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Multispecies trade-offs and opportunities for reducing megafauna bycatch in tuna purse seine fisheries

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Abstract

Bycatch mitigation in fisheries has typically focused on single species or taxonomic groups. Many fisheries are now under pressure to reduce impacts on multiple ecologically diverse taxa simultaneously. This is a core challenge for tuna purse seine fisheries, which account for roughly two-thirds of global tuna catches and 5% of wild marine catch destined for human consumption. The proliferation of Fish Aggregating Devices (FADs) has increased purse seine efficiency but also the risk of capturing protected species. Using four years of observer data with 100% coverage of a western Pacific tuna purse seine fishery, we examined catch rates of seven megafauna taxa representing three major bycatch groups of global concern: cetaceans, elasmobranchs, and sea turtles. We used Generalized Additive Models, multivariate ordination, and joint species distribution modelling to identify operational, environmental, and vessel-level drivers of bycatch. Composition of the primary tuna species, a proxy for targeting strategy, was the strongest and most consistent predictor of bycatch rates, followed by vessel identity and FAD type. Strong taxon-specific vessel effects indicate fishers use nuanced, undocumented fishing strategies that influence bycatch risk, with potential trade-offs among species. These findings highlight the importance of prioritising feasible mitigation actions while considering ecological consequences across multiple taxa. Encouragingly, some vessels achieved relatively low bycatch across several groups, suggesting fishers are already developing more selective fishing practices, including when fishing on FADs. Facilitating knowledge transfer among fishers could be an important addition to the toolkit for reducing mortality of species at risk from bycatch in global fisheries.

Introduction

Fisheries can have tremendous impacts on non-target (“bycatch”) species with slow growth and reproduction, such as marine mammals, sea turtles, and many sharks and rays (elasmobranchs) (Gray & Kennelly, 2018). Apart from elasmobranchs, which are widely targeted or retained as valuable byproducts, megafauna species are not typically the intended target of fishing operations (James et al., 2016; Komoroske & Lewison, 2015; Wosnick et al., 2023). Yet, fishing is the primary direct threat to population persistence of many iconic marine species globally (Dulvy et al., 2021; Lewison et al., 2014) (Dulvy et al., 2021; Lewison et al., 2014).

Bycatch has been a persistent issue for fisheries targeting tuna and similar pelagic species, which operate throughout the world’s tropical and subtropical oceans and interact with a wide range of megafauna species (Poisson et al., 2021). Tunas are one of the world’s most important target species groups, accounting for eight percent of global marine capture fisheries production (FAO, 2024). These species are traded in all forms and at all scales, from a relatively cheap product in small local markets to one of the most expensive seafood items available in luxury restaurants. Given their importance for global protein provision and to many national economies, considerable attention has been directed towards improving the environmental sustainability of tuna fisheries, particularly reducing impacts on non-target species (Hall et al., 2017).

Industrial tuna fisheries primarily use pelagic longlines and purse seines, with substantial use of gillnets and other gears in some regions (Gilman et al., 2017). All the major gear types have associated bycatch issues, with the exception of pole-and-line fishing, which is highly selective (at least on free schools of tuna) but less common (Gilman, 2011). Bycatch mortality rates in purse seines, which actively encircle tuna schools, are typically lower than in passive gears with longer soak times, such as longlines and gillnets (Gilman, 2011). However, the sheer magnitude of purse seine fishing—which contributes two-thirds of the world's tropical tuna catches—generates substantial cumulative impacts on non-target species (Gilman et al., 2017; Murua et al., 2023).

Concerns about purse seine bycatch have intensified over the past three decades with the rapid and growing adoption of Fish Aggregating Devices (FADs) (Tolotti et al., 2020). These floating objects are made from materials such as plastic, wood, and netting, and often extend up to 80 m below the surface (Swimmer et al., 2020). These structures can either be anchored to the seafloor or left to drift, usually equipped with satellite trackers. Fishing vessels also opportunistically set their nets on floating objects such as logs, marine debris, or dead animals. This technique attracts tuna and increases fishing efficiency compared to searching for free schools, but substantially decreases selectivity because a variety of animals—including juvenile tuna, sharks, and sea turtles—congregate around floating objects (Guillotreau et al., 2024). In addition to floating objects, many purse seiners set on live animals that co-occur with tuna, particularly whales, dolphins, and whale sharks (Escalle et al., 2019).

Bycatch mortality is reduced by avoiding interactions with the animal in the first place—the ideal scenario for biodiversity and for the fishers—or by improved handling and release of captured individuals. There are numerous operational strategies used to reduce capture of non-target species in purse seines, including operational modifications (e.g. "backing down" to allow dolphins or whales to escape from nets) or gear adjustments designed to minimize entanglement risk (Swimmer et al., 2020). Time-area closures and other controls on where and when fishing occurs are a common but often controversial regulatory tool to reduce interactions (Pons et al., 2023). These include permanent protected areas, or seasonal or short-term closures in high-risk areas. Dynamic time-area closures based on predictive models of species occurrence have been widely proposed for a range of bycatch species, but are rarely implemented in tuna purse seine fisheries due to operational challenges and concerns about loss of target catch (Crespo et al., 2024; Cronin et al., 2023; Hazen et al., 2018; Pons et al., 2023). For entangled animals, various operational and technical strategies have increased post-release survival in purse seines, such as mobulid sorting grids and other release devices, or deploying smaller boats to safely release entangled animals (Cronin, Croll, et al., 2022; Swimmer et al., 2020).

A persistent challenge is that bycatch mitigation measures have been implemented in a piecemeal and fragmented manner—both at regional and national scales and within individual fisheries (Gilman et al., 2019). Furthermore, bycatch mitigation has largely followed a taxon-specific framework, from the "best practices" promoted by environmental organizations and seafood industry partnerships to domestic fisheries regulations and the conservation measures adopted by regional fisheries management organizations (Gilman et al., 2019; Tolotti et al., 2023). The earliest and most visible example of this

approach was the suite of programs and regulations designed to address dolphin bycatch in purse seine fleets in the Eastern Tropical Pacific (Hall et al., 2017). Over time, similar efforts emerged for sea turtles, seabirds, and other marine mammals (Swimmer et al., 2020). More recently, initiatives to reduce elasmobranch bycatch have emerged, usually beginning with iconic species such as whale sharks or manta rays, but gradually expanding as awareness of bycatch impacts increases (Cronin et al., 2023).

Taxon-specific measures can be effective but can have unintended consequences. Changes in fishing behavior designed to reduce catch of one species can inadvertently increase another (Gilman et al., 2022). For example, adjusting hooks and bait to reduce sea turtle bycatch in longlines sometimes increases elasmobranch catches (Gilman et al., 2016), and measures implemented in the Indian Ocean to reduce yellowfin tuna (*Thunnus albacares*) catch led to a substantial increase in the catch of silky sharks (*Carcharhinus falciformis*) (Tolotti et al., 2023). Even theoretical dynamic spatial management simulations have shown that in some regions and gear configurations, no single combination of space and time is likely to avoid multiple bycatch taxa while maintaining viable tuna catches (Pons et al., 2022).

The lack of effective, multi-taxa mitigation strategies remains a major obstacle to the sustainability of tuna and other major fisheries. Both empirical and theoretical work indicates that mitigation technologies that reduce bycatch across multiple taxa are rare (Huang et al., 2024), and the difficulty of identifying solutions that both protect vulnerable species and maintain profitable target catches has hindered their broader adoption (Drynan et al., 2026; Swimmer et al., 2020). This challenge is particularly salient for oceanic elasmobranchs, which have large ranges that overlap closely with tuna fisheries and have proven to be especially difficult to avoid or release alive (Cronin, Amaral, et al., 2022; Drynan et al., 2026; Pacoureau et al., 2023). For example, silky sharks are a primary concern for tuna purse seine fisheries. They are one of the most frequently captured elasmobranchs in tuna fisheries globally, are listed as Vulnerable on the IUCN Red List, and were added to Appendix II of the Convention on International Trade in Endangered Species (CITES) in 2016 (Rigby et al., 2021).

As additional protections and restrictions on fishing are introduced to curb declines in imperiled megafauna populations, pressure is mounting on tuna fleets to reduce multiple types of bycatch while still maintaining profitable tuna catches. Rising to this demand will require a portfolio of solutions, including technological advances, innovations in fishing tactics, and more adaptive management approaches. One critical but underutilized tool is fisher knowledge (Gilman, Chaloupka, Bellquist, et al., 2023; Murua et al., 2023; Parsa et al., 2020). Emerging evidence highlights the overlooked role of individual fishers in driving what is generally described as a fleet-wide problem (Roberson et al., 2024). Catch rates are typically reported at the fleet level or as nominal catch-per-unit-effort metrics (e.g., average per vessel or purse seine set). While useful for identifying emerging bycatch issues or areas of elevated risk, these measures can be confounded by variation in fishing practices, technology, environmental conditions, and other factors that strongly influence catchability (Gilman et al., 2024). Analyses of multiple fisheries, gear types, and bycatch taxa indicate that a relatively small number of vessels often make a disproportionate contribution to the fleet's total bycatch, while many high-

performing vessels maintain target catches with comparatively low bycatch rates (Roberson et al., 2024; Roberson & Wilcox, 2025; Stram & Lanelli, 2015).

The idea that some fishers are consistently more effective at catching their target species (the "fisher," "skipper," or "vessel effect") is anecdotally accepted among fishery stakeholders and well established quantitatively for target catch (Hilborn, 1985; Salas & Gaertner, 2004). It is logical to view "anti-targeting," or avoidance of non-target catch, as another component of the same skill (Roberson & Wilcox, 2025). However, the fisher effect on bycatch has only been rigorously tested in fleets with low observer coverage, offering a skewed picture of variability among individual vessels (Parsa et al., 2020; Roberson et al., 2024; Roberson & Wilcox, 2025). The combination of uneven observer effort and the relative rarity of megafauna bycatch have led studies to focus on single species or taxa in isolation, rather than how different vessels perform across multiple bycatch types.

We capitalize on a rare opportunity to analyze patterns in fleet and vessel-level bycatch of multiple megafauna taxa using data from a tuna purse seine fleet in the Western Pacific, which maintained 100% observer coverage throughout the COVID-19 pandemic. This Marine Stewardship Council certified fishery operated by the Fishing Industry Association of Papua New Guinea (FIA-PNG) consists of large purse seine vessels flagged to PNG and the Philippines. Like other purse seine fisheries in the region, the fleet fishes using both free sets and associated sets, including on drifting and anchored FADs, logs and debris, and previously on whale sharks and live whales. Currently, the fishery's most pressing bycatch issue is silky sharks but there are interactions with other species of concern, including whale sharks, cetaceans, sea turtles, and mobulid rays (FIA-PNG, 2024). The management agency and industry association have worked together to implement a number of bycatch mitigation measures in recent years, including transitioning to non-entangling drifting FAD designs, encouraging vessels to avoid setting on protected species, and training crews in best-practice release protocols for entangled animals (FIA-PNG, 2024; Gilman et al., 2024).

The availability of this high quality dataset presents a unique opportunity to rigorously examine patterns in bycatch of multiple megafauna species at both fleet and sub-fleet levels. If significant vessel-level heterogeneity in bycatch rates exists within the fleet of physically similar vessels, this suggests that some captains and crews have developed effective strategies for reducing multiple types of bycatch, including for problematic species such as oceanic elasmobranchs. Identifying and incentivizing the practices of these high-performing fishers could provide a powerful, underutilized pathway to improving bycatch outcomes in tandem with existing technological and regulatory tools (Squires & Garcia, 2018). Conversely, understanding and quantifying which vessels disproportionately contribute to bycatch can help managers design more targeted and efficient interventions.

Methods

Description of Fisheries observer data

We analysed vessel and fleet-level variability in interactions with seven bycatch species or taxonomic groups (hereafter “bycatch taxa”), spanning three broad taxonomic categories with diverse life histories. Sea turtles included green (*Chelonia mydas*), olive ridley (*Lepidochelys olivacea)*, hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and flatback turtles (*Natator depressus*). Elasmobranchs included silky sharks (*Carcharhinus falciformis*), whale sharks (*Rhincodon typus*), and mobulids (*Manta birostris* and unidentified Mobulidae). The three cetacean taxa were false killer whales (*Pseudorca crassidens*), baleen whales (humpback *Megaptera novaeangliae*, Bryde’s *Balaenoptera edeni,* sei *Balaenoptera borealis*, blue *Balaenoptera musculus*, minke *Balaenoptera acutorostrata*, and unidentified baleen whales), and small to medium-sized dolphins (bottlenose *Tursiops truncatus*, common *Delphinus delphis*, Indo-Pacific bottlenose *Tursiops aduncus*, pantropical spotted *Stenella attenuata*, spinner *Stenella longirostris*, rough-toothed *Steno bredanensis*, and striped dolphins *Stenella coeruleoalba*).

The scientific observer data provided by the National Fisheries Authority of PNG has 100% coverage of fishing activity for the FIA-PNG fleet. The raw dataset included records from 45 vessels, with 8-481 observed sets per vessel (10,712 sets total) between January 2019 and August 2023. For each fishing event (set), the data included the vessel identity and information about the fishing activity and catch, including weights and counts of landed catch and bycatch of non-target species. Observer estimates were collected following the SPC/FFA Regional Observer Programme protocols, which record the weight or number of captured non-target species and, where possible, species of special interest observed within or interacting with the net (SPC & FFA, 2012). Target tuna catches were sampled using established observer methods that employ a combination of grab and spill sampling to reduce selectivity bias (Hoyle et al., 2024; Lawson, 2013). For non-target species, catch estimates were derived from observer counts, visual assessments and sampling protocols applied during catch sorting (Briand et al., 2018; Forget et al., 2021). Most bycatch records were recorded as counts, except for silky sharks and mobulids, for which both counts and corresponding weights were usually recorded. We used species-specific mean weights and counts derived from complete records to interpolate missing counts or weights for these taxa.

Observers also recorded the fate of the animal. Although they do not specifically record life status, most of the standardized fate codes indicate the animal’s condition (e.g., “Discarded - Protected species - Alive”). Our focus was on the occurrence and magnitude of bycatch interactions rather than post-capture mortality. Accordingly, “bycatch” included animals that were recorded in the net during hauling or onboard during catch sorting, irrespective of their life status. This included large individuals that could not be brought onboard, such as baleen whales, which were recorded by observers when they were encircled in the net.

Single taxon models

To evaluate the operational factors driving bycatch rates, we fitted separate Generalized Additive Models (GAMs) for each bycatch taxon using the mgcv package in R (Wood, 2015), with bycatch count or weight per set as the response variable. We explored a range of parameters recorded by observers that could affect bycatch occurrence and magnitude, including year, month, fishing location, time of day the set began, and set type. Latitude and longitude were parameterized as a two-dimensional smooth spatial surface to account for spatial variation across the fishing area.

There were nine categories of set types: two “unassociated” categories (unassociated free schools of tuna, and free schools feeding on baitfish) and seven “associated” categories: drifting natural FADs (e.g., logs, debris, or dead animals), drifting man-made FADs (e.g., rafts, payaos), live whales, live whale sharks (only permitted if unintentional, meaning the shark was not visible before initiating the set), other FADs, and “no tuna associated” (a broad category of object investigations or exploratory sets with no tuna observed). The latter two categories were grouped as “Other” due to ambiguity in their classification, resulting in eight set types overall. There are observed ecological and behavioural differences in both tuna and bycatch aggregations associated with the different set types. For example, silky sharks and juveniles of some tuna species are known to strongly associate with FADs (Tolotti et al., 2020), whereas free-school sets frequently catch larger tuna (Lennert-Cody et al., 2018).

To test the relationship between bycatch and target catch, we included the combined retained catch volume (metric tonnes) of the three principal tuna species: yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye (*Thunnus obesus*). Skipjack and yellowfin were the primary targets (totalling 253,980 t and 140,624 t retained, respectively), while bigeye comprised a smaller but economically important component (4,996 t) due to its higher market value. The fleet also retained small quantities of other tuna and tuna-like species, such as frigate tuna (*Auxis thazard*) and rainbow runner (*Elagatis bipinnulata*). Catch weight was used rather than counts because it contained fewer missing values.

In addition to the documented covariates, we derived a variable to capture unobserved fishing tactics used to target different tuna species, which may also influence bycatch risk (He et al., 1997). These tactics could include variation in net depth, environmental factors such as moon phase, setting and hauling speed or other nuanced operational tactics, and FAD deployment strategies that are not documented as part of the eight set type categories, such as the amount of time it was deployed (Murua et al., 2023). Fishing sets were categorised according to inferred targeting strategy using k-means clustering based on the catch composition of the three principal tuna species. For each set, we calculated the proportional contribution of each species to the total retained tuna catch to standardise for differences in catch volume and emphasise relative composition. K-means clustering was applied to these proportional data to group sets with similar species profiles. The number of clusters was set to k = 3 based on inspection of the within-cluster sum of squares (elbow method), which indicated diminishing improvement beyond this value, and on the interpretability of the resulting clusters. The algorithm was run with 50 random initialisations to ensure convergence on a stable solution. Clusters were interpreted as yellowfin-dominated, skipjack-dominated, or mixed-species sets with no single dominant tuna

species. Sets with zero catch of the focal tuna species were excluded from clustering and subsequently assigned to a fourth “zero main targets” category. This approach classified setting practices into discrete strategies reflecting relative targeting preferences, independent of overall catch volume, which was included separately as a covariate.

Vessel identity was included as a random effect to account for unobserved heterogeneity among vessels, including differences in vessel and gear characteristics, as well as crew behaviour, decision-making, and skill that may influence bycatch but are not captured in other covariates (Roberson & Wilcox, 2025). Vessels with fewer than 50 observed sets were excluded based on preliminary data exploration. Information on observer identity was not available and therefore could not be included.

No effort offset was included because the dataset did not contain explicit measures of fishing effort (e.g., net length or set duration, as set end times were not recorded). Information from the management agency indicated that vessels, gear configurations, and set durations were relatively homogeneous across the fleet. As a result, variation in fishing effort was assumed to be limited, and the vessel effect is interpreted as primarily capturing residual differences among vessels, including both technical and behavioural components. However, some influence of systematic differences in effort cannot be accounted for.

Our primary aim was to characterise patterns and drivers of bycatch across multiple taxa, with particular emphasis on the role of individual vessels and targeting strategies. Accordingly, the analysis was designed to isolate vessel level differences while accounting for other factors influencing catchability. This differs from prediction focused bycatch models that prioritise environmental drivers of bycatch occurrence (Gilman et al., 2024). Consequently, and because most bycatch taxa were extremely rare, we did not include additional environmental covariates (e.g., sea surface temperature, lunar phase, or El Niño-Southern Oscillation indices), instead focusing on vessel and operational factors.

We used an iterative model selection approach guided by the Akaike Information Criterion (AIC), diagnostic assessment of model fit. For each bycatch taxon, we first built a global model that included all covariates. We used the *dredge* function in the MuMIn package (Barton, 2015) as an initial tool to identify a set of well-supported candidate models. If multiple models were similarly supported ($\Delta AIC < 2$), we iteratively simplified the model and compared alternative formulations to select the best model. Following inspection of model diagnostics, we adjusted the functional form of predictors where necessary, including evaluating linear versus smooth representations of continuous covariates and increasing basis dimensions (k) when warranted. We also compared alternative parameterisations of categorical predictors as fixed or random effects. Given the zero-inflated and over dispersed nature of the bycatch data, we evaluated both Tweedie and negative binomial model families during model development (Shono, 2008). Based on model performance and their ability to accommodate both excess zeros and positive continuous or count observations, we selected the Tweedie distribution for all analyses.

If the final model included the vessel as a fixed effect, we applied a penalisation term “paraPen” from the mgcv package to the vessel coefficients to stabilise estimates for vessels with low or zero observed bycatch (Wood, 2015). We used deviation (sum) contrasts instead of default treatment contrasts, where vessel coefficients represent deviations from the overall mean rather than from an arbitrary reference level. For silky sharks and mobulids, which were recorded as both counts and weights and included a small number of interpolated records, we repeated the model selection process to confirm that results were consistent between the count and weight response variables.

Multivariate analyses

We used multivariate analyses to quantify differences in bycatch assemblages among targeting strategies, set types, and individual vessels. We assembled taxon specific effects estimated from the final GAMs into matrices describing variation among targeting strategies, set types, and vessels. For the set type and targeting strategy analyses, we extracted species coefficients from the final models regardless of whether terms were fitted as fixed or random effects. For the vessel analysis, we extracted vessel effects from GAMs, with vessel as a random effect for all species to ensure a common parameterisation across vessels.

For the set type and vessel analyses, we aligned taxon specific effect estimates to a common set of factor levels and combined them into matrices in which rows represented factor levels and columns represented species or species groups. We then conducted separate principal component analyses (PCAs) on centred and scaled matrices to reduce dimensionality and identify dominant gradients in species assemblage structure (Maechler et al., 2026). A PCA is a distance-based approach to classifying multivariate data that is useful for exploratory purposes and commonly used for ecological applications, such as comparing species assemblages across sampling sites. Here, the seven bycatch taxa and the primary target species catches represent the species assemblage, and the sampling site is either the set type or the vessel.

We opted for a PCA because both factors contained a relatively large number of categories, particularly the vessels, and therefore benefited from dimensionality reduction. We used ordination plots of the first two principal components (PC1 and PC2) to visualise similarities among vessels and set types, and we examined species loadings to interpret the contribution of individual species or groups to the observed gradients. To identify groups of set types or vessels with similar bycatch profiles, we applied k-means clustering to the PCA scores. We selected the optimal number of clusters using the elbow method applied to the first two principal components and evaluated cluster separation using silhouette widths.

We evaluated targeting strategies separately using a heatmap of species-specific GAM coefficients. Because targeting strategy comprised only four discrete categories (yellowfin-dominated, skipjack-dominated, mixed-species, and zero-main-target sets), direct visualisation of species associations was more interpretable than PCA ordination. We standardised coefficients across species and displayed

them as a heatmap to highlight positive and negative associations between individual bycatch taxa and targeting strategies relative to the reference (mixed species) assemblage.

Latent variable models

To further examine species co-occurrence patterns and shared responses to operational and spatial drivers, we fitted a generalized linear latent variable model (GLLVM) using the gllvm package in R (Niku et al., 2019). GLLVMs, also referred to as joint species distribution models, provide a complementary approach to PCA by jointly modelling species responses while accounting for residual correlations among species through latent variables. This framework allows observed predictor variables and unobserved sources of variation (represented by latent variables) to be analysed simultaneously, providing a way to tease apart some of the causes of species co-occurrence across sites (Niku et al., 2019).

The response matrix included the seven bycatch taxa and tuna catch, represented by the log-transformed combined catch volume of the three principal tuna species. We standardised all response variables (catch per set) to ensure comparability among species with different scales and units. The predictor matrix included the same temporal, operational, and spatial covariates used in the GAMs to facilitate direct comparison between modelling approaches. We included year as a categorical factor and modelled seasonal and diel patterns using sine and cosine transformations of month and set time, respectively, to account for cyclic variation in occurrence. We incorporated spatial variation using basis functions derived from a two-dimensional smooth of latitude and longitude, providing a flexible representation of spatial structure analogous to the smooth terms used in the GAMs. We included set type and vessel identity as categorical predictors but excluded targeting strategy because it was derived from tuna catch composition, and would therefore be collinear with the response matrix. We fit models using a Gaussian error distribution applied to the standardised response matrix.

Results

The final dataset, after removing records with missing data and four low-effort vessels, comprised 10,675 sets from 41 vessels over a four-year period. Silky sharks were by far the most frequently encountered bycatch taxon, both in terms of total individuals recorded and the proportion of sets with positive catches, followed by mobulids **(Figure 1).** Whale sharks and the three cetacean taxa were comparatively rare and sea turtles had the lowest total number of recorded interactions. The apparent temporal trends varied. Average catch rates of silky sharks and whale sharks declined from 2019 before showing a slight increase in 2023 **(Figure 1)**. Baleen whale catch rates also appear to decline, whereas mobulids, false killer whales, and sea turtles showed no clear temporal trend. The average dolphin catch rate appears to increase over time; however, dolphin interactions were extremely rare and characterised by occasional events involving large numbers of individuals. Survivability is not measured directly but immediate mortality rates can be inferred from the recorded fate at the time of release. Silky sharks had

the highest mortality during hauling (most were dead when landed), although mobulids may also have low short-term survival if the individuals with unknown life statuses did not survive release **(Figure 1)**.

Species differed in the factors associated with bycatch rates, although several predictors were consistently important across taxa **(Table 1)**. The only factor retained in all seven final models was the targeting cluster, derived from k-means classification of the catch composition of the three primary tuna species. Targeting strategies comprised skipjack-dominated (41.1% of sets), yellowfin-dominated (27.7%), mixed-species (28.0%), and sets with no recorded yellowfin, skipjack, or bigeye tuna (3.3%). Set type was retained in all models except sea turtles and included six object-associated categories and two free-school categories. Baitfish-associated free-school sets were by far the most common (67.8% of sets), followed by unassociated free-school sets (9.9%), whereas drifting FAD sets were the most common object-associated category (6.8% of sets) **(Figure S1).**

Table 1: Summary of the final generalized additive models (GAMs) for the seven bycatch taxa. Continuous predictors fitted as linear or smooth terms are indicated by significance level (*** p < 0.001, ** p < 0.01, * p < 0.05); retained categorical predictors fitted as fixed or random effects are denoted by F and R, respectively. Target catch volume is the combined retained catch of yellowfin, skipjack, and bigeye tuna. Month was fitted as a cyclic smooth and location as a two-dimensional spatial smooth. Targeting cluster was derived from k-means clustering of tuna catch composition. Time of day refers to set start time. Set type comprises eight categories of free school and object-associated sets. Vessel flag indicates Papua New Guinea or Philippines registration. EEZ indicates whether fishing occurred within or outside the PNG Exclusive Economic Zone. Vessel denotes the unique identifier of each vessel (>50 observed sets). Dev = deviance explained by the final model.

Bycatch species	Target catch volume	Year	Month	Location	Target species cluster	Time of day	Set type	Vessel flag	EEZ	Vessel	AIC	Dev. (%)
Silky shark wt	***	***	***	***	F	***	F			F	8364.9	25.5
Mobulids count	**		***	***	F	***	R***			R***	8834.2	20.1
Whale shark count				***	F	***	R***	F		R***	955.5	48.9
Baleen whales count			**	***	F	*	R***		F	R***	683.4	51.1
Dolphins count				*	F	***	R***				575.3	54.1
False killer whale count			**		F		R***			R***	598.0	33.8
Sea turtles count			**	*	F					R***	593.0	20.2

Vessel identity was included in the final models for all taxa except dolphins, meaning there was significant variation in bycatch rates among individual vessels that was not explained by the other covariates **(Table 1)**. Vessel effects were highly significant when fitted as random effects and, despite the associated increase in model complexity, inclusion of vessel as a fixed effect resulted in a substantial improvement in model fit for silky sharks. Geographic location, seasonal effects, and time of day were also commonly retained, although their influence was species-specific. Additionally, there were significant taxon-specific relationships with certain covariates (**Figures S2-S8**). Silky shark catch had a non-linear relationship with retained tuna catch volume, with uncertainty increasing at the highest catch volumes where observations were sparse. Baleen whale interaction rates were higher within the PNG EEZ; however, because 91.5% of observations occurred within PNG waters, this effect was likely confounded with geographic location, vessel identity, and set type. Similarly, whale shark interactions were higher for Philippines-flagged vessels, which accounted for only 1.3% of observations and likely captured residual variation not captured by vessel identity or fishing location. Year was retained only for silky sharks, consistent with this species being the primary focus of bycatch mitigation efforts during the study period. Vessel flag and EEZ were the least informative predictors overall.

Model explanatory power varied among taxa, ranging from 20.1% to 54.1% deviance explained **(Table 1).** Explanatory power was highest for dolphins, baleen whales, and whale sharks, intermediate for false killer whales, and lowest for silky sharks, sea turtles, and mobulids. Overall, model diagnostics indicated that the GAMs provided an adequate representation of bycatch patterns (**Figures S2-S8**). Concurvity was low to moderate in all final models, and basis dimension diagnostics indicated that most smooth terms were appropriately specified. Diagnostic performance was strongest for baleen whale, dolphin, false killer whale, and sea turtle models, with no evidence of residual non-uniformity, overdispersion, or excess outliers. Whale shark models also performed well, although there were minor departures from residual uniformity and expected outlier frequencies.

Residual diagnostics were poorest for silky sharks and mobulids despite these being among the most frequently encountered taxa. Both species had occasional large aggregation or catch events that were systematically underpredicted by the models of both counts and weights. For mobulids, this was reflected primarily in residual overdispersion, whereas silky shark weight models showed residual non-uniformity, overdispersion, and excess outliers even after substantial increases in basis dimensions. For silky sharks, persistently low *k*-indices for tuna catch volume and spatial smooths suggest that important sources of variation remained unaccounted for, potentially reflecting ecological processes not captured by the available covariates, such as oceanographic conditions, ENSO-related productivity patterns, or other environmental drivers (Gilman 2024). Nevertheless, the models were considered suitable for the primary objective of describing broad patterns and identifying similarities among species across key operational drivers.

Overall, these models are not well-suited to predictive applications, such as forecasting bycatch rates across seasons or fishing areas (Gilman et al., 2024). This is especially true for silky shark and mobulids because of the models' inability to accurately capture rare, high magnitude bycatch events. However,

these extreme catches were verified with the data owners and were consistent with observations from other Pacific tuna purse seine fisheries. Although the remaining models performed well diagnostically, most bycatch taxa were extremely rare (<2% of sets), and dolphin and false killer whale interactions were additionally characterised by infrequent but occasionally very large capture events.

The heatmap revealed clear differences in bycatch assemblages among targeting clusters **(Figure 2).** Relative to mixed species sets, skipjack-dominated and yellowfin-dominated sets generally exhibited similar or lower bycatch rates for most taxa. The main exception was mobulids, which showed stronger positive associations with single-species targeting strategies than with mixed species sets. In contrast, sets with zero catch or only catch of secondary targets ("zero main targets"), such as lower value tuna species, were associated with substantially higher bycatch rates for most taxa. Silky sharks were the only exception, showing little difference between zero main target and mixed species sets. The similarity in colour patterns among several taxa (e.g., whale shark, false killer whale, and dolphins) suggests bycatch species responded consistently to variation in tuna targeting strategies, although the magnitude and direction of these responses differed among species **(Figure 2)**. Because targeting strategy was derived from catch composition rather than directly observed fishing behaviour, these patterns likely reflect differences in fishing tactics and decision making that were not explicitly recorded in the observer data.

Principal component analysis indicated that variation in species assemblages among set types was driven primarily by differences in the relative abundance of multiple bycatch taxa rather than by entirely distinct species assemblages **(Figure 3, Figure S9)**. Drifting and anchored FAD sets were positioned closest to the origin, indicating assemblages that were broadly representative of the average across all set types. In contrast, the most extreme positions in ordination space were occupied by the heterogeneous "Other" category, free school tuna sets, live whale shark sets, and live whale sets. These set types therefore differed most strongly from the average bycatch assemblage.

Hierarchical clustering provided only weak support for discrete grouping among set types, consistent with the gradual transitions apparent in the PCA. Surprisingly, the strongest division separated free school tuna and "Other" sets from the remaining set types, instead of associated from unassociated sets **(Figure S10).** Notably, free school baitfish sets (by far the most common set type) clustered most closely with anchored FAD sets, which were uncommon, suggesting some similarity in bycatch assemblage structure. However, low silhouette widths indicated substantial overlap among categories.

Species loadings highlighted a small number of strong associations between bycatch taxa and set types **(Figure 3)**. As expected, whale sharks were strongly associated with live whale shark sets. In contrast, baleen whales were not closely associated with live whale sets. This pattern may partly reflect differences in animal visibility during setting: regulations prohibit setting on visible whale sharks, which often remain below the surface and are therefore more likely to be encountered incidentally. In contrast, whales are more readily detected from vessels and sets are permitted, although discouraged, in their vicinity. The result may also reflect the diversity of species within the baleen whale group, which included

species with differing migratory and foraging behaviours. Consequently, vessels may have intentionally set on certain whale species (e.g. humpback whales, which are usually more visible at the surface) while interactions with more cryptic species like Bryde's whales may have occurred under different conditions. However, both set types were uncommon, and their use declined over the four-year period with the introduction of management measures discouraging or prohibiting sets on live animals **(Figure S1)**.

Other notable set type associations included drifting log and debris sets, which were closely aligned with false killer whales and moderately aligned with silky sharks **(Figure 3)**. Dolphins were oriented towards the "Other" category, although this association was weaker than those observed for whale sharks and false killer whales. Baleen whales and mobulids showed less specific associations with individual set types and instead contributed to broader compositional gradients across the ordination. Importantly, silky sharks, the most frequently encountered bycatch taxon, were negatively associated with both types of unassociated sets. Free-school sets on baitfish accounted for the vast majority of fishing effort during the study period, although the fleet steadily shifted towards increased use of drifting FADs and drifting logs or debris relative to unassociated sets **(Figure S1)**. This suggests that other factors besides set type were important drivers of the significant fleet wide decrease in silky shark bycatch over time.

Once individual vessels were identified as an important source of variation in bycatch rates for all species except dolphins, we examined whether vessels could be grouped according to their overall bycatch assemblages. Principal component analysis revealed substantial variation among vessels in both the magnitude and composition of vessel specific bycatch effects **(Figure 4)**. The first two principal components explained 52.5% of the total variation and captured the major gradients in vessel level bycatch patterns. Three broad vessel groupings were identified through K-means clustering (k = 3) applied to the PCA scores, although separation among clusters was moderate **(Figure 4).** These groups corresponded primarily to gradients in both overall bycatch intensity and taxonomic composition. One cluster comprised vessels associated with elevated cetacean and sea turtle interactions, a second was characterised by stronger associations with elasmobranch bycatch (silky sharks, whale sharks, and mobulids), and a third consisted of vessels with comparatively weak bycatch effects across most taxa.

The first principal component (PC1) represented a dominant gradient in vessel specific effects across multiple bycatch taxa. Vessels with strongly negative PC1 scores had consistently larger positive vessel effects, indicating higher than average bycatch relative to other vessels after accounting for targeting strategy, set type, location, and other model covariates **(Figure 4)**. Vessels with strongly positive PC1 scores were the opposite, and vessels located closer to the origin had vessel effects closer to the fleet-wide average. The second principal component (PC2) captured the primary compositional trade-off in vessel effects, separating vessels more strongly associated with cetaceans and sea turtles from those more strongly associated with elasmobranchs. Together, these axes indicate that vessel level variation reflected not only differences in the overall magnitude of bycatch effects, but also consistent differences in the taxonomic composition of those effects.

Higher order axes revealed additional ecological structure within these broad groups **(Figure S11)**. PC3 primarily contrasted whale sharks and baleen whales, while PC4 was associated with variation in false killer whale interactions. Although these axes explained additional variation, inclusion of higher order principal components reduced clustering quality, suggesting that they primarily captured within group heterogeneity (e.g., differences within the elasmobranchs group) rather than defining additional vessel types. Collectively, these results indicate that vessels vary along continuous gradients in both bycatch propensity and species composition, with a subset of vessels exhibiting consistently elevated associations with particular taxonomic groups.

To quantify vessel performance across multiple bycatch taxa spanning a wide range of morphologies and ecological niches, we examined vessel scores along PC1 from the PCA of GAM-derived vessel effects. Because all six taxa with significant vessel effects loaded negatively on PC1, this axis can be interpreted as a gradient in overall bycatch propensity, with more negative scores indicating consistently higher bycatch across multiple taxa after accounting for other predictors included in the GAMs.

Reducing bycatch in tuna purse seine fisheries is only practical if vessels can simultaneously maintain profitable target catches. Comparison of each vessel's bycatch score, average retained tuna catch, and fishing effort revealed substantial heterogeneity in overall performance across the fleet **(Figure 5)**. Vessels with the highest average tuna catches were distributed across the full range of bycatch scores, indicating that high target catch did not necessarily require elevated bycatch. Notably, the vessels with the best bycatch intensity scores all occurred within the upper quartile of tuna catch volume and generally exhibited above average target catches.

Conversely, vessels with the lowest tuna catch volumes tended to have average rather than extreme bycatch scores **(Figure 5)**. There was therefore little evidence for a group of consistently poor-performing vessels characterised by both high bycatch across multiple taxa and very low target catch. Instead, variation among vessels appeared to reflect multiple performance outcomes, with some vessels achieving both low bycatch and high tuna catches.

This interpretation of PC1 provides a quantitative measure of vessel level bycatch performance that accounts for differences in operating conditions, including location, season, targeting strategy, and set type. However, the mean catch volume of the three principal tuna species combined is a rough measure of target catch performance that does not account for differences in catch value or operating costs (such as fuel consumption). For example, vessels targeting larger individuals or higher value species such as bigeye tuna may achieve lower average catch volumes while maintaining comparable economic performance. In addition, several of the vessels with the lowest overall effort, including those that entered or exited the fishery during the study period, occurred near the extremes of the bycatch gradient. This suggests that longer observation periods may be required to reliably characterise vessel performance in a highly variable system.

Finally, we used a generalized linear latent variable model (GLLVM) to examine co-occurrence patterns among tuna and the seven bycatch taxa while accounting for the same environmental and operational

covariates considered in the GAMs. Specifically, we asked whether catches of different bycatch taxa were consistently associated with one another and whether vessels with elevated bycatch also tended to have higher tuna catches. We initially fitted a model containing all candidate covariates and two latent variables and then progressively simplified the model until it converged. The final model did not include latent variables or a vessel effect, indicating that no residual correlation structure remained among taxa after accounting for the measured spatial, temporal, and operational predictors. This means that co-occurrence patterns among tuna and bycatch taxa were largely explained by the observed covariates rather than by unmeasured ecological processes or persistent associations among species **(Figure 6)**. Repeating the analysis with target tuna catch excluded produced a similar result.

The GLLVM coefficients describe how the relative occurrence of each taxon changes under different environmental and operational conditions after standardising responses to a common scale. Several strong and biologically interpretable patterns emerged **(Figure 6)**. The most prominent negative responses included the decline in silky shark occurrence over time, reduced tuna catches in live whale-shark-associated sets, and lower mobulid occurrence across all set types relative to free-school tuna sets. The strongest positive responses were higher whale shark occurrence in sets on live whale sharks, and higher baleen whale occurrence in sets on live whales. Overall, these patterns were broadly consistent with the taxon specific GAM results, indicating that the same operational factors drove variation in both the univariate and multivariate analyses.

The absence of a vessel effect in the GLLVM appears inconsistent with the GAM and PCA results, which identified significant vessel effects for six of the seven bycatch taxa and revealed groups of vessels with similar bycatch assemblages. However, these findings address slightly different questions. The GAMs showed that vessels differed in their effects on catch rates of individual taxa (excluding dolphins) after accounting for other predictors, while the PCA demonstrated that vessels could be characterised by different combinations of positive and negative effects for specific taxa. In contrast, the GLLVM evaluated whether vessel identity explained residual variation in the combined tuna and bycatch assemblage after accounting for spatial, temporal, and operational covariates. The absence of a vessel effect indicates that vessels were not consistently associated with higher or lower catches across all taxa simultaneously. Instead, vessel specific differences reflected trade-offs among species, with vessels exhibiting distinct bycatch profiles rather than consistently elevated catches of both target and non-target species. Together, these results suggest that species co-occurrence is primarily determined by environmental and operational conditions but vessels differ in how they operate within those conditions, which influences how effects are distributed across multiple bycatch taxa.

Discussion

As threats to marine biodiversity accumulate and awareness of population declines grows, fisheries face mounting pressure to reduce impacts on a wide range of non-target species. To explore potential opportunities and trade-offs in multispecies bycatch mitigation, we analysed a high resolution observer dataset from a tropical tuna purse seine fishery in the western Pacific. We examined catch rates of

seven bycatch taxa representing three groups of global conservation concern: sea turtles, cetaceans, and elasmobranchs. Our approach focused on operational and environmental factors that could most directly be monitored or regulated, including fishing location, season, time of day, targeting strategy, and set type. We also explicitly considered the role of individual vessels, because understanding whether bycatch is a fleet wide issue or concentrated among particular vessels could help managers design more effective interventions.

Using a combination of taxon specific GAMs, multivariate ordination, and joint species distribution modelling, we identified significant spatial, temporal, and operational drivers of bycatch of seven taxonomic groups. Overall, targeting strategy, set type, and vessel identity consistently emerged as the dominant sources of variation in catch rates. During the study period, several mandatory and voluntary mitigation measures were introduced for protected species, particularly silky sharks. Our results suggest that overall, the fleet responded to these interventions, but the responses differed among vessels. The findings also suggest that individual fishers used a variety of nuanced operational strategies, some of which may reduce risk for certain taxa while increasing risk for others.

This analysis included several bycatch taxa that were rarely encountered and occasionally occurred in very large aggregations. Although the models performed well for describing fleet and vessel-level patterns, they would not be suitable for predicting extreme bycatch events, such as captures involving multiple whale sharks, dozens of dolphins, or hundreds of mobulids or silky sharks. These events are highly stochastic and may also be difficult for observers to quantify accurately, particularly when animals escape before being brought alongside the vessel, when large target catches are processed simultaneously, or when estimates must be extrapolated from subsamples of the catch (Briand et al., 2018; Forget et al., 2021) (Briand et al., 2018; Forget et al., 2021). More generally, bycatch estimates derived from onboard observers are subject to uncertainty because non-target catches are often estimated from visual observations, limited sampling during catch sorting, or counts from a subset of brails, which may not fully represent the composition of the entire set (Briand et al., 2018; Forget et al., 2021; Hutchinson et al., 2015). Smaller species or individuals may also be under-recorded when observers have limited visibility of all areas where catch is processed (Forget et al., 2021).

Despite these limitations, we are confident that the observer dataset provides a reliable representation of fishing activity and broad bycatch patterns. Observer skill and experience vary, and observer presence can influence fisher behaviour, but complete observer coverage substantially reduces these potential sources of bias (Wakefield et al., 2018). Furthermore, observer protocols are designed to minimise reporting errors by requiring counts only when accurate enumeration is possible and weight estimates only when large catches cannot be counted directly (SPC & FFA, 2018). Therefore, while there is uncertainty around the magnitude of individual bycatch events, we do not expect these sources of error to substantially affect the fleet and vessel-level patterns that were the focus of this study.

Variation in fishing strategies and individual decision making

These results demonstrate that individual vessels are an important source of variation in bycatch rates. A major component of this vessel effect appears to be related to fishers' decisions about targeting strategies and set types, which is unsurprising in an industrial purse seine fishery (Murua et al., 2023). However, while FAD use is often the focus of discussions surrounding purse seine bycatch mitigation, our results suggest that behavioural changes were more complex than a simple shift from object associated to unassociated fishing. Although free school baitfish sets remained the dominant fishing strategy throughout the study period, unassociated sets declined relative to associated sets as the fleet increased its use of drifting man-made FADs and drifting logs or debris.

One explanation for why this shift did not result in higher silky shark catch rates may be increased adoption of non-entangling FADs, which replace entangling netting with hanging ropes and have been actively promoted within the fishery (Escalle et al., 2023). Because the observer data do not distinguish between conventional and non-entangling FADs, the set type variable represents a broad category of anchored and drifting FADs. This may also help explain why FAD associated set types had less distinct bycatch assemblages than more specific set types like whale shark sets.

While targeting strategy and set type are related, they capture different aspects of fishing behaviour (Torres-Irineo et al., 2014). Set type is recorded by the observers, whereas targeting strategy was inferred from retained tuna catch composition and therefore reflects a broader suite of undocumented tactics and decisions (Murua et al., 2023; Tidd et al., 2017). These likely include where and when fishers deploy FADs, how long they allow aggregations to develop, how they interpret acoustic information from echosounders, and other operational choices not captured in the observer data (Tidd et al., 2017). The fact that targeting strategy was retained in all seven bycatch models and the latent variable model suggests that these decisions influence not only target catches, but also bycatch risk across multiple taxa.

The effect of individual vessels on bycatch outcomes is rarely examined directly, even though it is anecdotally understood by many managers (Roberson & Wilcox, 2025; Tidd et al., 2017). By standardising catch rates after accounting for spatial, temporal, and operational factors, our analysis isolated vessel effects from other drivers of bycatch risk. Strong vessel effects emerged for six of the seven bycatch taxa, indicating that some vessels consistently had higher or lower bycatch than other vessels operating under similar conditions. These patterns suggest that vessel specific differences in fishing tactics, decision making, technology, knowledge of the environment, and operational skill of the captain and crew contribute substantially to bycatch risk (Hamilton & Baker, 2019; Seidu et al., 2022). In this technologically advanced purse seine fleet, fish finding equipment is likely an important but undocumented contributor to vessel level variation. Vessels are equipped with echosounders of varying capability, and captains differ in their ability to interpret information on biomass, species composition, and fish behaviour (Dagorn et al., 2012; Melvin, 2002). In the western Pacific, most FADs are also

equipped with echosounders, allowing captains to monitor and optimise their fishing strategies across large networks of FADs (Wain et al., 2021).

Although fishing around FADs is generally portrayed as requiring less skill than fishing for free schools of tuna, effective FAD fishing involves numerous strategic decisions (Lennert-Cody et al., 2018; Tang et al., 2019). The composition and abundance of species associated with a FAD depend on factors such as soak duration and time of day, and many target tunas and bycatch species have distinct patterns of movement around FADs (Gilman et al., 2024; Lennert-Cody et al., 2018). Fishers must balance these ecological considerations against operational constraints, including competition from other vessels for access to productive FADs (Macusi et al., 2015). Collaborative fishing arrangements and coordinated FAD teamwork among vessels add further complexity to these decisions (Lennert-Cody et al., 2018).

Additional differences in fishing tactics may also contribute to vessel effects. Some vessels use helicopters to locate tuna schools, which reduces search times and could potentially lower bycatch risk if protected species are detected from the air and communicated to the skipper (Waldo et al., 2024). Vessels may deploy support boats to help release larger animals (Swimmer et al., 2020), modify net characteristics to alter sinking rates, or operate equipment with different hauling capabilities (Tang et al., 2019). Crew experience, familiarity with the vessel, and captain knowledge of oceanographic conditions, prey distributions, lunar cycles, and weather patterns may all influence catch rates of both target and non-target species (Barz et al., 2020; Seidu et al., 2022; Squires & Garcia, 2018). Collectively, these factors could explain the strong vessel effects detected in the GAMs.

However, in complex and dynamic fisheries, it is difficult to distinguish fisher skill from stochastic variation ("luck") (Alvarez & Schmidt, 2006). This challenge is amplified for rare species and infrequent, exceptionally large bycatch events, which are difficult to predict. Consequently, some of the variation in bycatch outcomes among vessels may reflect stochastic processes rather than consistent differences in fishing practices. Additionally, much of the variation in bycatch risk remained unexplained by our models, likely reflecting a combination of unmeasured factors and inherent stochasticity. Nevertheless, the persistence of vessel effects across years, together with the extensive coverage of fishing events in our dataset, suggests that genuine vessel specific differences can still be detected despite the considerable variability inherent in the system.

Multispecies bycatch avoidance

We found little evidence that vessels consistently performed either exceptionally well or poorly across all target and bycatch species. Instead, vessels appeared to trade off among species groups. Broadly, three patterns emerged: vessels associated with elevated cetacean and sea turtle bycatch, vessels associated with elevated elasmobranch bycatch, and vessels with relatively low bycatch across most taxa. Trade-offs were also evident among targeting strategies and set types, particularly between mobulids and silky sharks. These findings are consistent with studies showing that silky sharks are strongly associated with floating objects, while mobulids are caught in both free school and object associated sets (Cronin et al.,

2026; Escalle et al., 2019; Wang et al., 2025). Encouragingly, some vessels maintained relatively low bycatch of silky sharks and mobulids, suggesting this trade-off is not inevitable.

Our findings add to growing evidence that reducing bycatch across a diverse range of taxa is challenging, particularly when fishers must simultaneously avoid elasmobranchs and air-breathing species (Drynan et al., 2026; Poisson et al., 2021; Pons et al., 2022). Some management and conservation organisations have adopted ambitious "zero bycatch" targets, which tend to receive substantial pushback from industry due to concerns about feasibility (Crowder & Murawski, 1998; Gilman et al., 2022; Good et al., 2020). While fishers can clearly influence bycatch risk through operational decisions, some component of bycatch remains stochastic and unpredictable with the currently available information and technologies; some interactions are just bad luck (Hall, 1996). This is not an argument for abandoning ambitious conservation goals, but rather for prioritising interventions that target the most important and manageable sources of risk and incentivise continuous improvement (Dolman et al., 2016; Gilman et al., 2022).

In the FIA-PNG purse-seine fleet, the management agency's focus on silky sharks appears well justified given their relatively high capture frequency and mortality rates. Sea turtles, whale sharks, and baleen whales rarely died as a direct consequence of capture, while dolphins and false killer whales also experienced relatively low immediate mortality. Nevertheless, interactions should still be minimised to reduce stress and sublethal impacts (Zollett & Swimmer, 2019). Mobulids may warrant greater management attention because they exhibited relatively high catch rates, potentially substantial mortality, and no clear declining trend through time. Their slow growth, low reproductive output, and vulnerability to multiple fisheries have resulted in all mobulid species being classified as Vulnerable or Endangered on the IUCN Red List (IUCN, 2025). However, safe handling and release practices are likely to improve post-release survival for mobulids and larger or more robust species like sea turtles, medium to large cetaceans, and whale sharks (Clavareau et al., 2020; Zollett & Swimmer, 2019).

In contrast, silky sharks—particularly juveniles—are highly susceptible to mortality during capture because they can be crushed beneath large tuna catches during brailing operations (Clavareau et al., 2020). Consequently, reducing initial capture is likely to be more effective than improving release practices. Spatial management measures and move-on rules have been proposed in many regions (Crespo et al., 2024), and voluntary spatial measures focusing on silky sharks were introduced in the FIA-PNG fleet following spatial risk analyses of silky shark, mobulid, whale shark, sea turtle, and false killer whale bycatch (Gilman et al., 2024). However, our results corroborate previous findings that broad spatial closures targeting multiple bycatch taxa would be difficult to implement effectively because bycatch hotspots vary among species, and rarer species are inherently difficult to predict spatially (Gilman et al., 2024). Real-time information sharing and move-on rules may therefore be particularly valuable for mitigating interactions with rare species and responding to occasional large bycatch events (Gilman et al., 2024). Some vessels may already be using and adapting these strategies informally.

Management implications

Encouragingly, the vessel-level patterns observed in this study suggest that fishers are already adopting effective, albeit largely undocumented, strategies to reduce bycatch. Identifying these practices and facilitating peer learning may therefore provide a practical pathway for reducing bycatch across multiple protected species simultaneously (Cronin et al., 2026; Murua et al., 2023). Managers may be able to accelerate this process by rewarding innovation and good performance, facilitating knowledge exchanges, and focusing attention on raising consistently poorer performers to a higher standard (Gilman, Chaloupka, Booth, et al., 2023; Squires et al., 2021). Such incentives can operate through formal mechanisms, including individual transferable bycatch quotas, bycatch risk pools, and other performance based management tools (Booth et al., 2021; Gilman, Chaloupka, Bellquist, et al., 2023; Gilman, Chaloupka, Booth, et al., 2023; Hilborn et al., 2026; Squires & Garcia, 2018). Informal incentives could also be effective. In the FIA-PNG fleet, anecdotal evidence suggests that company reputation and Marine Stewardship Council certification have both encouraged behavioural change. Regardless of the mechanism, mitigation is likely to be most effective when fishers retain flexibility to develop solutions suited to their specific vessel and operating conditions (Eayrs & Pol, 2019; Suuronen, 2022).

Some solutions, such as non-entangling FADs and safe-release trainings, could be applied broadly across tuna fisheries. Voluntary or mandatory move-on rules or dynamic spatial management could also be effective in some fleets (Gilman et al., 2024). Yet, even in a technically advanced, highly regulated, and monitored purse seine fleet, our results demonstrate that the decisions and behaviours of individual fishers and crews remain important determinants of bycatch outcomes. Because tropical Pacific purse-seine fleets already operate under 100% observer coverage, there is an opportunity to place greater emphasis on performance-based management rather than overly prescriptive rules governing where, when, and how fishing occurs. Providing fishers with flexibility to achieve bycatch objectives may encourage the development of solutions that are more effective and adaptable than those imposed through top-down regulation alone (Barz et al., 2020; Gilman, Chaloupka, Booth, et al., 2023).

Conclusions

The proliferation of FADs across the world's oceans is a major concern for biodiversity and the sustainability of tuna stocks (Pons et al., 2023; Tolotti et al., 2020). Our results are encouraging because they suggest that fishers are already combining a diverse suite of bycatch mitigation tactics, including strategies that maintain relatively low bycatch rates while continuing to fish on floating objects. Completely eliminating bycatch across a diverse assemblage of commonly and rarely encountered species is unlikely with current tools. However, understanding the trade-offs among species and fishing strategies can help managers develop interventions that prioritize conservation needs and encourage continuous improvement towards zero bycatch, while still maintaining viable fisheries (Gilman, Chaloupka, Booth, et al., 2023). As fisheries management increasingly incorporates broader sustainability objectives, including carbon emissions and animal welfare, solutions will need to be developed collaboratively with vessel managers, skippers, and crews. The remaining bycatch challenges

are complex and unlikely to be solved through regulation alone; continued improvement will depend on combining scientific evidence with the operational knowledge and adaptive capacity of fishers.

Declarations

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Data Availability Statement

The fisheries observer data used in this study are owned by and are available from the National Fisheries Authority of Papua New Guinea (https://www.fisheries.gov.pg/; nfa@fisheries.gov.pg) and restrictions apply to their availability. As reported in the Methods section, the query of the observer program database conducted for this study was for the period between 01 January 2019 and 31 August 2023; for purse seine vessels flagged to Papua New Guinea and the Philippines that form part of the Fishing Industry Association of Papua New Guinea’s Marine Stewardship Council certified fleet; and for all recorded catch groups. Papua New Guinea government rules prevent the authors from making the observer data publicly available. However, a vignette describing the modelling framework, model selection procedures, and model diagnostics will be made available through a public GitHub repository: https://github.com/lroberson/PNG-multispecies-bycatch-pub.

Conflict of Interest Statement

The authors declare no conflicts of interest.

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Figures

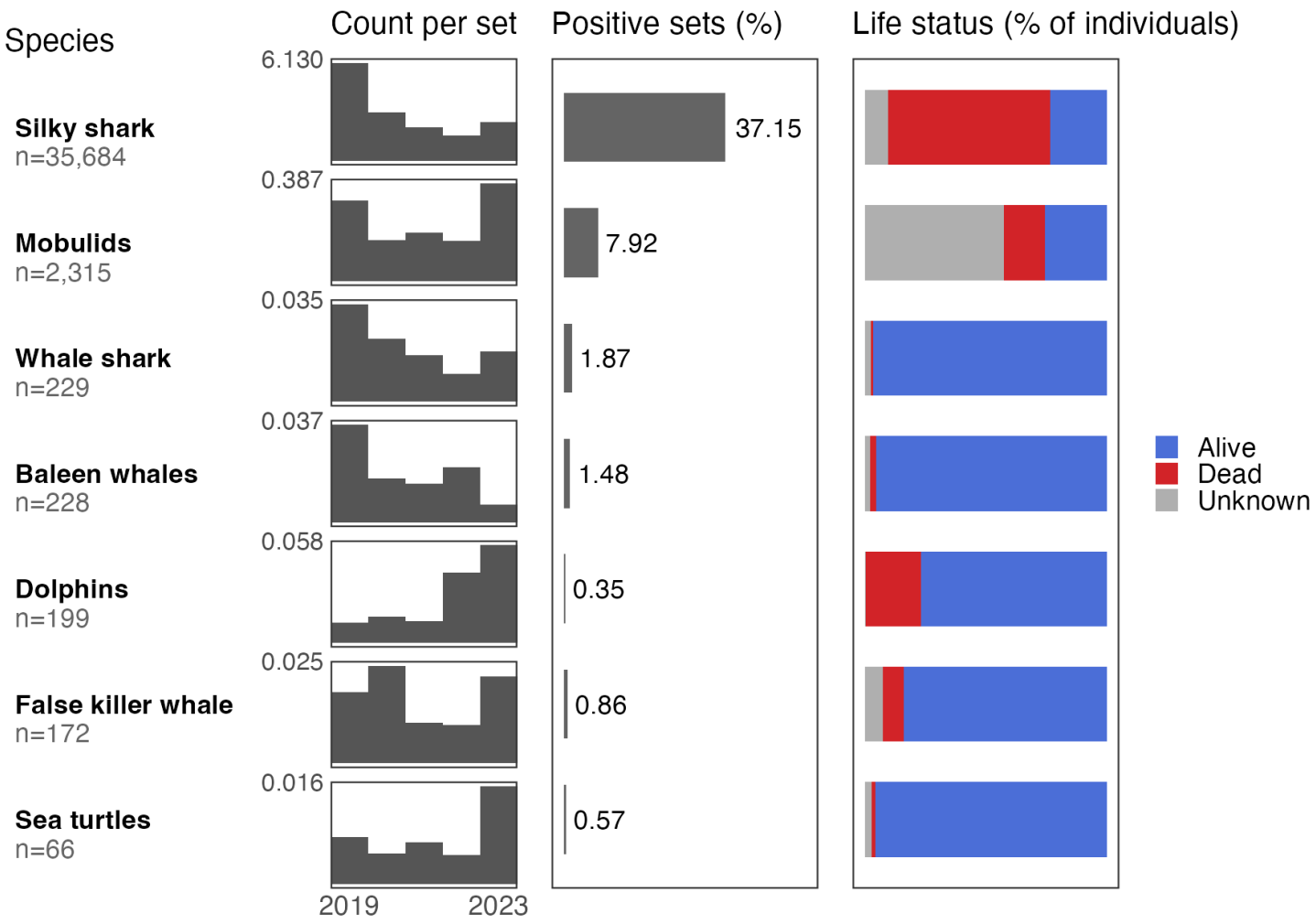


Figure 1

Bycatch of seven focus taxa recorded in the observer data from 2019—2023, ordered top to bottom by total number of individuals recorded (*n* includes some interpolated counts for silky sharks and mobulids). Positive sets had at least one individual. Life status was inferred from the description of the fate code recorded at the time of release. All individuals were released regardless of their life status, except for four retained silky sharks and three retained mobulids.

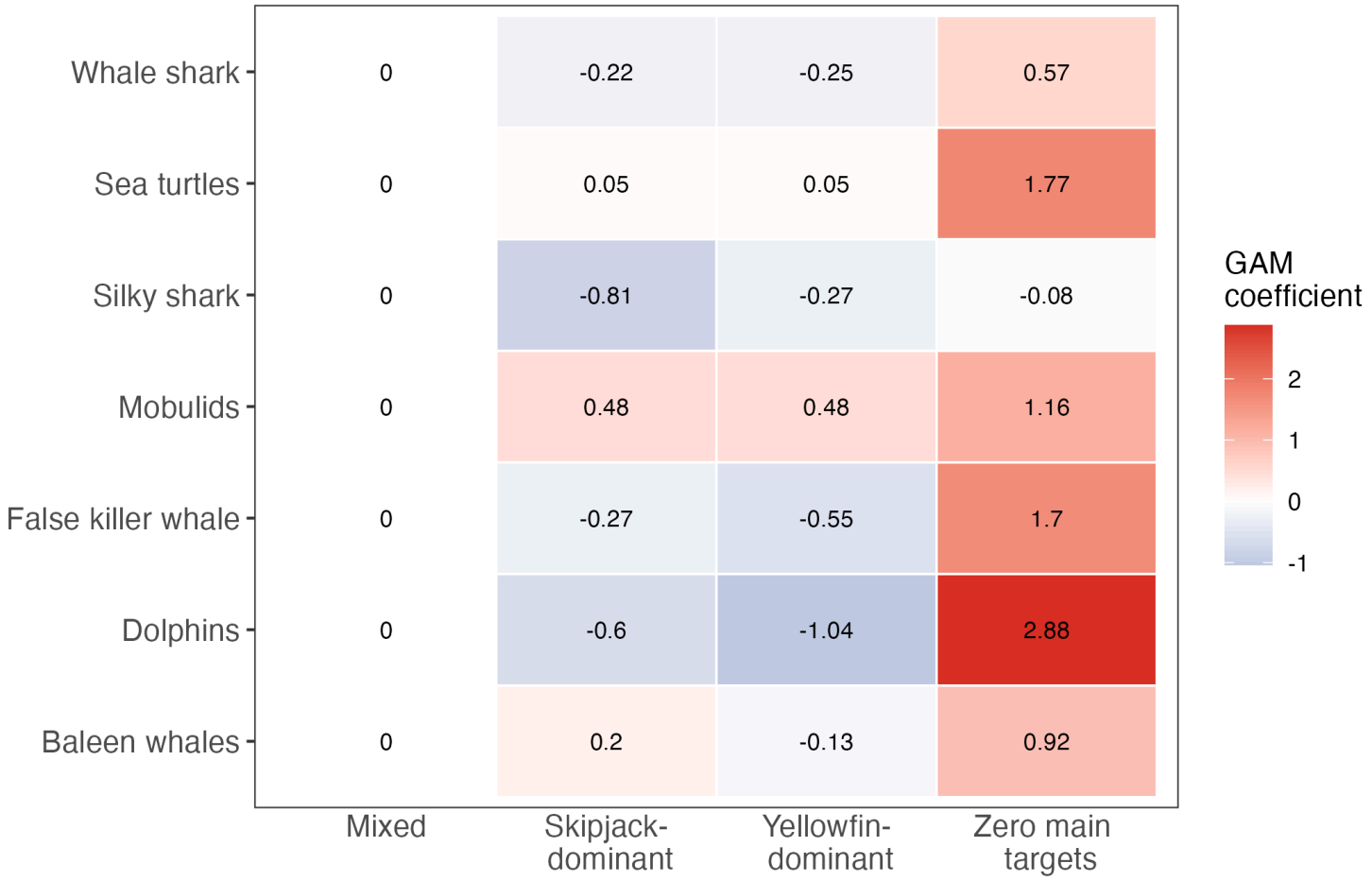


Figure 2

Heatmap of species-specific responses to tuna targeting strategies based on coefficients from the final generalized additive models (GAMs). Targeting clusters were derived from *k*-means clustering of retained tuna catch composition and comprised mixed-species, skipjack-dominated, yellowfin-dominated, and zero main target sets. Values represent model coefficients for each targeting cluster relative to the mixed species strategy, which served as the reference category (coefficient = 0). Red shading indicates higher bycatch rates and blue shading indicates lower bycatch rates relative to mixed species sets. Rows with similar colour patterns indicate similar responses among bycatch species (e.g., whale shark, false killer whale, and dolphins).

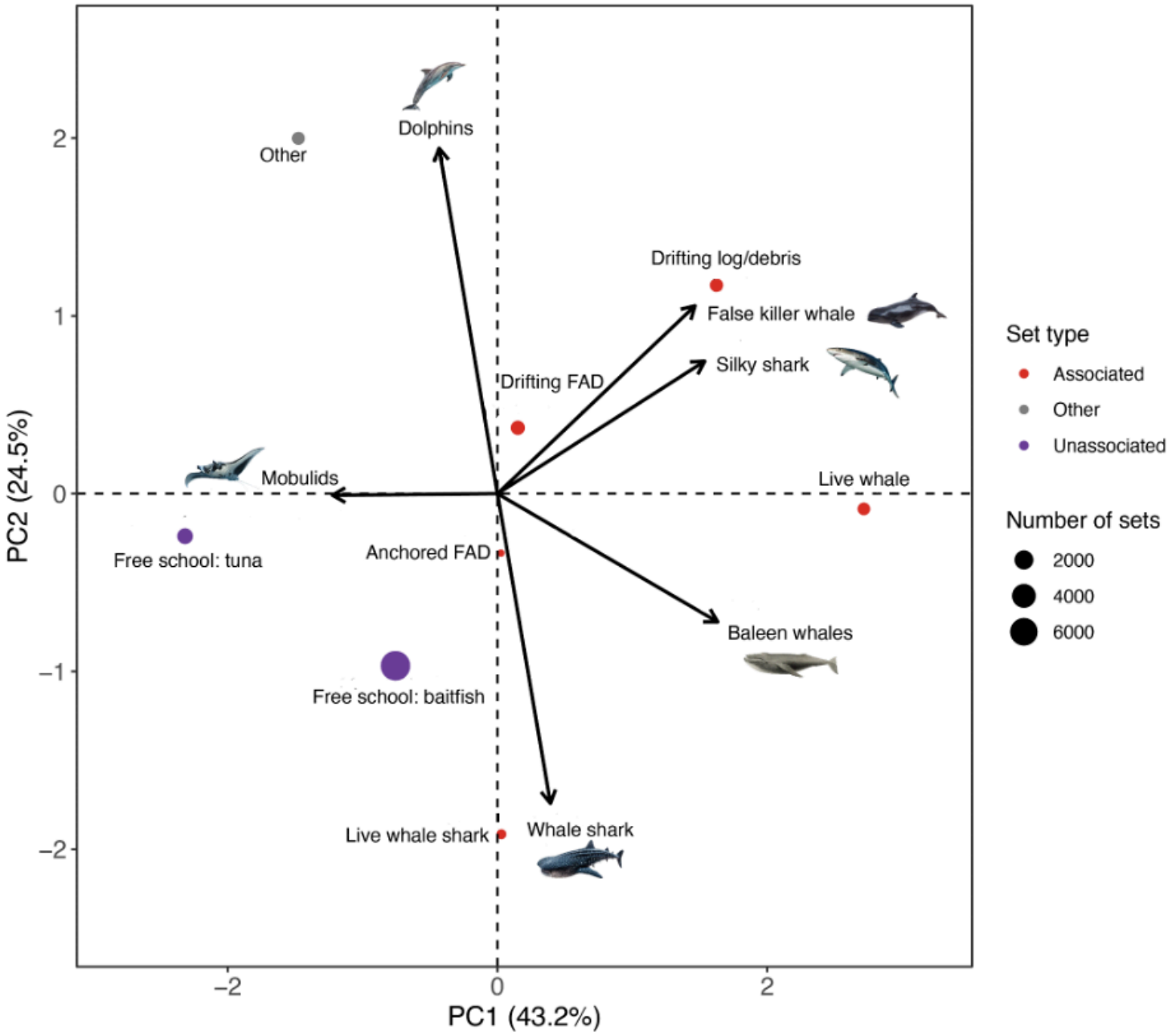


Figure 3

Principal component analysis (PCA) of bycatch assemblages for fishing set types based on taxon specific GAM coefficients for the final models that included set type as a predictor variable (all bycatch taxa except sea turtles). Points represent set types and are plotted according to the first two principal components (PC1 and PC2), which together explained 68.8% of the variation in assemblage structure. Point size is proportional to the number of observations and point colour indicates set-type category. Distances between points reflect similarity in species assemblage composition, while distance from the origin reflects the magnitude of deviation from the average assemblage. Arrows represent species loadings, with arrow length indicating the strength of each species' contribution to the ordination and arrow direction indicating association with particular set types.

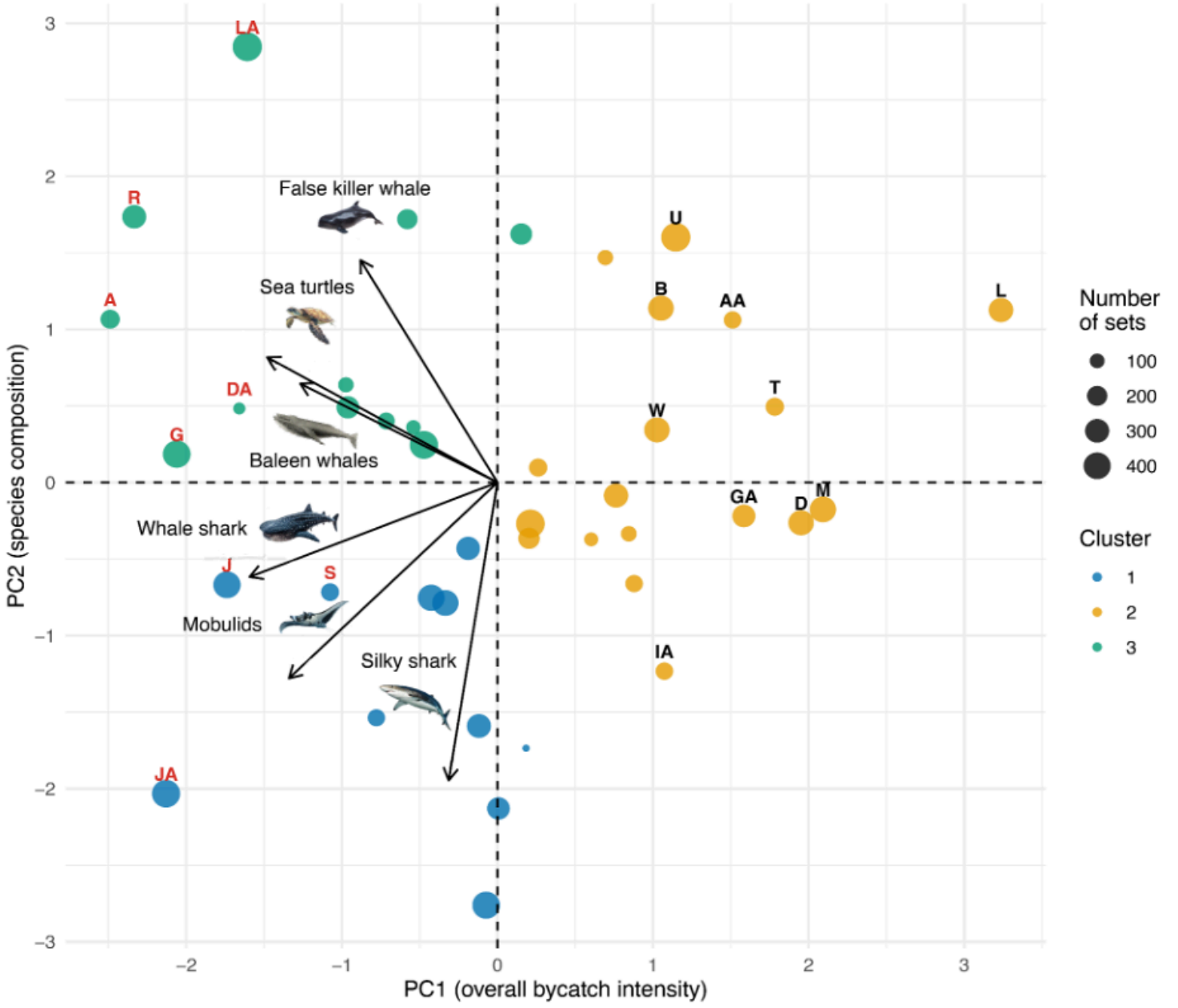


Figure 4

Principal component analysis (PCA) of vessel-level bycatch composition, with vessels grouped using k-means clustering (*k* = 3). Points represent individual vessels positioned according to their scores on PC1 (overall bycatch intensity) and PC2 (species composition), with point size proportional to the number of sets. Colours indicate cluster membership, highlighting groups of vessels with similar bycatch profiles. Arrows show species loadings, with direction and length indicating their contribution to variation in bycatch composition. Dashed lines at zero mark the origin of the PCA space. Selected vessels at the extremes of PC1 are labelled to illustrate differences between low (black labels) and high (red labels) bycatch profiles.

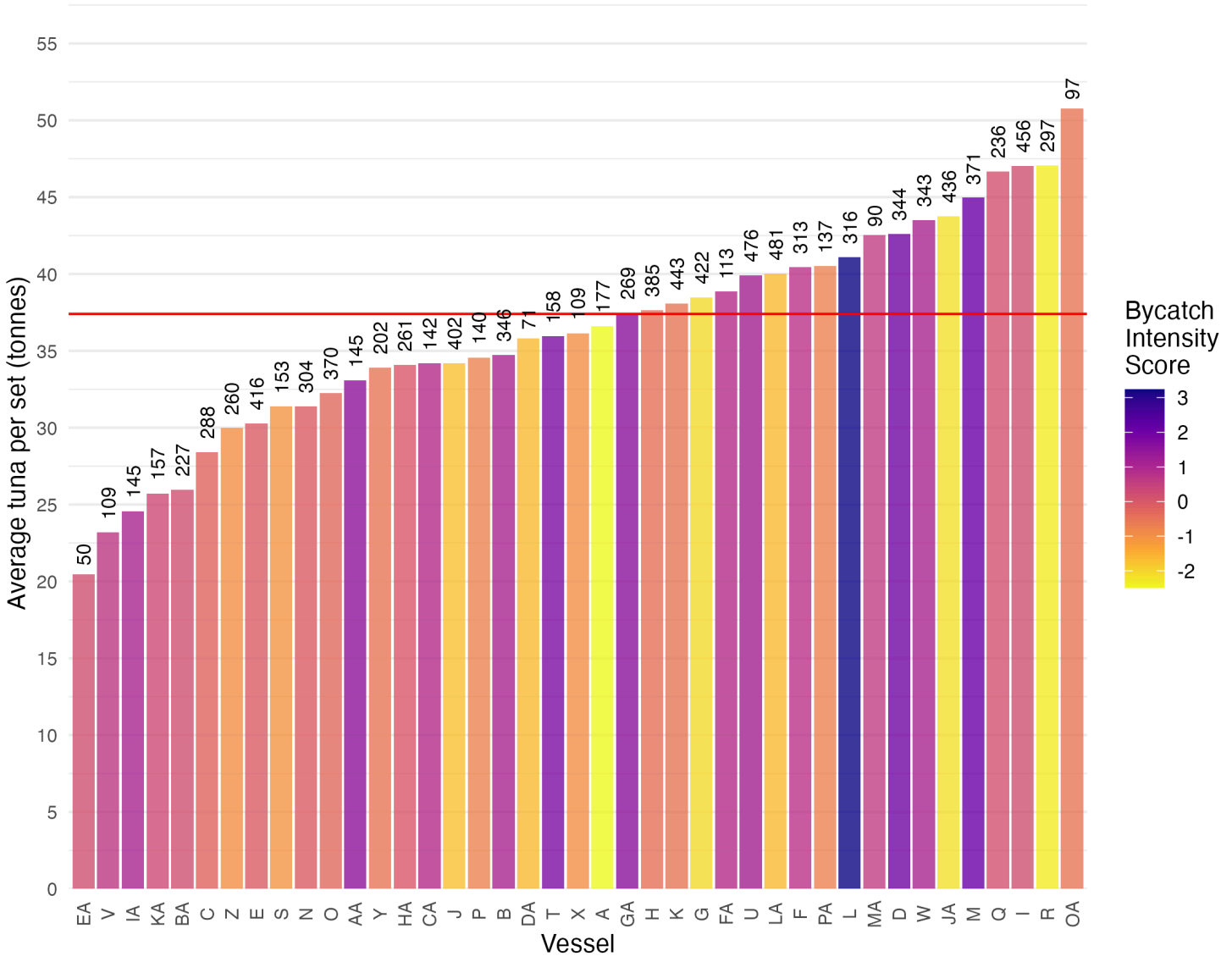


Figure 5

Vessel-specific bycatch intensity score (PC1) and average retained tuna catch per set. Colour corresponds to each vessel's PC1 score from the PCA of GAM-derived vessel effects for the six bycatch taxa in which vessel identity was retained in the final model (all taxa except dolphins). The PC1 value represents a bycatch intensity score. More negative PC1 values (yellows) indicate vessels associated with consistently higher bycatch across multiple taxa, while positive values (purples) indicate lower bycatch relative to the fleet average. Numbers above bars denote the number of observed sets per vessel. The red line shows the fleet-wide mean retained tuna catch per set (37.4 t; *n* = 10,657 sets).

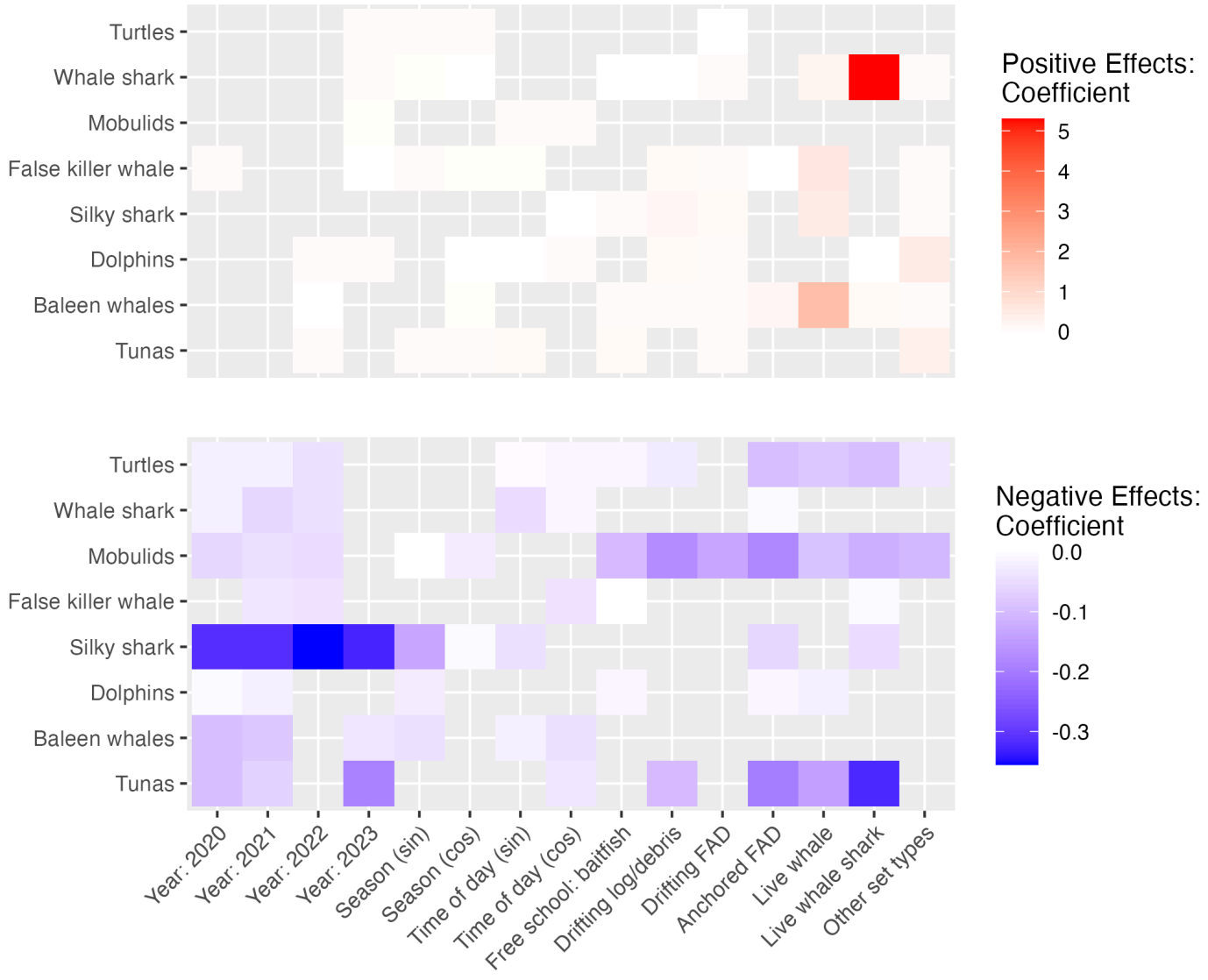


Figure 6

Relative responses of tuna and bycatch taxa to environmental and operational covariates estimated using a multivariate generalized linear latent variable model (GLLVM) with Gaussian error distribution and standardised responses. Heatmaps show taxon specific coefficients representing deviations from each species' mean response under different conditions, enabling comparison across taxa on a common scale. Positive (top) and negative (bottom) panels indicate conditions associated with higher or lower relative occurrence, respectively. Coefficients for categorical predictors are expressed relative to reference levels (e.g. baseline set type is a free tuna school and baseline year is 2019). Weak effects (coefficient < 0.05) are shown in grey. Spatial smooth terms are excluded from the figure.

Supplementary Files

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