale Take Reduction Plan was not mandated to require consideration of regulatory impacts on other species (50 CFR 229.37). Yet, as demonstrated here, effort redistribution from the SEZ closures altered interaction risks for the protected species. When the SEZ was closed, relative interaction risk increased for all species—except loggerhead sea turtles—in concentrated fishing areas outside the SEZ. Oceanic whitetip sharks, giant manta rays, and olive ridley sea turtles showed the most concentrated risk near the SEZ boundary when the SEZ was closed, indicating high susceptibility to overlap with the displaced fishing effort. Scalloped hammerhead sharks and green and leatherback sea turtles experienced moderate increases in risk near concentrated fishing efforts. In contrast, loggerhead sea turtles and false killer whales exhibited more diffuse risk patterns, suggesting broader spatial ranges or less overlap with fishing activity. These varied responses underscore the trade-offs of spatial closures and the differing vulnerabilities across species. This tradeoff is not exclusive to the Hawai'i longline fishery. In the US North Pacific demersal trawl fishery, an area closure reduced the bycatch rate of the red king crab, *Paralithodes camtschaticus*, but increased the bycatch rate of Pacific halibut, *Hippoglossus stenolepis*, due to displaced fishing effort (Abbott and Haynie 2012). Likewise, model results from the North Atlantic swordfish longline fishery showed that closing one area might reduce bycatch rates of sea turtles and two shark species, but would increase bycatch rates for 11 other shark species as effort shifted (Baum *et al.* 2003). The SEZ closures follow this pattern, illustrating that regulatory actions aimed at a single species inherently alter the risk profile for the suite of species in the system.

Fragmented bycatch management hinders effective mitigation. Taxon-specific legislation often results in piecemeal management strategies that fail to address bycatch risks comprehensively (Moore *et al.* 2009). In the Hawai'i longline fishery, separate regulations exist for seabirds, sea turtles, odontocetes, and sharks in the regional and domestic fisheries management systems (NMFS 2005, 2012, 2015, 2016, Gilman *et al.* 2014, 2019b). This approach can create unintended tradeoffs (Gilman *et al.* 2019b, Yan *et al.* 2024). For example, switching between fishing depths changes the bycatch risk

for different shark and sea turtle species (Gilman *et al.* 2016, O'Farrell *et al.* 2024). Additionally, replacing J-style hooks with circle hooks in the swordfish and tuna longline fishery (Yokota *et al.* 2006, Boggs and Swimmer 2007) reduces sea turtle bycatch risk but increases catch rates for six shark species (Reinhardt *et al.* 2018). Night setting decreases longline interaction rates with many seabirds including the protected albatross species, *Thalassarche* spp., but increases interaction rates with the nocturnal white-chinned petrel, *Procellaria aequinoctialis* (Melvin *et al.* 2013). The 2005 expansion of the Bornholm MPA in the Baltic Sea, intended to conserve Baltic cod populations (*Gadus morhua callarias*) led to effort displacement that increased the exploitation and discarding of juvenile cod and counteracted the goal of the expansion (Suuronen *et al.* 2010). Although these examples illustrate the opposing consequences of legislative action on some species, such measures can also yield mutual benefits for other species (Melvin *et al.* 2013, Ochi *et al.* 2024, Yan *et al.* 2024). Therefore, it is essential to evaluate these tradeoffs through a holistic approach.

Closure effectiveness and broader implications

While we are not advocating for the removal of the SEZ as a mitigation measure, its broader impacts on the fishery warrant careful consideration. Some time-area closures have successfully protected marine megafauna (Beets and Friedlander 1999, Moore *et al.* 2009, Goldsworthy *et al.* 2022), but their effectiveness depends heavily on spatial scale, duration, and how well they align with the movement of the species they aim to protect. For example, a North Atlantic longline closure failed to reduce leatherback sea turtle bycatch because the closed area was much smaller than the turtles' range (James *et al.* 2005). Similarly, closures in the Gulf of Maine were ineffective at reducing harbor porpoise, *Phocoena phocoena*, bycatch in the sink gillnet fishery due to their limited spatial and temporal coverage (Murray *et al.* 2000). In these instances, moving to longer and larger closures could better meet single-species management objectives, provided the cascading impacts of such a change were acceptable. However, in some cases, if a species requires a large spatial area for protection, enforcement may not be plausible. The vaquita, *Phocoena sinus*, in the Gulf of California is on the brink of extinction (ESA Listing Rule 50 FR 1056, 1985) due to bycatch from artisanal gillnets (D'agrosa *et al.* 2000). Despite the implementation of time-area closures in 2005 aimed at protecting vaquitas, these measures proved ineffective because of inadequate enforcement and insufficient coverage of their habitat range (Gerrodette and Rojas-Bracho 2011).

In the Hawai'i Pacific region, many protected areas are located within or around high seas fishing grounds, where domestic longline fleets compete with foreign vessels. In these spaces, unilateral conservation efforts by a single nation may be insufficient. Protecting wide-ranging or migratory species under these conditions often requires coordinated international agreements through Regional Fishery Management Organizations. One major consequence of expanding closures without this coordination is the displacement of fishing effort into regions with fewer bycatch regulations. This could involve shifting activity within the same fleet, as was seen with the SEZ closure, or a broader restructuring of the global seafood supply chains. For instance, a four-year closure of

the HI longline swordfish fishery redirected the US swordfish supply to foreign longline fleets with higher bycatch rates and fewer regulations to mitigate sea turtle interactions (Sarmiento 2006, Gilman et al. 2006b, Chan and Pan 2016). This market-driven shift resulted in an estimated 2882 additional sea turtle interactions, ultimately negating the intended conservation benefits of the closure (Rausser et al. 2009). The potential consequences of mitigation measures aimed at a single stock should be evaluated so that potential trade-offs across the species and protected species are understood even when the legal framework is focused on stock-specific outcomes.

Even if the cap-based closure successfully protects the target species and has neutral or positive impacts on other pelagic species, it still raises the question of how the closure affects the fishery itself. In 2016, the Papahānaumokuākea Marine National Monument expansion permanently closed 68% of the fishable EEZ to fishing. When the SEZ is closed, only 17% of the entire EEZ is open to fishing, inevitably influencing fleet behavioral response and affecting the socio-economics of the fishery. In response to the SEZ closures, the Hawai'i DSLL fishing fleet shifted its efforts further south, and "fished the line" in areas immediately outside the closed area. The effort was extended significantly beyond the EEZ and into the high seas, where less than 30% of the fleet fished within the EEZ for 10 consecutive quarters (Fig. 1d). Although catch of target species was reported as unaffected for vessels that historically fished in the SEZ (Ovando and Hilborn 2020), this change in effort can result in financial losses for fishing vessels by also increasing competition with foreign fleets, travel time, and fuel costs (O'Keefe et al. 2014, Seary et al. 2022). While our analyses did not directly examine economic outcomes or operational impacts beyond effort, these shifts in behavior are expected (O'Keefe et al. 2014, Cabral et al. 2017) and highlight potential downstream effects of the closure. Thus, the consequences of the SEZ closure extend beyond the scope of false killer whale bycatch reduction.

Current legislative frameworks for bycatch mitigation are not structured to assess the impact of mitigation measures on other species. Under the MMPA, the SEZ was designed to minimize false killer whale bycatch but was not mandated to consider its effect on other species (50 CFR 229.37). We showed that SEZ provided limited benefits to false killer whales and inadvertently concentrated bycatch risk for other protected species. While a cap-based area closure is among the many bycatch mitigation strategies that exist (Gray and Kennelly 2018, Swimmer et al. 2020), effective bycatch mitigation strategies inherently introduce tradeoffs for the range of species in the system and for the fishery itself (Huang et al. 2024). Growing evidence, including our findings here, suggests that single protected species management could create unintended consequences and reduce management efficiency (Gilman et al. 2019b, Ochi et al. 2024). It is essential we evaluate the multispecies impact—positive or negative—of current and future bycatch mitigation measures and frequently reevaluate their associated tradeoffs.

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Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

The fisheries-dependent datasets in this article are not available for public dissemination due to confidentiality requirements.

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