



Get them off the deck: Straightforward interventions increase post-release survival rates of manta and devil rays in tuna purse seine fisheries

Joshua D. Stewart^{a,b,*}, Melissa R. Cronin^{b,c,d}, Erick Largacha^e, Nerea Lezama-Ochoa^{f,b,c,g}, Jon Lopez^h, Martin Hallⁱ, Melanie Hutchinson^h, Emma G. Jones^j, Malcolm Francis^k, Maitane Grande^l, Jefferson Murua^l, Vanessa Rojo^m, Salvador J. Jorgensen^{n,o}

^a Ocean Ecology Lab, Marine Mammal Institute, Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Newport, OR, USA

^b The Manta Trust, Dorchester, Dorset, UK

^c Mobula Conservation, La Paz, BCS, Mexico

^d Duke University Marine Lab, Nicholas School of the Environment, Duke University, Beaufort, NC, USA

^e Formerly: Inter-American Tropical Tuna Commission Field Office, Manta, Ecuador

^f Institute of Marine Science, University of California Santa Cruz, Santa Cruz, CA, USA

^g Ecosystem Science Division, Southwest Fisheries Science Center, NOAA Fisheries, Monterey, CA, USA

^h Inter-American Tropical Tuna Commission, Ecosystem and Bycatch Program, La Jolla, CA, USA

ⁱ redCID (Network for the Study of Incidental Captures and Discards), La Jolla, CA, USA

^j National Institute of Water and Atmospheric Research (NIWA), Auckland, New Zealand

^k National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand

^l AZTI, Herrera Kaia, Portualdea z/g, 20110 Pasaia, Gipuzkoa, Spain

^m Instituto Español de Oceanografía, Centro Oceanográfico de Canarias, Santa Cruz de Tenerife, Spain

ⁿ California State University at Monterey Bay, Seaside, CA, USA

^o Formerly: Monterey Bay Aquarium, Monterey, CA, USA

ARTICLE INFO

Keywords:

Bycatch

Mobulid

Post-release mortality

Conservation

Mitigation

RFMOs

Best practices

ABSTRACT

Bycatch remains a major challenge in commercial fisheries, with large numbers of threatened species impacted by incidental capture. One of the most vulnerable bycatch groups in global tuna fisheries are the manta and devil rays (mobulids), which have experienced significant population declines in response to both targeted and incidental capture. The retention of mobulids has been banned by many countries and Regional Fisheries Management Organizations (RFMOs), but major knowledge gaps exist in the group's survival rates following release after incidental capture. Mobulids are accidentally captured in purse seine fisheries, and in recent years, many RFMOs have mandated handling and release procedures for mobulids in an effort to maximize survivorship and reduce impacts of fishery bycatch. We synthesize data from four empirical studies using satellite tags ($n = 89$) to estimate survival rates of four species of mobulids (*Mobula birostris*, *M. mobular*, *M. tarapacana* and *M. thurstoni*) released from tuna purse seine vessels in three global regions. We directly estimate the effects of intrinsic, environmental, and operational factors, and handling and release methods on mobulid survival rates. We found a significant negative effect of time spent on deck; likely negative effects of the brailer number in which a ray was brought out of the sacked net, and remaining in the sacked purse seine net until after brailing was complete; and likely positive effects of being captured in a floating object set and body size on survival probability. The observed survival rates of mobulids with known fates were 50 % for *M. birostris*, 74.2 % for *M. mobular*, 33.3 % for *M. tarapacana*, and 20 % for *M. thurstoni*. The median predicted survival probability under optimal handling conditions was 83.7 % for *M. birostris*, 95.3 % for *M. mobular*, 82.2 % for *M. tarapacana*, and 53.7 % for *M. thurstoni*. These empirical estimates can improve handling methods and vulnerability assessments of these endangered species in global fisheries.

* Corresponding author at: Ocean Ecology Lab, Marine Mammal Institute, Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Newport, OR, USA.

E-mail address: joshua.stewart@oregonstate.edu (J.D. Stewart).

<https://doi.org/10.1016/j.biocon.2024.110794>

Received 25 June 2024; Received in revised form 8 September 2024; Accepted 13 September 2024

Available online 30 September 2024

0006-3207/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

1. Introduction

Manta and devil rays (collectively mobulids) are large, filter-feeding rays comprising nine recognized species distributed circumglobally in tropical to temperate waters (Couturier et al., 2012). Mobulid rays have one of the lowest reproductive rates of all sharks and rays, giving birth to just one pup per pregnancy after a 13-month gestation period (Stewart et al., 2018). Mobulids reach sexual maturity after 5–10 years (species dependent) and have inter-birth intervals of 2–7 years (species and region dependent), resulting in extraordinarily low intrinsic population growth rates (Dulvy et al., 2014; Stewart et al., 2018). These biological characteristics make mobulids highly susceptible to population declines, especially in response to direct and indirect (i.e. bycatch) effects of fisheries (Dulvy et al., 2014; Pardo et al., 2016). Seven out of the nine species of mobulid rays are listed as Endangered, and two as Vulnerable by the International Union for the Conservation of Nature (IUCN) Red List. While data on absolute abundance of mobulid populations remain extremely limited, relative abundance trends and fisheries landings suggest severe and rapid population declines in many species and regions, with very few examples of stable or increasing populations (White et al., 2015; Fernando and Stewart, 2021; Pacoureau et al., 2021; Carpenter et al., 2023).

The primary threat to most mobulid populations is harvest or incidental mortality in fisheries (Croll et al., 2016), although sub-lethal impacts from vessel strikes, fishing gear entanglements, habitat degradation and disruptions from unregulated tourism have been proposed as growing secondary threats (Stewart et al., 2018). Targeted fisheries for mobulid rays and retention of bycaught mobulids were widespread in the late 2000s and early 2010s in response to surging demand for mobulid gill plates in east Asia, and may have been a primary driver of population declines in the western Pacific and Indian Oceans (O'Malley et al., 2016). Consequently, several major international and national management measures for mobulids have been established over the past decade. These include listing on the Convention for the International Trade in Endangered Species (CITES), the Convention on the Conservation of Migratory Species of Wild animals (CMS), retention bans by Regional Fisheries Management Organizations (RFMOs; Cronin et al., 2023b), and fishing bans in Indonesia, one of the largest fisheries for mobulids globally (Booth et al., 2021; Setyawan et al., 2022). Despite these management efforts, the impact of discarded bycatch in international tuna fisheries is poorly understood. In addition, retained bycatch in major mobulid fishing nations such as Sri Lanka appears to have remained high years after international management implementation (Fernando and Stewart, 2021), and it remains unclear to what degree the international trade in mobulid gill plates (and thus market demand) has decreased.

Although targeted fisheries for mobulids have received the most public attention and management action due to their association with the gill plate trade, bycatch of mobulids remains widespread globally across a variety of fisheries and gear types (Mas et al., 2015; Croll et al., 2016; Alfaro-Cordova et al., 2017; Fernando and Stewart, 2021; Keznine et al., 2024). Mobulids are captured incidentally in gillnet, purse seine, longline, and trawl gears, both in subsistence/artisanal and commercial/industrial fisheries. Mobulid bycatch in industrial purse seine fisheries targeting tuna and tuna-like fishes is estimated at 13,000 mobulids per year (Croll et al., 2016). Mobulid bycatch in gillnet fisheries is likely to be far greater, but global estimates are not available (Alfaro-Cordova et al., 2017; Fernando and Stewart, 2021). Retention and landing bans, which mandate prompt release of incidentally entangled mobulids, may not be effective at avoiding bycatch or reducing their mortality in gillnet fisheries, as survival rates of mobulids (and other ram ventilators that must swim actively to breathe) released from gillnets are expected to be low due to long soak times of unattended nets (Dapp et al., 2016; Benson et al., 2018). However, at-vessel mortality rates (i.e. mortality prior to release) of mobulid rays captured in longline fisheries are low (1–5 %; Coelho et al., 2012; Mas et al., 2015; National Marine Fisheries Service,

2023), and early indications from tagging studies suggest that post-release mortality rates of mobulids in purse seine fisheries may be lower than the expected mortality rates in gillnets, depending on handling methods and operational characteristics (Francis and Jones, 2017; Hutchinson et al., 2017). This suggests that improving handling and release methods may be a potentially effective mitigation solution for mobulids in these ubiquitous and large-scale fisheries (Poisson et al., 2014; Cronin et al., 2023b).

All RFMOs have recently implemented retention bans for mobulid rays (Cronin et al., 2023b; ICCAT, 2024). In addition, many have mandated specific handling practices or banned practices that may reduce survivorship, such as the use of gaffs, hooks, and cables to maneuver and offload mobulids from the vessel. Simulations of spinetail devil ray (*Mobula mobular*) vulnerability status in the eastern Pacific suggest that increasing post-release survivorship for the species could be more effective at reducing the population's vulnerability to declines than closing all purse seine and longline fisheries in the management jurisdiction for nine months each year (Griffiths and Lezama-Ochoa, 2021), highlighting the potential value of improving post-release survivorship as a management and mitigation option for these species.

To date, a single peer-reviewed study has evaluated post-release survival of mobulids (Francis and Jones, 2017), leaving major knowledge gaps in baseline survival rates across species and how environmental, operational, and handling and release characteristics may influence survival probability. Here, we use archival satellite tags deployed on the four most common species of mobulid rays incidentally captured in purse seine fisheries in three global regions to compare species-specific post-release survival probabilities and to estimate the effects of handling practices, environmental conditions, and fishery operational characteristics on survival probability. Based on our results, we make recommendations for best handling and release practices to maximize survival probability and minimize impacts on mobulid rays in tuna purse seine fisheries.

2. Methods

2.1. Data collection

We compiled survivorship data from four separate empirical studies on mobulid rays released alive from tuna purse seine fisheries in the Eastern Tropical Pacific (ETP), New Zealand (NZ), and the Eastern Atlantic (ATL). Four mobulid species were targeted in these studies: *M. birostris*, *M. mobular*, *M. tarapacana*, and *M. thurstoni*, all of which are cosmopolitan species found in all ocean basins in tropical, sub-tropical, and some temperate regions (Couturier et al., 2012). Methodological details varied slightly across studies, as they were planned and conducted separately and in most cases at different times. Below we describe the specific methodology for each study, but first we provide a general description of tuna purse seine operations and archival tag deployments that were consistent across studies.

Tuna purse seine vessel sizes and capacities (metric tons) vary greatly both across and within regions. Purse seine vessel capacities in this study ranged from 205 to 1355 mt in NZ, 299–1369 mt in the ETP, and > 1200 mt in ATL. Vessel capacities reflect the maximum tuna catch volume that can be captured and stored, and the broad range of vessel capacities included in this study reflects the variability of catch volumes in most industrial purse seine fleets globally. In the purse seine fishing modality, tuna schools are first encircled with the main purse seine net, which varies in length and depth depending on vessel size. Across the four studies, purse seine sets were either made on unassociated / free tuna schools, or on floating objects (natural objects or fish aggregating devices; FADs). In the ETP, sets are also made on schools of dolphins that associate with tuna, but no tags were deployed in dolphin sets. After setting, the bottom of the net is closed ('pursed'), entrapping the target catch and any bycatch. Over the course of several hours the main net is hauled in, reducing the volume of the encircled tuna, and constraining

the catch into a dense sack at the side of the vessel ('sacking') for increased efficiency during loading onto the vessel ('brailing'). Catch is then loaded onto the vessel via a large dip net (the 'brailer') lowered into the sack using a crane from the deck. The catch from each brail (~2–10 mt) is sorted on deck and emptied into refrigerated holds. Bycatch species are typically identified by the crew either in the sacked main net or in the brailed catch. When a bycaught species is brought on board using the brailer, it is typically maneuvered onto the deck to await release by the crew. In some cases, mobulid rays became entangled in the sacked main net and therefore were released after the entire catch was brailed, usually by using the sack itself to lift and maneuver the ray onto the deck. Trained observers and scientists deployed archival satellite tags on bycaught mobulids on deck after they were brailed or brought on board entangled in the net, or occasionally while the ray was in the sacked main net awaiting release.

Across all four studies, observers deployed either a survivorship pop-off archival tag (sPAT) or a MiniPAT tag (Wildlife Computers, Redmond WA) attached to the ray using a short (~10 cm) tether and a large plastic umbrella anchor. The tags were affixed into the dorsal musculature approximately 15 cm behind the anterior margin of the pectoral fin, in the crease between the pectoral fin and the body cavity to minimize interference with normal swimming behaviors. Tags were programmed to detach after a fixed number of days (described below for each study),

after remaining at a constant depth for 24–72 h (variable among deployments), or if the tag reached a depth of >1700 m, the latter two scenarios indicating a mortality. In the case of MiniPAT tags, depth, temperature, and light level archives were recorded and transmitted for the full deployment period. In the case of sPAT tags, the final five days of depth and temperature archives were transmitted after release.

Differing metrics of animal status or condition and behavior upon release were collected across the four studies, making standardized reporting of condition challenging. In addition, condition was not included as a covariate in analyses due to potentially confounding effects (see 2.3 Statistical Analysis). We therefore do not report further on the details of condition and behavior metadata from each study.

2.1.1. Eastern tropical Pacific

From 2017 to 2024, we trained fishery observers from the Inter-American Tropical Tuna Commission (IATTC) and the Tuna Conservation Group (TUNACONS) to deploy satellite tags on mobulid rays and collect relevant data on the specimen, operational characteristics, environmental data, and handling and release methods. We conducted in-person training workshops in Manta, Ecuador, provided all observers with a written protocol in English and Spanish, and created an instructional video on the tagging procedure for observers to refresh their skills prior to being assigned a tagging kit.



Fig. 1. Example handling and release methods. A) *Mobula mobular* being released by hand. B) *M. thurstoni* being released using a stretcher. C–D) *M. tarapacana* and *M. birostris* being released using cargo nets. Note the satellite tags visible in (A) and (B), indicated by red arrows. Photos courtesy of TUNACONS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Observers noted the species and took a reference photograph that included the side of the head, eye, cephalic fin, spiracle, and anterior margin of the pectoral fin, which was used for expert species confirmation (Stevens et al., 2018). Observers collected disc width and/or disc length using a flexible measuring tape. In four cases, observers took an image of the full disc length with a provided 25 cm scale for reference, and the disc length was estimated by measuring the pixel distance relative to the pixel distance of the 25 cm scale. Disc length was converted to disc width using the mean body proportions reported in Notarbartolo di Sciara (1987) for *M. tarapacana*, *M. mobular*, and *M. thurstoni*, and in Marshall et al. (2009) for *M. birostris*. Observers recorded the sex of the ray when possible, the time that the ray was brought aboard, the brailer number containing the ray, the position of the ray in the brailer (bottom, middle or top), the time that the ray was released back into the water, the set size (tons of catch), and the water temperature. Observers described and, in most cases, filmed the release methods, which were categorized into manual release (by hand), release using a stretcher, and release using a cargo net (Fig. 1). In some cases, mobulid rays were caught in sets with zero tuna catch (otherwise known as a “skunked” set) or were entangled in the sack of the main net and brought on board by hauling in the main net after the entire tuna catch was brailed. In these situations, rays that were brought on board and released using the sack of the main net were considered cargo net releases, and we applied an additional effect to account for either being left in the main net until brailing was completed, or for the potential effect of being entangled and immobilized in the net (see 2.3 Statistical Analysis). Other less common release methods included pushing a ray down a ramp, or lowering the floats of the sacked net and pushing the ray out without first bringing it on board or removing it from the water (see 3. Results). Animals were only tagged if they appeared to be alive. Satellite tags (both MiniPAT and sPAT) were programmed to detach after 30 days, or if constant depth or maximum depth conditions were exceeded.

2.1.2. Atlantic

In July of 2018, during a commercial tropical tuna purse seine fishing trip onboard a 107 m, 3177 mt ton vessel in the Eastern Atlantic Ocean within the Exclusive Economic Zone of Gabon, six incidentally captured *M. tarapacana* were tagged. One ray was entangled in the net and landed early during net hauling, while all other rays were brought on board using the brailer. Scientists recorded time of sack formation, brail number, set size (tons of catch) disc width, sex, handling and release methods used, and time from landing to release. All rays were tagged with MiniPAT tags, programmed for 100-day deployment periods. The rays were released using the vessel's standard handling procedures of release by transferring animals from the brailer onto a cargo net and using a winch to release the animals on the opposite side of the vessel than the hauling operations. The single ray that was entangled in the net was released by hand.

From 2019 to 2023, a mobulid ray tagging program was conducted by AZTI and funded by the Basque Government and OPAGAC on tropical tuna purse seiners (ANABAC and OPAGAC tuna purse seiner vessels) operating in the Atlantic Ocean. On-board observers were trained by personnel from Instituto de Español de Oceanografía (IEO), DataFish and AZTI to deploy satellite tags on mobulid rays and to collect specific data on the fishing operation (location, date and time of the set, total catch, and net sacking start time), individual metrics (species, sex, length and disc width in cm), and handling information (brailer number containing the position in the brail (top, middle, bottom), time when brailed on board, time when released, and mode of release (using the brailer, a light stretcher, cargo net, using specific equipment such as a hopper or lateral doors, manually from deck, after disentangling from hauling net). When possible, observers collected pictures from the tagged animals for species identification confirmation. sPAT tags were programmed for 30 to 60-day deployments, and MiniPAT tags were programmed for 180-day release.

2.1.3. New Zealand

Following protection of *M. mobular* and *M. birostris* under the New Zealand Wildlife Act in 2011, fishery observers were provided with data forms to document captures of mobulid rays during tuna purse seine fishing activities. The fishery operates seasonally around northern parts of the North Island, with vessels ranging from 30 to 80 m length, and FADs not permitted. Observers were trained to deploy Wildlife Computers MiniPAT and sPAT tags on bycaught mobulid rays. The format of data forms varied over time but included the following: size (disc width measured with a flexible measuring tape) and sex if pelvic fins were visible, information on the stage in the fishing operation that rays were observed and removed, and handling and release methods, including time out of the water. Brailer number and location in brail were recorded in only some instances due to changes in data form format. Additional information was sometimes available from trip reports, diaries, and photographs, as well as information on location, depth, set size (tons of catch), and water temperature from the commercial fishery catch and effort data from the Fisheries New Zealand Enterprise Data Warehouse (EDW).

When a ray was tagged, a tagging sheet was also completed with information on the tag, the status of the ray, attachment location, and release location. Observers were instructed to treat tagged rays using normal handling practices. MiniPAT and sPAT tags were programmed to release after 30 days. The archived data was transmitted at the end of the deployment and processed and analyzed following protocols outlined in Francis and Jones (2017).

The handling of rays as they were brought onboard and released was categorized using the data forms along with supplementary information such as observer diaries, photographs and videos where available. Rays were classed as either brailed onboard or lifted onboard in the sack of the main net (including from unsuccessful skunked sets). Release methods observed included being released by hand, being lifted from the water and then cut and dropped out of the main net directly, release from the brailer, and release using a cargo net or rope sling. All of these methods aside from manual release were classified as a cargo net release as they involved lifting and maneuvering the ray with a net attached to a crane or winch.

2.2. Fate determination

We identified post-release mortality based on sinking behavior and subsequent release of a satellite tag due to the tag exceeding either its maximum depth or allowable time at a constant depth (Francis and Jones, 2017; Benson et al., 2018), both of which trigger an active release (Fig. 2). We considered rays that had tags remain attached for >15 days to have survived, as this was almost five times the average time at liberty of rays with tag-recorded mortalities (mean 3.24 days to mortality, maximum 10 days; Fig. S2). For tags that detached in fewer than 15 days, we visually inspected dive profiles to determine if the ray was exhibiting normal dive behavior similar to rays with longer tag retention times (e.g. rapid dives to >200 m) or abnormal dive behavior similar to rays that died (e.g. remaining in the top 50 m for multiple days, no diel dive cycle; Fig. 2), and considered a ray to have survived if it was exhibiting normal dive behavior for the three days prior to premature tag release (Francis and Jones, 2017).

2.3. Statistical analysis

We used a Bayesian logistic regression to estimate the effects of recorded covariates on the survival probability of released mobulid rays. We modeled survival as the outcome, with a tag-recorded survival represented by 1 and a mortality represented by 0. We excluded tag failures where fates were unknown. Covariates included in the model are reported in Table 1. In the case of continuous covariates, we centered and scaled them such that they each had a mean of 0 and a standard deviation of 0.5, so that covariate effects would be comparable in scale

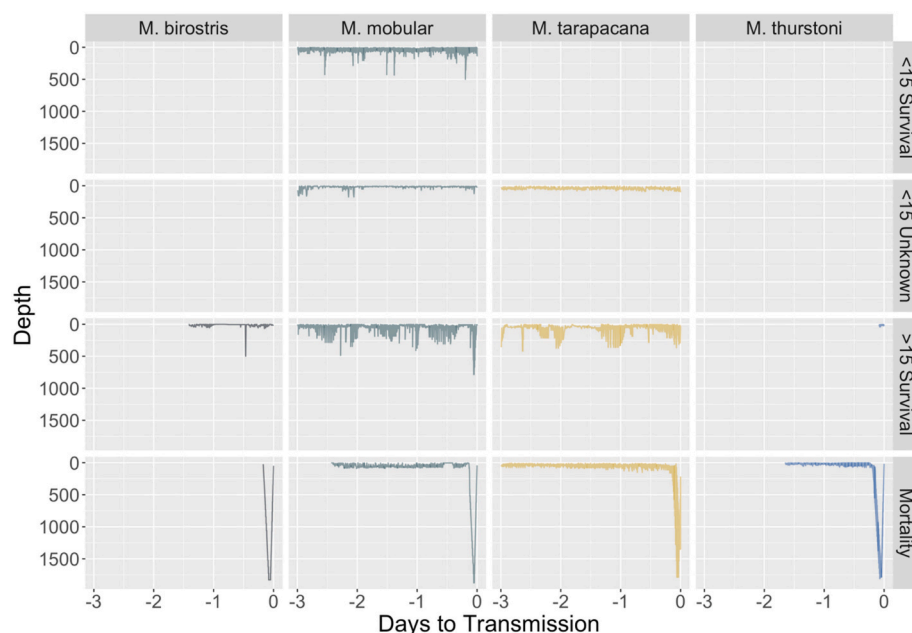


Fig. 2. Dive behavior of tagged mobulid rays. Tag-recorded depth records from the three days prior to tag release were used to determine the fate of tagged rays. Individuals that died sank, with tags releasing after maximum depth thresholds or time at constant depth thresholds were exceeded ('Mortality'). Individuals with >15 day tag deployments were considered survivors. Dive profiles of individuals whose tags released in <15 days were inspected to determine if individuals engaged in normal dive behaviors (e.g. deep frequent deep dives) prior to tag release, in which case they were considered survivors. Two tags released in <15 days and had ambiguous dive profiles; one *M. tarapacana* that appeared to be moribund, and one *M. mobular* that exhibited some >100 m dives but may also have been moribund. Note that the one surviving *M. thurstoni* tag released after 30 days, but due to battery issues only a very short time series of dive data was transmitted via satellite. In some cases, depth time series from multiple tags are plotted in a single panel.

Table 1

Covariates included as explanatory variables for survival probability in the analysis. Covariates that were centered & scaled were subtracted from the mean value and divided by the standard deviation such that mean = 0 and standard deviation = 0.5. For all binary covariates, 0 indicates 'No' and 1 indicates 'Yes'. FAD Sets refer to purse seine sets made on a fish aggregating device or floating object, and all other sets were made on unassociated tuna schools.

Covariate	Type	Centered & scaled?	Units	Range
Species	Categorical	–	<i>M. birostris</i> , <i>M. mobular</i> , <i>M. tarapacana</i> , <i>M. thurstoni</i>	–
Body Size (Disc Width)	Continuous	Y	cm	110–554
Male	Binary	–	Yes/No	0–1
Brailer Number	Continuous (integer)	N	–	0–17
Time Spent on Deck	Continuous	Y	Minutes	0–48
Release Method	Categorical	–	By Hand/Stretcher/Cargo Net	–
Entangled in Sack (Normal set)	Binary	–	Yes/No	0–1
Entangled in Sack (Skunked set)	Binary	–	Yes/No	0–1
Tons of Catch	Continuous	Y	Tons	0–200
Water Temperature	Continuous	Y	°C	21.0–29.1
FAD Set	Binary	–	Yes/No	0–1

between continuous and binary variables (Gelman et al., 2008). However, we did not center and scale brailer number in order to allow missing values to be imputed as categorical values (see below). We did not include brailer position (top/middle/bottom) as all but two specimens in the eastern Pacific were on the top of the brailer, and this information was not consistently recorded in either the Atlantic or New Zealand. We considered release by hand (manual) to be the intercept, and applied fixed effects for stretcher and cargo net releases. We did not include reported specimen condition as a covariate both because the condition scales were inconsistent across studies, and because we believe condition is likely to be a confounding covariate for survival probability, as many of the other included covariates are likely to influence condition in addition to survival probability, and it would therefore mask the potential causal effects of upstream covariates on survival if it were included alongside them in the model (D'Agostino McGowan et al., 2023).

Data were missing in some cases for brailer number, sex, time on

deck, and temperature, and we allowed the model to estimate these missing values. For missing sexes, we used a Bernoulli prior with a probability of 0.5 so that missing sexes had an a-priori equal chance of being male or female. For missing brailer numbers, we used a categorical prior with equal prior probabilities of categories 1–5, as all but three specimens with known brailer number was brought on deck in brailers 1–4 (92 % in brailers 1 or 2). For missing time on deck and temperature values, we used a prior with a normal distribution of mean 0 and standard deviation 1, which provided twice as much variance as the observed data distributions for the missing data to be freely imputed without constraints. Because brailer number was not centered and scaled within the model, we transformed the posterior estimate of the covariate effect post-hoc by multiplying it by 2 times the standard deviation of the observed distribution of brailer numbers to make it directly comparable to other covariate effect sizes.

For all covariate coefficients, we used uninformative priors that were normally distributed with mean 0 and standard deviation 1.5. We note

that these priors were for logit-transformed covariates, and $N(0,1.5)$ on the logit scale provides an approximately flat, uninformative prior on the proportional (0,1) scale. We compared three variations of the same basic linear model. The first model ('Shared') estimated shared covariate effects for each species, and a separate intercept term for each species' baseline survival probability. The second model ('Fixed Effects') estimated covariate effects independently for each species, such that each species had its own relationship to each covariate except for release method (which was shared across species), and a separate intercept term for each species. The third version ('Hierarchical') had a hierarchical structure such that there was a global mean effect for each covariate, and species-level effects normally distributed around that mean effect with model-estimated variance. This model assumed that there was a general (global mean) relationship between each covariate and mobulid survival probability, but that individual species could have departures from that mean relationship. In the hierarchical model, intercept terms for species were estimated separately (not hierarchically) as with the other two model formulations, and the effect of release method was shared across species.

We compared the three model formulations above using leave-one-out information criteria (LOOIC), and selected the model with the lowest LOOIC value (Vehtari et al., 2017). We also considered Pareto k values from the LOOIC calculations as a metric of model performance. Pareto k values indicate the relative influence of individual data points on a model by determining the extent to which posterior estimates change when one observation is held out (Vehtari et al., 2017). If a model is misspecified, it is likely to have many highly influential data points (large Pareto k values) and therefore poor predictive performance. To assign significance to covariate effects, we used a threshold of 95 % posterior probability that a covariate effect was less or >0 , and we also noted likely negative or positive effects for covariates with >90 % probability of an effect less or >0 . We coded and ran models using JAGS (Plummer, 2003) and R (R Core Team, 2021), and ran three MCMC chains for 400,000 iterations with a burn-in period of 200,000 and thinning interval of 200, resulting in 3000 retained posterior samples. We evaluated model convergence based on visual inspection of chains and \hat{R} values <1.05 , which indicates that an infinite number of iterations would lead to potential reduction of posterior intervals by <5 % (Gelman and Rubin, 1992).

To test the sensitivity of the model estimates to the inclusion of data from mobulids that were released using the main net and thus had estimated times on deck of zero minutes, we excluded the single individual with a known fate (a *M. mobular* tagged in New Zealand), re-ran the final selected model, and compared the posterior effects for covariates with the model including all data.

3. Results

3.1. Tag deployments and operational characteristics

We deployed a total of 89 satellite tags on 4 *M. birostris* (3 in ETP, 1 in ATL), 41 *M. mobular* (20 in ETP, 16 in NZ, 5 in ATL), 32 *M. tarapacana* (19 in ETP, 13 in ATL), and 12 *M. thurstoni* (11 in ETP, 1 in ATL). Of those deployed tags, 58 reported data and 31 failed to report. Tag failure rates were highest in ETP deployments (23 failures out of 53 deployments; 43.4 %), slightly less common in ATL (6 out of 20 deployments; 30 %), and uncommon in NZ deployments (2 out of 16; 12.5 %). Tag failures were most common in *M. thurstoni* (7 out of 12 tags failed; 58.3 %), followed by *M. birostris* (2 out of 4 failed; 50 %), *M. tarapacana* (13 out of 32 failed; 40.6 %), and *M. mobular* (9 out of 41 failed; 22 %). In total, we recovered data from working tags on 2 *M. birostris*, 32 *M. mobular*, 19 *M. tarapacana*, and 5 *M. thurstoni*.

Tags that reported remained attached for an average of 14.7 days. Tags from surviving individuals remained attached for mean 24 days (range 6–82). The mean time to death for individuals that died was 3.24

days (range 0–10). Two tags (one *M. mobular* that detached after 10 days and one *M. tarapacana* that detached after 13 days) had ambiguous fates based on dive profiles (Fig. 2) and were excluded from statistical analyses. The *M. tarapacana* tag exhibited restricted dive behavior likely indicative of an impending mortality, but the tag detached prior to recording the event. The *M. mobular* tag exhibited some dives >100 m, but with a far more surface-associated profile than other *M. mobular* tags, possibly indicating that the ray was moribund. We did not include these two tags in the survival analysis as the fates were unknown. The observed survival rates of mobulids with known fates were 50 % for *M. birostris*, 74.2 % for *M. mobular*, 33.3 % for *M. tarapacana*, and 20 % for *M. thurstoni*.

Mean disc widths of tagged specimens were 454 cm (range 335–554) for *M. birostris*; 225 (110–270) for *M. mobular*; 267 (196–300) for *M. tarapacana*; and 178 (154–224) for *M. thurstoni*. Mean minutes spent on deck were 5.67 (range 0–12) for *M. birostris*; 7.10 (0–48) for *M. mobular*; 6.93 (0–16) for *M. tarapacana*; and 6.45 (2–10) for *M. thurstoni*. Mean disc widths of individuals released by hand were 219 cm (range 130–297); 211 cm (110–297) by stretcher; 266 cm (178–554) by cargo net; one 185 cm *M. thurstoni* was released using a ramp; and one 292 cm *M. tarapacana* and one 475 cm *M. birostris* were released directly from the sacked net without being removed from the water. All three of the tags failed from individuals released by ramp or directly from the sacked net without being removed from the water, and thus only hand, stretcher, and cargo net releases were considered in survival analyses. Mobulids released by hand spent mean 8.6 min on deck prior to release (range 2–48); 6.3 (2–14) for stretcher releases; and 5.7 (0–15) for cargo net releases, including individuals that were lifted out of the water, maneuvered and released using the main net without first being lowered onto the deck (individuals with 0 min deck time). The *M. thurstoni* released using a ramp spent 6 min on deck. The longest that a ray with a confirmed survival spent on deck before release was 13 min (a *M. tarapacana* tagged in the ETP). The mean time spent on deck for all surviving rays was 5.9 min, and was 10.2 min for rays that died. In the ETP, 2 *M. birostris*, 2 *M. mobular*, 3 *M. tarapacana*, and 2 *M. thurstoni* were either brought on board or released directly from the sack of the main net, without being brailed. In NZ, 9 *M. mobular* were brought on board directly from the sack of the main net.

The mean catch size varied across bycaught mobulid species. The mean tons of catch in sets containing tagged *M. birostris* was 8.75 tons (range 0–12); *M. mobular* 18.86 tons (0–200); *M. tarapacana* 17.26 (0–77); and *M. thurstoni* 28.8 (0–100). Three *M. birostris* were captured in FAD sets and one in a free school set; 18 *M. mobular* were captured in FAD sets and 23 in free school sets; 22 *M. tarapacana* were captured in FAD sets and 10 in free school sets; and 8 *M. thurstoni* were captured in FAD sets and 4 in free school sets. In the ETP, the mean water temperature during sets containing *M. birostris* was 26.5 °C (range 24.9–27.7); *M. mobular* 25.7 °C (21.6–27.7); *M. tarapacana* 25.7 °C (23.5–27.3); and *M. thurstoni* 26.0 °C (20.9–28.7). The mean water temperature of sets containing *M. mobular* in NZ was 22.4 °C (21–24.1). In ATL, the mean water temperature during sets containing *M. mobular* was 24.9 °C (only one set with recorded temperature); *M. tarapacana* 25.5 °C (24.4–29.1); and *M. thurstoni* 27.2 °C (only one set).

The full biological, handling, environmental, and operational conditions associated with each tag deployment are reported in Supplemental Table S1, and in select summary plots in Supplemental Fig. S1.

3.2. Model results

3.2.1. Key findings summary

We found a significant negative effect of time spent on deck prior to release on survival probability. *M. mobular* had a significantly higher baseline survival probability than the three other species included in the analysis, although *M. birostris* and *M. thurstoni* have comparatively limited sample sizes. We found likely negative effects on survival probability of the brailer number that a ray was brought out of the

sacked net in, and of being left in the sacked purse seine net until after brailing is complete; and likely positive effects of being captured in a FAD set and body size.

3.2.2. Detailed model results

LOOIC scores were lowest for the *Shared* model formulation, 3.2 points higher for the *Hierarchical* model, and 8.8 points higher for the *Fixed* model, with standard errors of LOOIC scores ranging from 8.3 to 11.5 points, which made it impossible to choose a best performing model based on LOOIC as the standard errors of the LOOIC scores were larger than the differences in LOOIC scores. Instead, we selected the top model based on model fit diagnostics as indicated by Pareto k values (Vehtari et al., 2017). The *Shared* model formulation had 96.4 % of observations under the 0.7 Pareto k diagnostic threshold indicating there were few (3.6 %) highly influential data points that may indicate poor model performance or model misspecification, compared with 89.3 % < 0.7 in the *Fixed Effects* model and 82.1 % < 0.7 in the *Hierarchical* model. We therefore present results from the *Shared* model formulation.

The model estimated a significant (>95 % probability) negative effect of time spent on deck (median = 1.65; 95 % CI -3.42 - 0.32; 99.5 % probability < 0). The model estimated likely (>90 % probability) negative effects of the brailer number containing a ray (-1.63; -4.88–0.67; 90.8 % < 0) and of a ray being left in the sack of the main net and released after brailing was complete (-1.72; -4.0 - 0.42; 94.6 % < 0). In contrast, the model did not estimate a significant or likely effect of being left in the sack and released immediately from a skunked set (69.6 % < 0). The model estimated a likely positive effect of body size on survival probability (1.12; -0.50 - 2.88; 90.8 % > 0), and a likely positive effect of capture in a floating object or FAD set rather than an un-associated free school set (0.88; -0.49–2.44; 90 % > 0). No other covariate effects were significant, and we report all covariate effect estimates and significance levels in Table 2 and Fig. 3. Excluding the single tagged *M. mobular* with a known fate that was released using the main net without being brought onboard—and thus had a time on deck of zero minutes—had virtually no effect on posterior covariate effects (Table S2).

Species-specific intercepts were estimated on the logit scale and therefore the raw estimated species effects are mainly useful for comparing base survival effects between species, but the effects themselves are best interpreted as predicted survival probabilities combined with other covariates. *M. mobular* had a higher estimated base survival intercept than *M. tarapacana* (99.3 % probability) and *M. thurstoni* (99.2 % probability), but not *M. birostris* (91.8 % probability). There were no significant differences in base survival intercepts among *M. birostris*, *M. tarapacana*, or *M. thurstoni*, although the median intercept estimate was lowest for *M. thurstoni* (-0.76), followed by *M. birostris* (-0.17), *M. tarapacana* (-0.06), and *M. mobular* (1.87). To estimate realized

survival probabilities under typical operating conditions, we used the full posterior distributions to predict survival probability for each species using the model-estimated covariate effects applied to a female (no male effect applied) of the mean recorded disc width for each species, removed from the main net in the first brailer (no sack effect applied), released using a stretcher (*M. mobular*, *M. tarapacana* & *M. thurstoni*), or a cargo net (*M. birostris*), after capture in a set with the mean recorded tons of catch (19.1 tons), and mean recorded water temperature. We varied the number of minutes spent on deck (3, 8 and 15 min) to compare the predicted survival probabilities under this key operating characteristic and compared the survival probability of an individual released in 3 min after being brailed onboard in the first brailer versus being released after remaining in the sack of the main net through the entire brailing process. The median predicted survival probability after 3 min on deck was 83.7 % for *M. birostris*, 95.3 % for *M. mobular*, 82.2 % for *M. tarapacana*, and 53.7 % for *M. thurstoni*. This decreased to 57.2 % for *M. birostris*, 83.3 % for *M. mobular*, 52.3 % for *M. tarapacana*, and 21.9 % for *M. thurstoni* after 15 min on deck. Being left in the sack of the main net until the entire catch had been brailed decreased survival probability by approximately the same amount as spending ~15 min on deck. Predicted survival probabilities under these operational and handling conditions are reported in full with credible intervals in Table 3. Predicted survival probabilities for each species across a range of values for time on deck, alongside realized fates of tagged rays, are shown in Fig. 4. Predicted survival probabilities for each species at three intervals of time on deck are shown in Fig. 5.

4. Discussion

We provide the first global, multi-species comparative analysis of post-release survival rates of live mobulid rays released from tuna purse seine vessels, providing novel estimates of how environmental, handling, and operational characteristics influence survival rates in these vulnerable species. We find that in the case of ideal handling practices (release within three minutes), predicted survival ranged from 53 % to 95 %, depending on species. Our results suggest that the handling and rapid release guidelines currently mandated by four of the five major tuna RFMOs could be associated with ≥80 % survival probability for three of the studied mobulid species, if complied with by vessels. However, given the sensitivity of these survival rates to operational characteristics, especially handling time, achieving high post-release survival rates for mobulid species will remain challenging, especially for *M. thurstoni*, which had comparatively low survival rates even in optimal handling scenarios. The observed survival rates of 20 % (*M. thurstoni*) to 74 % (*M. mobular*) indicate that current survivorship remains far from the estimated maximum survival probabilities under optimal handling and release conditions. Although data on survivorship of mobulid rays is unavailable from before the implementation of improved handling practices, our estimates indicate a potential major improvement over the very low survival rates (previously assumed to be 100 % mortality) associated with harmful handling practices such as the use of hooks and cables to remove rays from the deck. Further, we find that a straightforward mitigation strategy—prioritizing the immediate release of bycatch species and altering deck operations to minimize mobulid release handling time and time spent on deck—can significantly increase survival probability. These results can be used to inform best handling practices to maximize the survivorship of these vulnerable species (Poisson et al., 2016; Hutchinson et al., 2017), and to improve estimates of the overall impact of purse seine bycatch on mobulid populations by refining fishing mortality scenarios (Griffiths and Lezama-Ochoa, 2021).

Tagged mobulid rays in our study were generally returned to the water in under 10 min, and many were released in under five min. The three categories of release method—by hand, stretcher, or cargo net—had minimum release times of 0–2 min, although we note that the very fast cargo net release times occurred when mobulids were released

Table 2

Model estimated covariate effects on mobulid survival probability. Estimated effects are reported as the median with 95 % credible intervals. Significance was assessed based on 95 % of posterior draws being less or greater than zero, and significant covariate effects are indicated with *. Likely positive or negative (>90 % of posterior draws) effects are indicated with ^.

Covariate	Estimated effect (95 % CI)	Probability < or > 0
Bag effect (after brailing)	-1.72 (-4–0.42)	94.6 %^
Bag effect (skunked set)	-0.43 (-2.12–1.36)	69.6 %
Body size	1.12 (-0.5–2.88)	90.8 %^
Brailer number	-1.63 (-4.88–0.67)	90.8 %^
FAD set	0.88 (-0.49–2.44)	90.0 %^
Male	-0.81 (-2.27–0.6)	87.7 %
Release - cargo net vs manual	-0.36 (-1.91–1.14)	69.0 %
Release - stretcher vs cargo net	1.33 (-1.06–4)	84.6 %
Release - stretcher vs manual	0.96 (-1.14–3.22)	81.8 %
Time on deck	-1.65 (-3.42 - 0.32)	99.5 %*
Tons of catch	-0.62 (-2.09–0.92)	80.0 %
Water temperature	-0.44 (-2.14–1.3)	68.4 %

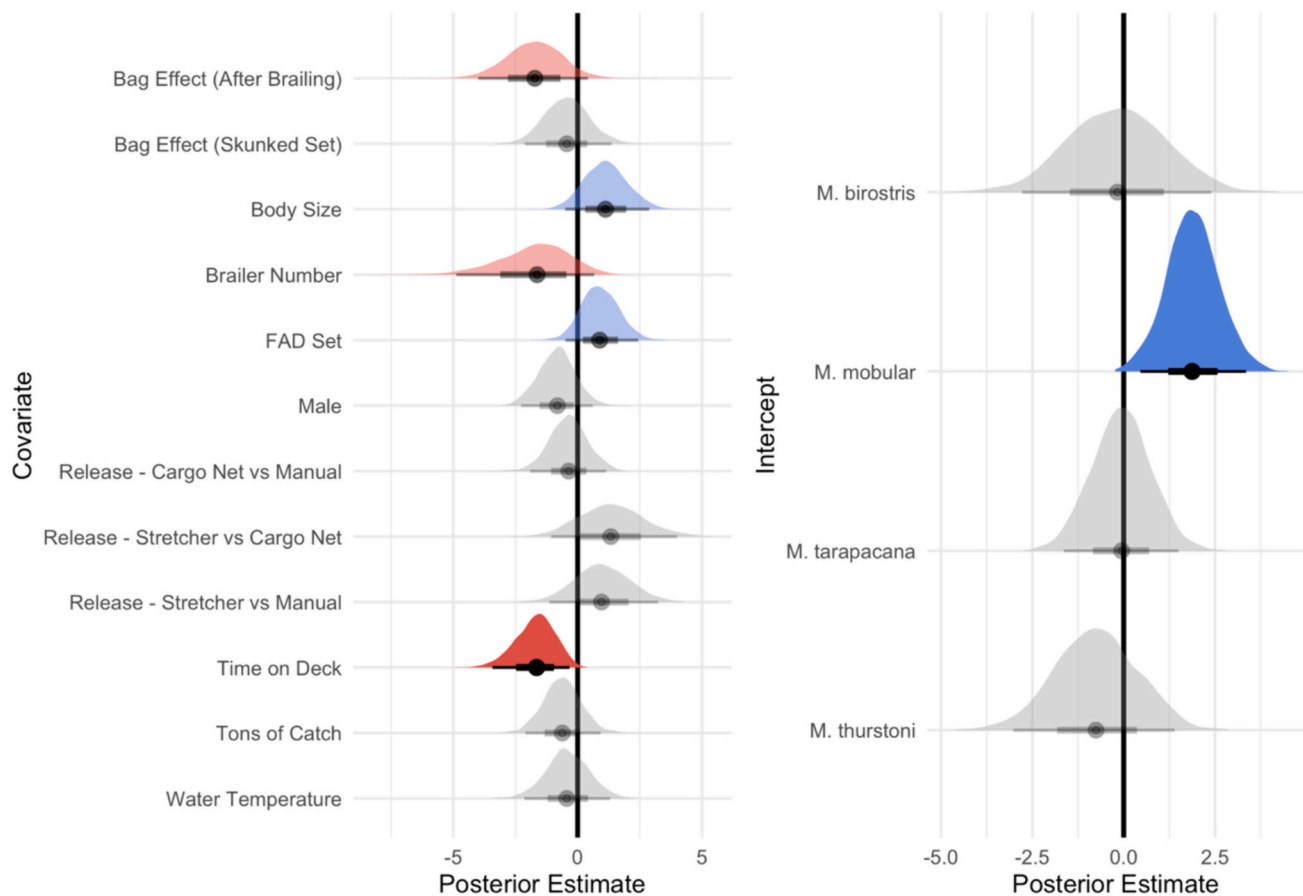


Fig. 3. Posterior estimates for covariate effects on mobulid survival probability and species-specific intercepts. Note that estimates are on the logit scale. Densities reflect the posterior distributions of covariate effects (left) and species-specific intercepts (right), dots are the median, thick horizontal lines are the 50th percentile, and thin horizontal lines are the 95th percentile intervals. Blue indicates positive and red indicates negative effects. Covariate distributions in solid colors are effects with >95 % of posterior draws greater or less than zero, whereas those in light colors are effects with >90 % of posterior draws greater or less than zero. Faded gray distributions had no significant or likely effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Predicted survival probabilities for mobulid species captured under average conditions for the observed sample, brought on board in the first brailer, and released after 3, 8, or 15 min on deck; and after 3 min on deck when the ray was brought on board after being entangled in the sack of the net for the duration of brailing. Note that the effect of a cargo net release was applied for *M. birostris*, as this was the only release method observed for the species, and it is generally too large to feasibly release with other methods. A stretcher release method was applied for the other three species. The observed survival rate (raw percentage of surviving tagged specimens with known fates) is presented for comparison with survival under different handling conditions.

Species	3 min	8 min	15 min	3 min, from sack after brailing	Observed survival rate
<i>M. birostris</i>	83.7 % (21.5 % - 99.4 %)	75 % (13.5 % - 98.9 %)	57.2 % (5.2 % - 97.8 %)	54.7 % (3.4 % - 97.8 %)	50 %
<i>M. mobular</i>	95.3 % (67.6 % - 99.7 %)	92 % (52.7 % - 99.3 %)	83.3 % (29.4 % - 98.7 %)	82.3 % (15.6 % - 99.2 %)	74.2 %
<i>M. tarapacana</i>	82.2 % (23.7 % - 98.6 %)	71.8 % (15 % - 97.6 %)	52.3 % (5.6 % - 95.1 %)	49.9 % (2.9 % - 97 %)	33.3 %
<i>M. thurstoni</i>	53.7 % (8.1 % - 93.2 %)	39 % (4.6 % - 87.9 %)	21.9 % (1.8 % - 79.6 %)	20.8 % (0.9 % - 86.6 %)	20 %

by using the sack of the main net to lift, maneuver, and release the ray, and not when the ray was physically transferred to a cargo net after being brailed onto the deck. The maximum release times of 48, 14 and 15 min for each method, respectively, were likely not associated with practical constraints of the release methods, but instead by priorities of on-deck operations and captain and crew behavior. Further, there was no apparent relationship between body size and time on deck, and even the largest recorded mobulids could be released in five minutes or less. In short, it appears that all species and sizes of mobulids can be released relatively quickly using the most common methods developed and employed in purse seine fisheries (manual, stretcher, and cargo net), which can be implemented in most or all vessel types. We believe that this is likely why we found no significant effect of release method on

survival probability, and that all three methods are major improvements over previous handling methods, as long as rays are released quickly. We do note that, despite the lack of significant differences, the median effect of using a stretcher to release a ray was positive both compared to cargo net and manual releases (Fig. 3). This suggests that stretchers may be a preferable method of release for mobulids that are not too large to lift without the aid of a crane or winch, and future studies should continue testing for effects of release method on the survival probability of mobulid rays.

We found a likely (>90% probability) negative effect of brailer number on survival probability, suggesting that mobulids that spend more time in the sacked net prior to release have a lower survival probability than those brailed and released early on. Brailer number

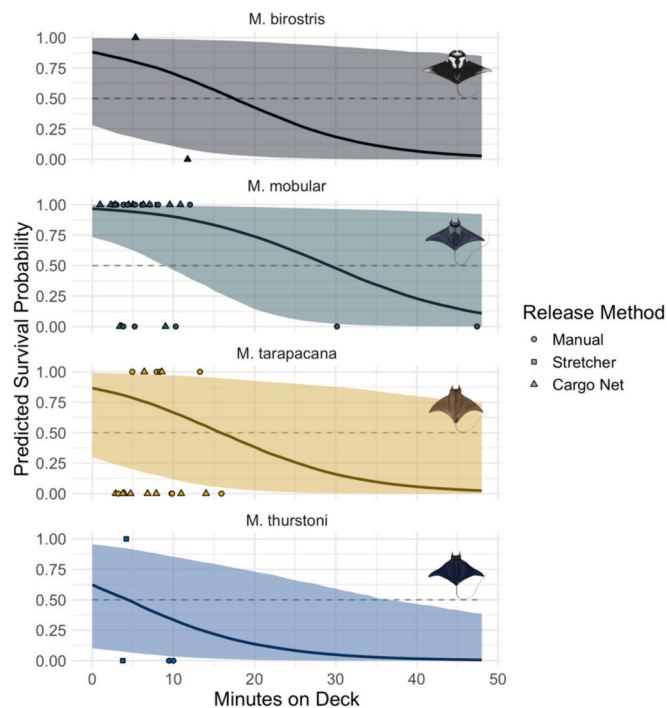


Fig. 4. Effects of time spent on deck prior to release on mobulid survival probability. The x-axis represents minutes on deck and the y-axis represents model-predicted survival probability under typical operating characteristics (see methods). Polygons represent 95 % credible intervals, and lines indicate median survival probabilities. A dashed line is at 50 % predicted survival probability for reference. Points at 0 and 1 indicate mobulids that survived (1) or died (0), and point shapes represent release method. Illustrations are by Julie Johnson, Life Science Studios.

may also be a proxy for a mobulid's position in the sacked net, with mobulids deeper in the net and thus subjected to greater crushing forces of the main catch being brailled later in the process. Similarly, being brought on board from the purse seine sack after the entire catch was brailled was associated with reduced survival probability, whereas being brought on board from the sack in a skunked set (a set with no or very little tuna, where the net retrieval operation is significantly reduced) had no effect on survival probability. This suggests that being entangled in the sack of the main net does not in itself contribute to reduced survival rates, especially in cases where the ray is quickly brought on board and released without the additional operational time associated with brailing a large set. Instead, time spent constrained in the main net and subject to crushing from the weight of the catch throughout the entire brailing process most likely restricts the ability of ram-ventilating mobulid rays to respire, increasing mortality probability.

The four species in our study exhibited substantially different realized and estimated survival probabilities, with *M. mobular* median survivorship of 95 % under optimal handling conditions (release in three minutes), in contrast to *M. thurstoni* median survivorship of 53 % under optimal handling conditions. Although sample sizes for *M. thurstoni* and *M. birostris* were much lower than *M. mobular* and *M. tarapacana*, the uncertainty around estimated survival probability was similar across *M. birostris*, *M. thurstoni*, and *M. tarapacana*. It would be reasonable to expect the larger-bodied mobulids to have lower post-release survival rates, as they may sustain more corporal and organ damage due the increased effects of gravity outside of the water. However, *M. thurstoni*, the smallest of the four species, had the lowest survival probability, and we found a likely positive effect of body size, with larger individuals having higher survival probability. It is possible that larger individuals are more robust to mechanical stresses associated with capture (e.g. physical damage from the large volume & weight of tuna in the net), or

may have physiological advantages over smaller individuals (e.g. greater gill surface area for respiration in a low-oxygen sacked net).

We found a likely positive effect of floating object or FAD sets on survival probability of mobulids, suggesting that mobulids captured in FAD-associated sets may have improved post-release outcomes when compared with free school sets. Tuna schools captured in free sets are often feeding, and can be pursued by the purse seine vessel for several miles before encirclement, whereas FAD sets are made on drifting floating objects with associated schooling tunas. In addition, FAD sets tend to be made earlier in the morning whereas free school sets are often made later in the day. As a result, it is possible that tunas and mobulid rays caught in free school sets are more metabolically active at the time of capture than those caught in FAD sets, which may increase oxygen consumption in the sacked net. This could reduce available dissolved oxygen for respiration, reducing survival probability for incidentally captured mobulids. We note that the effect of set type on survival probability had a > 90 % probability of being positive, but did not meet the 95 % significance threshold and should therefore be a focus of future confirmatory studies for all three set types (FAD, free school, and dolphin-associated sets in the ETP).

Several key factors have been shown to predict mortality risk of elasmobranchs during fishery interactions. The gear type and duration of the interaction are primary drivers of survival outcomes, both of which influence respiration by constraining active ventilation in elasmobranchs. Survival rates are typically higher in longline fisheries with short soak times and where animals are able to swim to move oxygenated water over their gills, whereas at-vessel mortality rates (mortality prior to handling and release) in net fisheries (e.g. gillnet or purse seine) are much higher because animals are constrained or entangled, prohibiting movement and respiration in obligate ram ventilators (Musyl and Gilman, 2019). In addition, species and body size effects on mortality rates are likely driven by the underlying physiology of some taxa, making them differentially sensitive to stress. In longline fisheries, at-vessel mortality rates are good indicators of which elasmobranch species are physiologically more or less resilient to capture stress (Skomal, 2007; Whitney et al., 2021). For example, hammerhead shark species are extremely sensitive to capture stress and have some of the highest at-vessel mortality rates, while blue sharks are relatively robust to the physiological stresses of capture and have very low at-vessel mortality rates (reviewed in Ellis et al., 2017). Differences in at-vessel mortality rates among species may be due to adaptive physiology for deep diving, foraging strategies (e.g. high metabolic demands in Lamnidae), or respiratory modality (e.g. scalloped hammerhead sharks were found to utilize breath holding behaviors to maintain body temperatures at depth; Royer et al., 2023). These patterns are broadly consistent with our results, as the factors that were related with survival probability (time on deck, body size, set type, and whether a ray was left in the main net until after brailing) all plausibly influence oxygen availability and respiration of bycaught rays.

4.1. Caveats and limitations

We requested that observers minimize the amount of time working with bycaught mobulids (e.g. tagging and collecting individual data such as size and sex) so that the time spent on deck and out of the water was not prolonged. In addition, the observers tagged mobulid rays that were clearly alive and thus demonstrated some signs of vitality. As such, the samples in this study may have an average release time faster than what occurs across industrial purse seine fisheries and reflect lower post-release mortality than in normal operations. Further, observers almost certainly elected to tag mobulids that came out of the main net earlier, biasing our sample towards individuals that may have been in better condition than those remaining in the main net for longer. As such, survival probabilities that we report here should be considered an optimistic scenario under near-ideal handling and operational conditions. We also emphasize that the observed survival rates for specimens

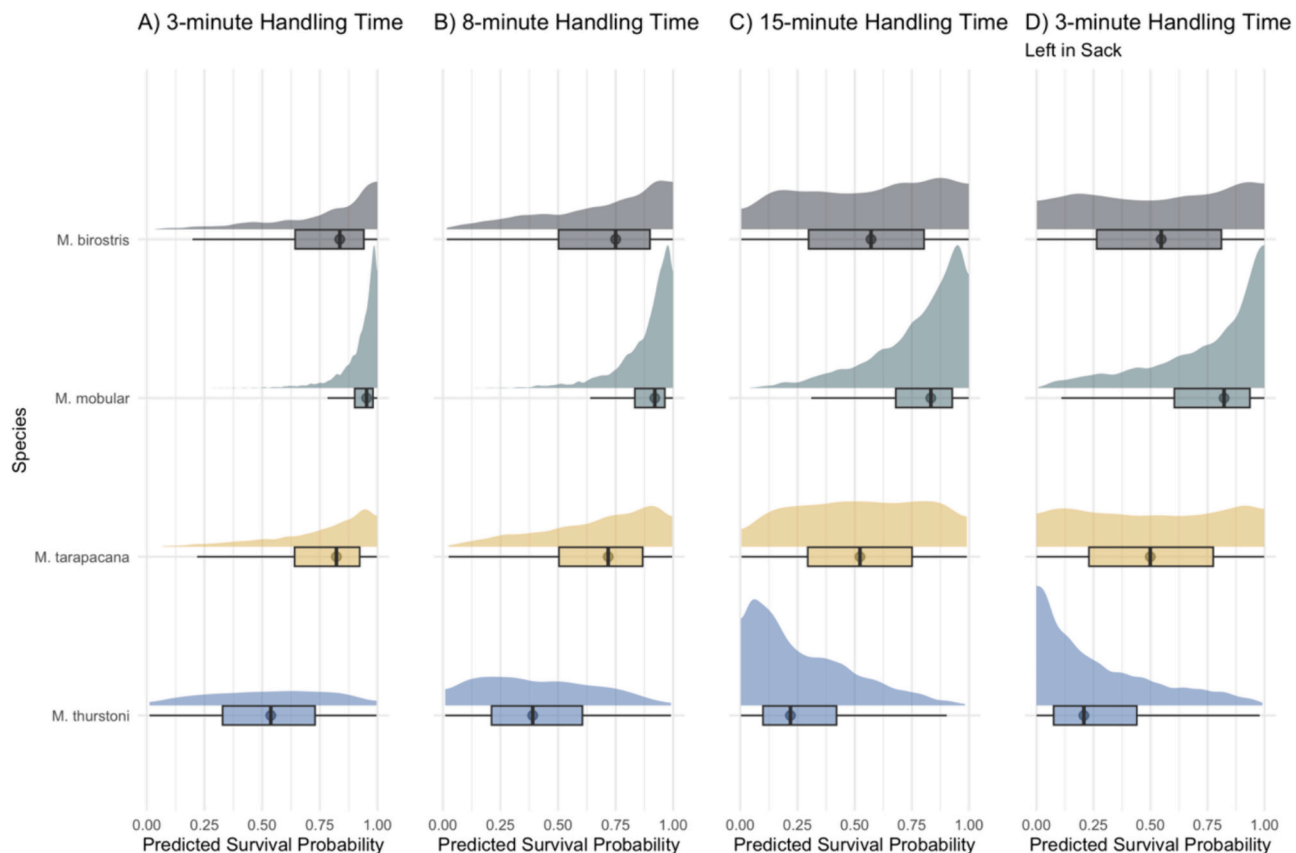


Fig. 5. Predicted mobulid survival probabilities under different handling and operational characteristics. Predictions were generated using the posterior estimates of covariate effects applied to mean observed covariate values, and varying time spent on deck. Note that the effect of a cargo net release was applied for *M. birostris*, as this was the only release method observed for the species, and it is generally too large to feasibly release with other methods. A stretcher release method was applied for the other three species. In (D) the effect was applied for a mobulid left in the sack of the main net until after brailing is completed. Densities reflect the species-specific posterior predicted survival probabilities. Box plots summarize the posterior predictions with median (dot and vertical line), 50th percentile (box), and 95th percentile (horizontal lines) intervals.

in this study were far lower than the potential estimated survival rates under optimal handling and release conditions.

The effects of satellite tag attachments on survival probability are unknown but expected to be low, as all four species in the study have previously been studied using archival satellite tags with similar tag deployment methodology, and no apparent effects on behavior or survivorship (Croll et al., 2012; Thorrold et al., 2014; Stewart et al., 2016). However, we note that those tag deployments were on healthy individuals either free-swimming or caught under controlled conditions, and it is possible that tag deployments could have a greater negative effect on already stressed or injured mobulids, such as bycaught specimens in our study. Nevertheless, given the extensive use of archival satellite tags to study the survivorship of bycaught elasmobranchs (Musyl and Gilman, 2019) and the relatively large proportion of surviving individuals in our study, we posit that tag deployments had little or no effect on survival probabilities reported here.

While we had large sample sizes for *M. mobular* and *M. tarapacana*, our sample sizes for *M. thurstoni* ($n = 5$) and *M. birostris* ($n = 2$) were very small. Our best-fit model employed shared parameters for covariate effects, and was selected using leave-one-out cross validation model performance metrics over alternative models that employed either hierarchical or fixed effects of covariate relationships for each species. We anticipated that hierarchical covariate effects would provide the best fit, as they allow for group-level effects that are informed by a mean effect, which would constrain the estimates for groups with low sample size while allowing effects for groups with large sample sizes to be estimated more precisely. The improved performance of the shared covariate effects model may reflect small sample sizes in *M. thurstoni* and

M. birostris limiting the ability of models to independently estimate covariate effects for those species. Future post-release survival studies should target these species, and others not included in our study, to further refine species-specific baseline survival rates and covariate effects.

We experienced unusually high rates of tag failures in this study, most of which occurred in the most recent Eastern Pacific and Atlantic deployments. Tags were deployed in harsh environments and tagged mobulids were released in some cases using nets that could potentially entangle and damage tags. However, during the ETP and second round of ATL deployments when most tag failures occurred, there was an ongoing battery issue that was later identified and resulted in a recall by the tag manufacturer. We posit that the unusually high tag failure rate (especially compared to earlier tag deployments using the same tag models with previous battery and firmware combinations in other regions) was due to battery failures. It is noteworthy that the species-specific tag failure rates roughly corresponded to species-specific mortality rates, with the highest tag failure rates in *M. thurstoni*, which had the lowest survival probability, and the lowest tag failure rates in *M. mobular*, which had the highest survival probability. Importantly, all recorded mortalities in the ETP and ATL regions resulted in tagged individuals sinking past 1700 m, triggering an active release by the tags before they reach their maximum depth rating of ~2000 m. This active release requires an electric current to be run through a corrodible link, severing the tag from its anchor and allowing it to float to the surface. In the case of poor battery performance, it may not have been possible for tags to activate the release mechanism, and they may have reached their crush depth and thus failed before detaching. In contrast, a tag with a

faulty battery may have been able to transmit a limited amount of data if it either pulled out prior to the programmed release date or performed an active release without the time constraint of sinking past its crush depth, both of which would be more likely to occur with a surviving individual. For example, the one *M. thurstoni* that survived in the ETP transmitted only a few hours of dive data before the battery failed. While it was sufficient to confirm that the individual survived, as the tag reported a full 30 days post deployment, this may be an example of mortality being more likely to be masked by tag failures than survival. Unfortunately, we cannot directly account for this possibility in our models without further information on tag failure rates under different circumstances or the impact of battery performance on the active release mechanism. However, if tag failures were biased to occur more frequently in dead, sinking individuals, then we would expect a positive bias in survival rates estimated from tags that did report. While we cannot confirm this with the current dataset, we caution that base survival probabilities, in particular for *M. thurstoni*, could be lower than those reported here if tag failures did not occur randomly. As tag failure issues are resolved with updated components and firmware, it will be important to replicate these findings to confirm or reject the potential effects of tag reporting bias.

4.2. Recommendations for best handling and release practices

Our results support several tangible recommendations for handling and release practices to maximize survivorship of mobulids released alive from purse seine vessels. First, we recommend that mobulids be returned to the water within three minutes of being brought on board. Predicted survivorship of all species except *M. thurstoni* was 80–95 % if released within three minutes. There was no significant difference in survival probability for mobulids released by hand, using stretchers, or cargo nets after accounting for time spent on deck (although further study of the effects of handling methods is warranted as we note above). This suggests that any of these non-invasive handling and release practices is likely viable, and that whichever approach allows mobulids to be released as quickly as possible is preferable. For small mobulids, release by hand may be most efficient. For larger mobulids, stretchers may be useful as it can be challenging for crews to maneuver large, heavy individuals quickly by hand. We recommend cargo nets only for the largest individuals that cannot be maneuvered by hand or with a stretcher, as using a cargo net will likely slow the release process compared to other methods. We highlight that brailer grids, sorting grids, ramps and other bycatch reduction devices are promising solutions for quickly and safely releasing mobulids, showing mean release times under two minutes (Jones and Francis, 2012; Murua et al., 2022), and we recommend their implementation alongside further post-release tagging studies to confirm their efficacy. We recommend that mobulids be brought on board from the sacked net as quickly as possible and not left to the end of the brailing process, as mobulids brought on board in later brailers and directly from the sack post-brailing had reduced survival probability. Captains and deck bosses could preemptively designate specific crew members to immediately pause hauling to accelerate the release of mobulids. In addition, preliminary evidence suggests that spotters in the crow's nest and pilots operating helicopters on purse seine vessels may be able to identify mobulids in the net early in the net hauling process to prepare the crew to quickly release bycaught rays (Cronin et al., 2023a; Waldo et al., 2024).

We recommend future studies explore options for avoiding mobulid capture (e.g. through dynamic ocean management) and releasing mobulids directly from the net by dropping the corkline and allowing them to swim out prior to sacking. This may benefit *M. thurstoni* in

particular, which had comparatively low predicted survivorship even under optimal on-deck handling and release procedures. Release directly from the unsacked net would likely reduce the probability of individuals being entangled in or brought on board from the sack, potentially increasing survival rates.

Finally, we suggest that observers collect information on the sacking time of the net, the brail number and the time spent by mobulids on deck prior to release, which could help vessels demonstrate compliance with policies that require “prompt release” in four out of five major tuna RFMOs. This information can also be used to more accurately estimate fleetwide realized survival rates for mobulids, as well as providing metrics to track progress towards the implementation of optimal handling procedures, or to determine the need for corrective measures (e.g., fisher training courses in best release practices) and incentive programs to encourage rapid release.

CRediT authorship contribution statement

Joshua D. Stewart: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Melissa R. Cronin:** Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization. **Erick Largacha:** Writing – review & editing, Project administration, Investigation, Data curation. **Nerea Lezama-Ochoa:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Jon Lopez:** Writing – review & editing, Resources, Project administration, Methodology, Investigation. **Martin Hall:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Conceptualization. **Melanie Hutchinson:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Emma G. Jones:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Malcolm Francis:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Maitane Grande:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jefferson Murua:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Vanessa Rojo:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Salvador J. Jorgensen:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Data availability

All of the data used in the analysis is presented in a supplementary table in the paper and is therefore freely available.

Acknowledgements

We thank observers from IATTC and TUNACONS for deploying satellite tags on mobulid rays in the Eastern Tropical Pacific, and Pedro Santistevan and Guillermo Moran of TUNACONS for making data collection and tag deployments possible on TUNACONS vessels throughout the ETP. We thank the vessel captains and crews who

participated in voluntary tag deployments and data collection efforts. We thank Ernesto Altamirano for assistance with IATTC data requests and data management. We thank Don Croll and Andre Boustany for early discussions on the development of the tagging program in the ETP, and Stefany Rojas for helping to facilitate training workshops in Manta, Ecuador. The Monterey Bay Aquarium and the Save Our Seas Foundation provided funding to support tag deployments from 2017 to 2023 in the ETP. The Save Our Seas Foundation provided support for open access publishing fees.

The International Seafood Sustainability Foundation provided funding and support for six tags deployed in the Eastern Atlantic Ocean in 2018. We thank the captain and crew of the F/V Pacific Star and Albacora for supporting the scientific crew in the deployment of tags during fishing operations.

The tagging program conducted in the Atlantic Ocean from 2019 to 2023 was funded by OPAGAC and the Basque Government. Tagging was conducted by observers of AZTI, IEO and Datafish and with the collaboration of the crew in OPAGAC and ANABAC purse seine fishing vessels. The Manta Trust helped in confirming the species identification of some of the tagged animals.

The Department of Conservation funded the New Zealand tagging program and data analysis. We thank Fisheries New Zealand (FNZ) fishery observers for documenting and tagging mobulid rays and are grateful for the cooperation of the crews of NZ purse seine vessels.

The authors declare no conflicts of interest.

All data is available in Supplemental Table S1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110794>.

References

- Alfaro-Cordova, E., Del Solar, A., Alfaro-Shigueto, J., Mangel, J.C., Diaz, B., Carrillo, O., Sarmiento, D., 2017. Captures of manta and devil rays by small-scale gillnet fisheries in northern Peru. *Fish. Res.* 195, 28–36.
- Benson, J.F., Jorgensen, S.J., O'Sullivan, J.B., Winkler, C., White, C.F., Garcia-Rodriguez, E., Sosa-Nishizaki, O., Lowe, C.G., 2018. Juvenile survival, competing risks, and spatial variation in mortality risk of a marine apex predator. *J. Appl. Ecol.* 55, 2888–2897.
- Booth, H., Mardhiah, U., Siregar, H., Hunter, J., Giyanto, Putra M.I.H., Marlow, J., Cahyana, A., Boysandi, Demoor A.Y.L., Lewis, S., Adhiasto, D., Adrianto, L., Yulianto, I., 2021. An integrated approach to tackling wildlife crime: impact and lessons learned from the world's largest targeted manta ray fishery. *Conservation Science and Practice* 3, e314.
- Carpenter, M., Parker, D., Dicken, M.L., Griffiths, C.L., 2023. Multi-decade catches of manta rays (*Mobula alfredi*, M. *Birostris*) from South Africa reveal significant decline. *Frontiers in marine. Science* 10.
- Coelho, R., Fernandez-Carvalho, J., Lino, P.G., Santos, M.N., 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. *Aquat. Living Resour.* 25, 311–319.
- Couturier, L.I.E., Marshall, A.D., Jaine, F.R.A., Kashiwagi, T., Pierce, S.J., Townsend, K. A., Weeks, S.J., Bennett, M.B., Richardson, A.J., 2012. Biology, ecology and conservation of the Mobulidae. *J. Fish Biol.* 80, 1075–1119.
- Croll D a., Newton KM, Weng K, Galván-Magaña F, O'Sullivan J, Dewar H (2012) Movement and habitat use by the spine-tail devil ray in the eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* 465:193–200.
- Croll, D.A., Dewar, H., Dulvy, N.K., Fernando, D., Francis, M.P., Galvan-Magana, F., Hall, M., Heinrichs, S., Marshall, A., McCauley, D., Newton, K.M., Notarbartolo-Di-Sciara, G., O'Malley, M., O'Sullivan, J., Poortvliet, M., Roman, M., Stevens, G., Tershy, B.R., White, W.T., 2016. Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 26, 562–575.
- Cronin, M.R., Croll, D.A., Hall, M.A., Lezama-ochoa, N., Lopez, J., Murua, H., Murua, J., Restrepo, V., Rojas-perea, S., Stewart, J.D., Waldo, J.L., Moreno, G., 2023a. Harnessing stakeholder knowledge for the collaborative development of Mobulid bycatch mitigation strategies in tuna fisheries. *ICES J. Mar. Sci.* 80 (3), 620–634.
- Cronin, M.R., Amaral, J.E., Jackson, A.M., Jacquet, J., Seto, K.L., Croll, D.A., 2023b. Policy and transparency gaps for oceanic shark and rays in high seas tuna fisheries. *Fish Fish.* 24, 56–70.
- D'Agostino McGowan, L., Gerke, T., Barrett, M., 2023. Causal inference is not just a statistics problem. *Journal of Statistics and Data Science Education* 0, 1–6.
- Dapp, D.R., Walker, T.I., Huveneers, C., Reina, R.D., 2016. Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality. *Fish Fish.* 17, 507–524.
- Dulvy, N.K., Pardo, S.A., Simpfendorfer, C.A., Carlson, J.K., 2014. Diagnosing the dangerous demography of manta rays using life history theory. *PeerJ* 2, e400.
- Ellis, J.R., McCully Phillips, S.R., Poisson, F., 2017. A review of capture and post-release mortality of elasmobranchs. *J. Fish Biol.* 90 (3), 653–722.
- Fernando D, Stewart JD (2021) High Bycatch Rates of manta and Devil Rays in the “Small-Scale” Artisanal Fisheries of Sri Lanka. *PeerJ*:1–35.
- Francis, M.P., Jones, E.G., 2017. Movement, depth distribution and survival of spinetail devilrays (*Mobula japanica*) tagged and released from purse-seine catches in New Zealand. *Aquat. Conserv.* 27 (1).
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7, 457–472.
- Gelman, A., Jakulin, A., Pittau, M.G., Su, Y.-S., 2008. A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.* 2.
- Griffiths, S.P., Lezama-Ochoa, N., 2021. A 40-year chronology of the vulnerability of spinetail devil ray (*MOBULA MOBULAR*) to eastern Pacific tuna fisheries and options for future conservation and management. *Aquat. Conserv.* 31, 2910–2925.
- Hutchinson M, Poisson F, Swimmer Y (2017) Developing best handling practice guidelines to safely release mantas, mobulids and stingrays captured in commercial fisheries. *PIDSC Working Paper WP-17-006*.
- ICCAT (2024) Compendium management recommendations and resolutions adopted by ICCAT for the conservation of Atlantic tunas and tuna-like species.
- Jones E, Francis M (2012) Protected rays – occurrence and development of mitigation methods in the New Zealand tuna purse seine fishery.
- Kezine M, Givos I, Mghili B, AL-Mabruk SAA, Aksissou M (2024) Elasmobranch bycatch in a bottom trawl fishery at Al Hoceima port in Morocco (Mediterranean Sea). *Thalassas* 40:685–691.
- Marshall, A.D., Compagno, L.J.V., Bennett, M.B., 2009. Redescription of the genus *Manta* with resurrection of *Manta alfredi*. *Zootaxa* 28, 1–28.
- Mas, F., Forselledo, R., Domingo, A., 2015. Mobulid ray by-catch in longline fisheries in the South-Western Atlantic Ocean. *Mar. Freshw. Res.* 66, 767.
- Murua J, Ferarios JM, Grande M, Onandia I, Moreno G, Murua H, Santiago J (2022) Developing bycatch reduction devices in tropical tuna purse seine fisheries to improve elasmobranch release.
- Musyl, M.K., Gilman, E.L., 2019. Meta-analysis of post-release fishing mortality in apex predatory pelagic sharks and white marlin. *Fish Fish.* 20, 466–500.
- National Marine Fisheries Service, 2023. Biological Opinion on the Authorization of the Hawaii Deep-Set Longline Fishery. Pacific Islands Regional Office, Honolulu, HI.
- Notarbartolo di Sciara, G., 1987. A revisionary study of the genus *Mobula Rafinesque*, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. *Zool. J. Linn. Soc.* 91, 1–91.
- O'Malley, M.P., Townsend, K.A., Hilton, P., Heinrichs, S., Stewart, J.D., 2016. Characterization of the Trade in Manta and Devil Ray Gill Plates in China and Southeast Asia through Trader Surveys. *Aquatic Conservation, Marine and Freshwater Ecosystems*, pp. 1–41.
- Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.-M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J. S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. *Nature* 589, 567–571.
- Pardo, S.A., Kindsvater, H.K., Cuevas-Zimbrón, E., Sosa-Nishizaki, O., Pérez-Jiménez, J. C., Dulvy, N.K., 2016. Growth, Productivity, and Extinction Risk of a Data-Sparse Devil Ray. *Scientific Reports*:1–10.
- Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing* 124.
- Poisson, F., Séret, B., Vernet, A.L., Goujon, M., Dagorn, L., 2014. Collaborative research: development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. *Mar. Policy* 44, 312–320.
- Poisson, F., Crespo, F.A., Ellis, J.R., Chavance, P., Bach, P., Santos, M.N., Séret, B., Korta, M., Coelho, R., Ariz, J., Murua, H., 2016. Technical mitigation measures for sharks and rays in fisheries for tuna and tuna-like species: turning possibility into reality. *Aquat Living Resour* 29, 402.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Royer, M., Meyer, C., Royer, J., Maloney, K., Cardona, E., Blandino, C., Fernandes da Silva, G., Whittingham, K., Holland, K.N., 2023. “Breath holding” as a thermoregulation strategy in the deep-diving scalloped hammerhead shark. *Science* 380, 651–655.
- Setyawan, E., Erdmann, M., Gunadharma, N., Gunawan, T., Hasan, A., Izuan, M., Kasimidi, M., Lamatenggo, Y., Lewis, S., Maulana, N., Mambasar, R., Mongdong, M., Nebore, A., Putra, M.I.H., Sianipar, A., Thebu, K., Tuharea, S., Constantine, R., 2022. A holistic approach to manta ray conservation in the Papuan Bird's head seascape: resounding success, ongoing challenges. *Mar. Policy* 137.
- Skomal, G.B., 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fish. Manag. Ecol.* 14, 81–89.
- Stevens, G.M.W., Fernando, D., Dando, M., Notarbartolo di Sciara, G., 2018. Guide to the manta and Devil Rays of the World. Wild Nature Press.

- Stewart, J.D., Beale, C.S., Fernando, D., Sianipar, A.B., Burton, R.S., Semmens, B.X., Aburto-Oropeza, O., 2016. Spatial ecology and conservation of *Manta birostris* in the indo-Pacific. *Biol. Conserv.* 200, 178–183.
- Stewart, J.D., Jaine, F.R.A., Armstrong, A.J., Armstrong, A.O., Bennett, M.B., Burgess, K. B., Couturier, L.I.E., Croll, D.A., Cronin, M.R., Deakos, M.H., Dudgeon, C.L., Fernando, D., Froman, N., Germanov, E.S., Hall, M.A., Hinojosa-Alvarez, S., Hosegood, J.E., Kashiwagi, T., Laglbauer, B.J.L., Lezama-Ochoa, N., Marshall, A.D., McGregor, F., Notarbartolo di Sciara, G., Palacios, M.D., Peel, L.R., Richardson, A.J., Rubin, R.D., Townsend, K.A., Venables, S.K., Stevens, G.M.W., 2018. Research priorities to support effective Manta and devil ray conservation. *Front. Mar. Sci.* 5, 1–27.
- Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B., Berumen, M.L., 2014. Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nat. Commun.* 5, 4274.
- Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* 27, 1413–1432.
- Waldo, J.L., Altamirano-Nieto, E., Croll, D.A., Palacios, M.D., Lezama-Ochoa, N., Lopez, J., Moreno, G., Rojas-Perea, S., Cronin, M.R., 2024. Bycatch mitigation from the sky: using helicopter communication for mobulid conservation in tropical tuna fisheries. *Front. Mar. Sci.* 11.
- White, E.R., Myers, M.C., Flemming, J.M., Baum, J.K., 2015. Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area. *Conserv. Biol.* 29 (4), 1186–1197.
- Whitney, N.M., Lear, K.O., Morris, J.J., Hueter, R.E., Carlson, J.K., Marshall, H.M., 2021. Connecting post-release mortality to the physiological stress response of large coastal sharks in a commercial longline fishery. *PloS One* 16, e0255673.