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**Risk to the Indo-Pacific Ocean whale shark population from interactions with
Pacific Ocean purse-seine fisheries**

WCPFC-SC14-2018/SA-WP-12 (rev. 1)

(Revision makes minor corrections (in track changes) to results shown in Figures 17 & 18 and deletes brief text that describes an under-prediction which no longer exists. There are no changes to the conclusions or covering note.)

Common Oceans (ABNJ) Tuna Project¹

¹ Coordinated by the Western and Central Pacific Fisheries Commission, implemented by the Food and Agriculture Organization of the United Nations, and funded by the Global Environment Facility

Risk to the Indo-Pacific Ocean whale shark population from interactions with Pacific Ocean purse-seine fisheries

Covering Note

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The whale shark (*Rhincodon typus*) was the first shark to be listed by the Convention on the Conservation of Migratory Species (CMS) in 1999, as well as one of the first two sharks to be listed by the Convention on International Trade in Endangered Species (CITES) in 2003. These designations and protections demonstrate a long-standing and broad-based concern for the conservation and management of the species which is particularly heightened in the Western and Central Pacific Ocean (WCPO) due to interactions with the world's largest purse seine fishery. Recognizing this, Parties to the Nauru Agreement (PNA) adopted a ban on "*fishing or related activity in order to catch tuna associated with whale sharks*" under their Third Implementing Arrangement in September 2010. In December 2012, the Western and Central Pacific Fisheries Commission (WCPFC) strengthened regional protections for the whale shark in two ways: by adopting a conservation and management measure (CMM) prohibiting "*setting a purse seine on a school of tuna associated with a whale shark if the animal is sighted prior to commencement of the set*" (CMM 2012-04); and by designating the species as a WCPFC key shark species for data provision and assessment. The IATTC prohibited intentional setting of purse seines on whale sharks in the Eastern Pacific Ocean (EPO) in 2015 (C-15-03).

Sharks listed as WCPFC key shark species for assessment are included in the WCPFC's Shark Research Plan² but in some cases application of a traditional stock assessment framework has proved impossible. As a result, some species, including the whale shark, have been the subject of descriptive or indicator-based analyses, but as yet there has been no formal quantification of the threats posed by fishing. Two of the assessments conducted thus far under the Common Oceans (ABNJ) Tuna Project (i.e. for porbeagle and bigeye thresher shark) have applied a spatially-explicit risk assessment framework to catch and catch rate data. In the case of the whale shark, it was recognized in a previous study by Harley et al. (2013)³ that it might be necessary to use habitat standardization techniques to develop a relative index of abundance based on the propensity of whale sharks to be in areas of purse seine fishing effort. This study takes that idea one step further by using data on whale shark interactions with the purse seine fishery to predict habitat suitability and whale shark densities across the Pacific, and then to overlay fishing effort, predict fishing mortality and assess risk.

The findings of the study can be summarized as follows:

- A nominal trend of high interactions in 2006-2008, followed by lower rates thereafter (Figures 6 and 7), was not altered by standardization and is consistent with trends found in the Eastern Pacific Ocean by Román et al. (2018)⁴ (p. 35). These decreasing annual trends

¹ Common Oceans (ABNJ) Tuna Project, Food and Agriculture Organization of the United Nations, Rome, Italy

² WCPFC Key Document SC-08: Process for designation WCPFC key shark species for data provision and assessment.

<https://www.wcpfc.int/system/files/Key-Doc-SC-08-Process-Designation-Key-WCPFC-Shark-Species.pdf>

³ Harley, S., J. Rice and P. Williams. 2013. Spatial and temporal distribution of whale sharks in the Western and Central Pacific Ocean based on observer data and other data sources. WCPFC-SC9-2013/EB-WP-01. <https://www.wcpfc.int/node/3699>

⁴ Román, M. H., A. Aires-da-Silva and N.W. Vogel. 2018. Whale shark interactions with the tuna purse-seine fishery in the Eastern Pacific Ocean: Summary and analysis of available data. IATTC, Working Group on Bycatch 8th Meeting, La Jolla, CA, USA. http://www.iatc.org/Meetings/Meetings2018/BYC-08/PDFs/Docs/_English/BYC-08-INF-A-EN_Whale-shark-interactions-in-the-tuna-purse-seine-fishery-in-the-EPO.pdf

in interactions do not appear to result from management measures as prohibitions on intentional setting of purse seines on whale sharks were adopted by the PNA in 2010, by the WCPFC in 2012 and by the IATTC in 2015. Furthermore, the trends may have been influenced by low WCPO observer coverage rates prior to 2010 (Table 1).

- Given the consistency in annual interaction trends over a broad area of the Pacific, it is possible that these trends relate to basin-wide oceanographic/ environmental conditions which mediate the overlap of whale sharks and the purse seine fishery (p. 35).
- Strong correlations were found between environmental variables and whale shark interaction rates for most set types except free school sets which show the highest interaction rates (Figure 7). One potential explanation for the lack of consistent correlations with free school sets is that whale sharks' habitat preferences relate to fronts and clines that are not well-resolved in the aggregated oceanographic data used in the predictive modelling and which are more important in determining the locations of free school sets (p. 35).
- The spatially predictive model was able predict 'hotspots' for whale sharks which are generally in line with known areas of occurrence (p. 35). However, environmental predictors used in the model did not explain temporal shifts in interaction rates (Figure 13 and p. 3).
- In recent years, the number of interactions recorded as resulting in an immediate whale shark mortality was less than 1 in 1000 sets (p. 21). However, the probability of post-release mortality, which was estimated at ~10% (with a significant tail extending to higher value; Figure 14) based on an expert survey, was the greatest source of uncertainty in the assessment (p. 37). Understanding and reducing post-release mortality is recommended as one of most effective approaches to maintaining acceptable risk levels (pp. 37-38).
- For all scenarios the risk ranged from near 0% to as high as 54% of the most precautionary notional reference point (which is defined as "MSM" or maximum sustainable fishing mortality which is equivalent to half of the maximum population growth rate (r_{max})) (p. 28). As the risk of exceeding any one of the three notional limit reference points is generally less than 20% since 2009, the risk from Pacific Ocean fisheries alone is considered moderate to low. The total risk to the Indo-Pacific whale shark population may however be higher if there are differential impacts to more vulnerable population segments within the Pacific and/or higher fishing mortalities outside of the region (e.g. the Indian Ocean) (p. 37).

SC14 is invited to consider whether to:

- Accept the results of the quantitative risk assessment of the impacts of Pacific Ocean purse seine fishing on Indo-Pacific whale sharks;
- Conclude that the available data indicate there is a moderate to low probability that the Indo-Pacific whale shark is at risk from Pacific purse seine fisheries (probabilities of generally <20% that current risk levels exceed a range of life history-based notional reference points); and
- Recommend that the WCPFC initiate concerted efforts to identify and promote best practice safe release methods for whale sharks and quantify post-release mortality rates under a variety of release scenarios.



Risk to the Indo - Pacific Ocean whale shark population from interactions with Pacific Ocean purse - seine fisheries

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Cover Notes

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EXECUTIVE SUMMARY

Whale sharks are globally distributed throughout tropical and sub-tropical seas. By occupying similar habitat to many tropical pelagic species, including tuna, they interact with purse-seine fisheries targeting these species. Due to their particular life-history, whale sharks are thought to be vulnerable to fishing mortality, but it is unclear whether present levels of fishing mortality pose a risk to whale shark populations.

Here, we examined observer data from the Western and Central Pacific Ocean tropical purse-seine fishery. First, we described whale shark interactions and trends within that fishery. We then attempted to standardise data from fishery interactions to investigate if fluctuations in oceanographic conditions (described by sea surface temperature and chlorophyll *a*) can explain temporal patterns in interactions.

Although changes in oceanic habitat variables could not account for the temporal shifts in interaction rates, we found that estimated environmental effects on spatial interaction rates produced estimates of spatial habitat suitability that appeared consistent with available information. We used this map of predicted habitat suitability to define the overlap between Pacific Ocean (Western and Central Pacific Fisheries Commission and Inter-American Tropical Tuna Commission) tuna fisheries and whale sharks, and to estimate total mortalities expected within these fisheries.

We also used life-history information and life-history theory to estimate risk for the Indo-Pacific Ocean whale shark population from Pacific Ocean purse-seine fisheries. To estimate the un-observable post-release mortality, we conducted a Delphi survey of experts, and summarised the information using a statistical model. The risk assessment model suggested that the risk from Pacific Ocean fisheries alone is moderate to low, but not insignificant given potential other sources of mortality and uncertainty. In accordance with suggestions from the experts in the Delphi survey, we suggest that a strict application of best-practice release protocols can significantly reduce post-release mortality and, therefore, risk for whale shark populations.

1. INTRODUCTION

Whale sharks (*Rhincodon typus*, Smith 1828) occur in tropical and sub-tropical seas around the globe. While early genetic studies suggested limited genetic differentiation on a global scale (Castro et al. 2007, Schmidt et al. 2009), larger datasets and analytical methods have more recently pointed to genetically distinct meta-populations in the Atlantic and Indo-Pacific oceans (Vignaud et al. 2014, Meekan et al. 2017), with most likely only infrequent migrations around Cape of Good Hope. In the Indo-Pacific Ocean, a lack of genetic differentiation suggests a single panmictic meta-population (Vignaud et al. 2014, Meekan et al. 2017).

Localised target fisheries have led to demonstrated declines in relative abundance indices in several regions worldwide (Hsu et al. 2012, Pierce

& Norman 2016), supporting the conclusion of sensitivity to fisheries impacts (reviewed in Pierce & Norman 2016). Regional population depletions suggest that there may be limited functional connectivity between regional populations, although there is limited genetic evidence for separate populations. The notion of limited connectivity is supported by photo-identification databases, which indicate limited connectivity between known whale shark hotspots, suggesting some level of geographic structuring of regional populations (Pierce & Norman 2016).

Whale sharks often migrate between areas of high productivity within their (sub-)tropical range, and are thought to have similar habitat requirements as most tuna species. This overlap in habitats leads to interactions between whale sharks and purse-seine fisheries targeting tuna and other pelagic species (Sequeira et al. 2012). Although many of these interactions are probably due to habitat overlap alone, whale sharks are also known to act as a *de facto* fish aggregation device that operators use to spot schools of tuna (Matsunaga et al. 2003). Some reports suggest that whale sharks usually survive encounters with purse seines when handled adequately (Matsunaga et al. 2003, Escalle et al. 2017). Although conservation measures are now in place and directed whale shark fisheries have been prohibited in most nations, total mortality associated with fishery interactions is currently unknown, and late maturation and a long lifespan make whale sharks vulnerable to overfishing (Clarke et al. 2015, Pierce & Norman 2016).

Fisheries interactions with whale sharks in the Western and Central Pacific Ocean (WCPO) were summarised by Harley et al. (2013). These authors noted a drop in occurrence of whale sharks in free-school sets, which could be interpreted as a decline in abundance in the area. However, it was also noted that a statistical standardisation of interaction rate trends should be considered to draw more robust conclusions about abundance trends. Furthermore, the authors suggested that spatial habitat models, in line with previous species distribution models (SDMs) for whale sharks (Sequeira et al. 2012, Sequeira et al. 2014), could provide a basis for such a standardisation model.

In this study, we first provided an updated characterisation of whale shark interactions with WCPO purse-seine fisheries. We then used a statistical model to standardise interaction rates in space and time, and estimated the effect of oceanographic habitat variables on whale shark interaction rates in these fisheries. Assuming that these variables describe habitat suitability, we used the estimated correlation with oceanic variables to predict whale shark densities across the Indo-Pacific Ocean basins. Combined with data on the spatial distribution of fishing effort, the predicted whale shark densities allowed us to predict total whale shark mortality for Pacific Ocean purse-seine fisheries. We used these estimates with a range of elicited limit reference points (or impact sustainability thresholds) to estimate risk from Pacific Ocean purse-seine fishery interactions for the Indo-Pacific Ocean whale shark population.

2. METHODS

2.1 Data sources

For this risk assessment, we obtained data from a number of datasets, derived inputs and model predictions to estimate risk to the Indo-Pacific Ocean whale shark population from Pacific Ocean purse-seine fisheries (see Figure 1 for an illustration of the overall procedure).

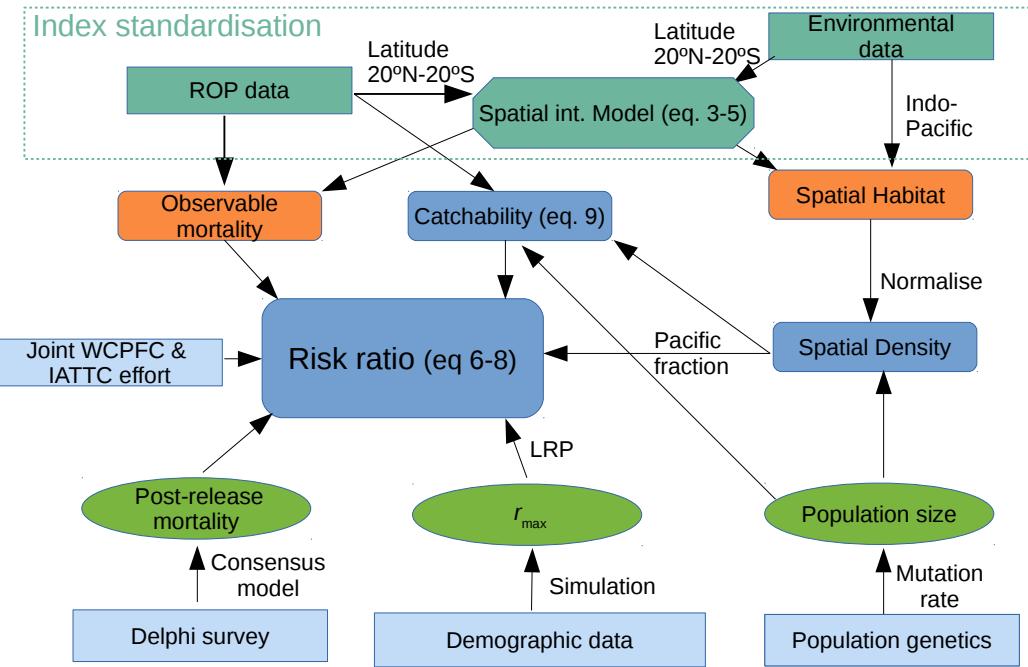


Figure 1: Illustration of the overall procedure of the whale shark risk assessment. Inputs are in square boxes, standardisation model-derived quantities with associated distributions are in boxes with rounded corners, and quantities with associated distributions that were derived outside of the model are shown in ellipses. The index standardisation procedure (teal-coloured components) used regional observer programme (ROP) interaction data and environmental layers in a Bayesian standardisation (CAR-GLMM) model (eq, equations are detailed in the text). Predictions of habitat suitability and estimates of observable mortality were obtained from this model (orange boxes). Demographic parameters (green ellipses; r_{\max} , maximum population growth) were obtained from other data sources, including expert input (Delphi survey). These parameters were combined with model-derived quantities to provide information of spatial densities, catchability and the risk ratio at different limit reference points (LRPs). (WCPFC, Western and Central Pacific Fisheries Commission; IATTC, Inter-American Tropical Tuna Commission).

2.1.1 Data availability

We obtained Western and Central Pacific Fisheries Commission (WCPFC) regional observer programme (ROP) data from the Pacific Community (SPC), with associated effort in the area covered by the ROP (i.e., between

Table 1: Summary of available data of interactions between whale sharks and Pacific Ocean purse-seine fisheries. Data were from the Western and Central Pacific Fisheries Commission (WCPFC) regional observer programme (ROP) database (total of 1800 whale shark interactions), logsheets and Annual Reports (AR1). Numbers refer to total reported interactions, interaction rates are per 1000 sets. The latter were calculated from observer-reported interactions and observed WCPFC tropical purse-seine fishery effort (ROP interaction rates), and from AR1 and total effort (AR1 interaction rates). Effort estimates were provided by SPC (Pacific Community) for the WCPFC tropical purse-seine fishing area between 20 degrees latitude North and South. Percentage ROP observed is total observed effort relative to total purse-seining fishing effort.

Year	Effort			ROP observed		Logsheets	AR1	
	Total in ROP area	Obs. ROP effort	% ROP observed	Total int.	Int. rate		Total Int.	Int. rate
2006	36233	2379	6.57	31	13.03	12		
2007	38876	2566	6.60	26	10.13	32		
2008	43839	3027	6.90	36	11.89	38		
2009	46219	8369	18.11	63	7.53	75		
2010	54645	28997	53.06	217	7.48	103		
2011	60279	26449	43.88	167	6.31	61		
2012	64298	30581	47.56	306	10.01	158		
2013	64568	36097	55.91	284	7.87	75		
2014	64308	32346	50.30	247	7.64	177	297	4.62
2015	54457	28063	51.53	281	10.01	206	382	7.01
2016	52077	23712	45.53	110	4.64	75	175	3.36
2017	18256	5737	31.43	32	5.58	165		

latitudes 20° N and 20° S, and east of longitude 140° E). We obtained Pacific Ocean-wide purse-seine effort data extending beyond the tropical purse-seine fishing area from published datasets by the WCPFC (WCPFC 2018) and Inter-American Tropical Tuna Commission (IATTC; IATTC 2018).

ROP data Observer programme data for WCPFC were requested from SPC for all observer records that included:

- sets marked by observers as being set on a live whale shark,
- observer catch records of whale sharks (as regular catch),
- observer catch records of whale sharks (as species of special interest).

We obtained two data extracts from the ROP database, which contained observer records from fishing activities between 20 degrees latitude North and South. One extract only contained data of whale shark interactions, whereas the second extract contained ROP-observed purse-seine effort for recent years (i.e., since 2006). Observed effort varied from a low value of 2379 sets in 2006 to a high value of 36097 sets in 2013 (Table 1). The supplied interaction dataset contained 2177 records from 2006 to 2017.

Log-sheet reporting and annual report summaries Data from log-sheet reporting were obtained from SPC. Observed interactions exceeded reported interactions in all years except 2008, 2009 and 2017 (Table 1). For the latter year, the observer data were incomplete, with only 5737 observed

sets (this fishing year was ongoing at the time data were extracted). Data for the years 2008 and 2009 were from early years of the ROP, when ROP observer coverage was relatively low.

Annual reports (AR1) were assessed for reported interactions, which were extracted for 2015 and 2016. 2017 AR1 reports were not available at the time of writing. Annual values for 2014 were obtained from Clarke (2015). AR1-reported interactions exceeded observed interactions in 2015 and 2016 by 101 and 65 interactions, respectively (Table 1).

Effort measures Purse-seine effort data were obtained in two formats: 1) the estimated number of purse-seine sets in the WCPFC tropical purse-seine fishing grounds between latitudes 20° N and 20° S were obtained from SPC on a 5x5 degree grid to minimise data restrictions owing to the three vessel data confidentiality rule, and 2) the estimated effort as the total number of sets from publicly available WCPFC (WCPFC 2018) and IATTC (IATTC 2018) purse-seine effort datasets (both on 5x5 degree grids). The latter contained effort data for areas that are not part of the tropical purse-seine area covered by the ROP, such as to the west of Papua New Guinea (PNG), in the South China Sea, and off Japan. Effort data reported at the level of individual sets in the tropical purse-seine area contained detailed information on set types (i.e., school association) and were, therefore, considered more adequate for the purpose of modelling whale shark interactions, in conjunction with observer-reported interactions for observed sets.

Other data sources We compared interaction rates found in the WCPO with those described in a recent IATTC analysis of whale shark interactions in the Eastern Pacific Ocean (EPO; Román et al. 2018). We also compared maps of total interactions from the EPO (reported in Román et al. 2018) to cross-validate spatial habitat suitability as inferred below from the more detailed (i.e., time resolved) WCPO data. Publicly available effort data from the IATTC (IATTC 2018) were combined with the public WCPFC effort data (WCPFC 2018) at the level of sets to obtain a pan-Pacific Ocean effort dataset (Figure 2) to estimate fishery overlap with an inferred Pacific Ocean whale shark distribution (see below).

2.1.2 Data preparation

Observer data The supplied ROP observer dataset on whale shark interactions contained 94 duplicate entries that were removed, resulting in 2083 records. Subsequently, it was evident that the identifications of a number of sets were doubled in the extract; 214 of these identifications were merged into single records for further processing, leaving a total of 1800 whale shark interactions for further analysis (Table 1). As the collection of observer data for 2017 was ongoing during the project, the cut-off year for data included in the analysis was 2016.

Table 2: Summary of publicly available fishing effort data for the Western and Central Pacific Ocean (WCPO) and Eastern Pacific Ocean (EPO) from Western and Central Pacific Fisheries Commission (WCPFC 2018) and Inter - American Tropical Tuna Commission (IATTC 2018) public domain effort datasets. Effort is presented as the proportion of effort in quarters 1 to 4 (Q1–Q4).

Year	WCPO					EPO				
	Sets	% Q1	% Q2	% Q3	% Q4	Sets	% Q1	% Q2	% Q3	% Q4
2006	69356	26.7	23.0	24.1	26.2	32060	33.9	27.4	20.7	18.0
2007	77593	23.8	23.8	24.4	28.1	28204	30.7	26.8	21.2	21.3
2008	81811	26.3	25.6	24.8	23.4	28902	30.1	28.3	20.3	21.3
2009	82465	21.7	24.6	25.8	27.9	27851	27.2	27.9	23.2	21.7
2010	93143	22.1	25.3	25.7	27.0	26802	25.2	29.1	24.5	21.2
2011	125529	20.3	28.3	28.4	23.0	26679	26.7	29.6	23.2	20.5
2012	103705	24.9	24.6	24.9	25.7	28175	26.3	29.2	24.7	19.9
2013	166334	20.6	27.4	28.8	23.2	29106	26.7	29.7	24.1	19.6
2014	129750	23.3	25.6	25.2	26.0	29749	26.4	28.1	24.3	21.2
2015	109282	24.0	25.3	26.1	24.7	32992	27.1	28.5	23.5	20.9
2016	150197	20.4	24.3	28.0	27.3	32437	24.7	31.2	24.2	19.8

2.2 Standardising interaction rates

Interaction rates were standardised using ROP data in conjunction with environmental layers on a fine spatial and temporal resolution (monthly) that was matched to observed sets. Environmental layers were compiled to ensure that we could account for variables that had previously been found to determine whale shark distributions (Sequeira et al. 2012, Sequeira et al. 2014).

2.2.1 Physical and Environmental layers

We extracted sea surface temperature (SST) and chlorophyll *a* (CHLa) data from satellite products as monthly averages on a spatial scale of 0.1 degrees at the equator. Depth and distance to land were calculated using high-resolution bathymetry and coast-line shapefiles. Observed purse-seine sets were then matched to the appropriate spatial and temporal component of environmental layers.

2.2.2 Standardising interactions

We standardised interaction rates using generalised linear mixed models (GLMMs) of whale shark occurrence in observed sets in the tropical purse-seine fishery. The mixed effects modelling was carried out at different levels of resolution and detail:

- At the set level, a logistic regression was used to standardise occurrence (presence-absence) with respect to environmental layers and also vessel-level variables such as flag state (i.e., state of vessel registration) and observer programme. We used flexible spline models to test the influence of environmental variables. These variables

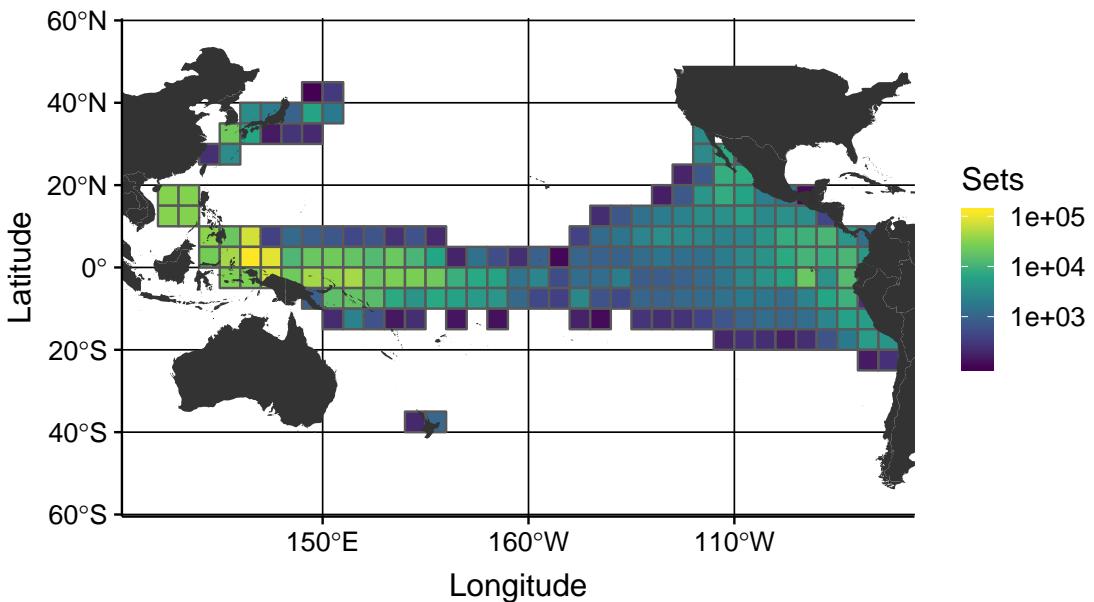


Figure 2: Total purse - seine fishing effort (number of sets) from publicly - available effort datasets for the Western and Central Pacific Ocean and Eastern Pacific Ocean for the period from 2006 to 2016 on a 5x5 degree grid. Only grid cells with more than 100 total sets are shown.

included SST, CHLa, depth and bathymetry slope. This initial standardisation was used to test if set level variables such as flag state and observer programme are important for the standardisation or if these can be ignored and data aggregated at a larger grid level without losing important information.

- Modelling was also conducted at a 5x5 degree grid level. By introducing a grid-cell indicator covariate, we accounted for spatial auto-correlation that is not influenced by measurable habitat variables (with a latent correlation structure for grid-level auto-correlation, assuming the grid is small relative to the residual correlation length scale). This grid level covariate also allowed us to link total effort from

WCPFC and IATTC public effort datasets.

Initial standardisation at set scale We initially standardised interactions using the full dataset including all observed effort and interactions (see Table 1), but not considering potential residual spatial structure after accounting for environmental predictors. We standardised interaction rates for year, quarter, set type, observer programme, vessel state flag and environmental layers. The relationship with environmental predictors was estimated as a smooth (thin-plate spline) term in a generalised additive mixed model (GAMM; Wood 2017). Observer programme and vessel flag state were treated as random effects, whereas all other variables were treated as fixed effects. The observation model was taken to be a binomial model with p the probability of interaction conditional on covariate. The full model for all interactions I was:

$$I \sim \text{Binomial}(1, p), \quad (1)$$

$$\text{logit}(p) = X\beta + Z\gamma + \sum f_i(E_i), \quad (2)$$

where I is an indicator variable that is one when an interaction occurs (i.e., we did not consider the number of whale sharks reported per interaction as few records had more than one individual per set); X is a matrix of fixed effect predictors, with associated regression weights β , and Z is the matrix of random effects with γ their estimated weights, E are environmental predictors and f is a set of smooth functions (splines). The model was estimated using the mgcv package (Wood 2017) in the software package R (R Core Team 2018).

Standardisation on 5x5 degree grid Standardisation at the 5x5 degree grid scale proceeded as above, but we also included a grid-level random effect in the analysis to account for spatial covariation that cannot be explained by physical covariates alone. For this model, we omitted set-level covariates such as set type, flag state and observer programme code, and used environmental covariates, year, quarter and grid cell as predictors, with the latter being a spatially correlated random effect. We aggregated environmental data of observed sets at the grid level using mean environmental data, and summing sets and interaction events so that n_s is the number of interaction events for ν_s sets in grid cell s . The model at the grid cell was then:

$$n_s \sim \text{Binomial}(\nu_s, p_s), \quad (3)$$

$$\text{logit}(p_s) = X\beta + Z\gamma + \omega_s, \quad (4)$$

$$\omega_s \mid \omega_q, q \neq s \sim \text{Normal}(\rho \sum_{q=1}^S a_{ij}\omega_q, \tau_\omega^{-1}), \quad (5)$$

where ρ is a common auto-regressive parameter, A is an adjacency matrix, and τ is a precision parameter. All priors were vaguely informative relative to the true scale of the parameters. The model was estimated using Bayesian inference via Markov Chain Monte Carlo using the inference software Stan (Stan Development Team 2018), within R using the brms package (Bürkner 2017). All priors were formulated as vaguely informative priors so as to exclude regions of parameter space that were implausible.

Data used for the final standardisation We used three subsets of data in the final standardisation and habitat suitability model:

1. the full observer dataset including all set types;
2. the full dataset, excluding sets identified as whale or whale shark associated sets. *A priori* identification of whale sharks may lead to avoidance, especially since the introduction of specific conservation measures, and could, therefore, introduce bias in estimated habitat suitability and decouple local whale shark abundance from interaction rates;
3. free school sets only; these data were used previously (by Harley et al. 2013), leading to the recommendation of standardising interaction rates based on this set type. This subset is included here to provide a link to this previous analysis, and may be akin to a random sample .

2.3 Integrated Bayesian risk assessment

To understand whether the current rate of interactions and associated mortality pose a risk to Indo-Pacific Ocean whale shark populations, we performed a spatially-explicit risk assessment. The risk assessment relied on a number of key inputs:

- The spatial density of whale sharks D relative to the total fishing activity E – this relationship defines the spatial overlap.
- Based on the overlap between fisheries and whale sharks, we derived the total estimated mortalities in each grid cell using an estimate of population size, catchability, and mortality from interactions.
- The total estimated mortality was then compared with a set of reference points.

The risk assessment can be separated in space and time. We used a quarterly breakdown of the total mortality, reflecting potential seasonal changes in habitat suitability and fishing effort distribution (c.f., Román et al. 2018). This approach allowed us to obtain more accurate estimates of total mortality. Nevertheless, we did not have any information about population trends at a three-monthly timescale, and relied on static estimates in

population size. Spatially, we retained the 5x5 degree spatial structure for convenience and as a reasonable compromise between spatial resolution, data availability and computational requirements. In the following, we omitted time-specific notation for convenience, but note that all quantities can, in theory, be derived for any temporal or spatial resolution that can be extracted from available data.

In detail, the present method estimated risk R_s in area s as the ratio of mortality M_s to a sustainability threshold S .

$$R_s = \frac{M_s}{S_s}, \text{ where} \quad (6)$$

$$M_s = q \cdot v \cdot E_s \cdot D_s \cdot N \quad (7)$$

$$S_s = \delta r_{\max} \cdot N \cdot D_s \quad (8)$$

Here, M_s is the total expected mortalities in area s , N is the total population size, D_s is the relative density of whale sharks (with $\sum_s D_s = 1$) in area s , E_s is the corresponding total purse-seine effort in that area; q is the catchability (here defined as the probability that a given set will interact with a whale shark conditional on its presence in the same grid cell), v is the proportion of whale sharks in any area that will die per interaction (i.e., the vulnerability), which can be split into $v^{\text{obs}} + v^{\text{post}}$, the observable mortality rate (i.e., mortality occurring during the interaction) and the post-release mortality; δ is a factor that determines the risk threshold (i.e., the reference point relative to r_{\max}). We used values of 0.5 (F_{MSM} ; Clarke & Hoyle 2014, Zhou et al. 2011), 0.75 (F_{Lim}) and 1 (F_{Crash}). The latter defines the fishing mortality that would lead to extinction (i.e., $F \geq r_{\max}$, with r_{\max} the maximum population growth rate at low population size [and in the absence of allee effects] and F the fishing mortality).

There are a number of unknown factors in this formulation that were derived either directly from available data (q and D_s), by combining life-history or genetic attributes and ecological theory (r_{\max} and N), or by summarising expert judgement (v^{post}). The parameter D_s is the normalised density of individuals per unit area (or grid cell s), which can be estimated for the Indo-Pacific Ocean region as the predicted mean interaction probability given environmental covariates, adjusted for cell size (i.e., cells further from the equator are smaller) and land cover, and normalised to sum to 1. Assuming that the spatial differences in interaction rates in the WCPO observer dataset reflected differences in relative local abundance, D_s is readily available by modifying equation 3 to predict yearly and quarterly interaction probabilities given covariates across all grid cells. It is important to note that we predicted D_s across the Indo-Pacific Ocean basins because population size N is estimated for the Indo-Pacific Ocean population, and we need to estimate how much of the total population we expect in the Pacific Ocean purse-seine areas alone. The latter quantity is $D_{s_P} \cdot N$, with s_P grid cells that overlap with Pacific Ocean purse-seine fishing effort. We also removed year and quarter random effects (i.e., temporal variation not associated with environmental variables) from the model, and

subsume these effects into the catchability parameter, effectively assuming that unexplained temporal variation is due to changes in availability that could not be related to included oceanographic variables.

Having determined D_s , the parameter q_y for year y can be estimated from observer data for a given N as

$$I_{s,y}^{\text{obs}} = q_y \cdot E_{s,y}^{\text{obs}} \cdot D_{s,y} \cdot N, \quad (9)$$

where $I_{s,y}^{\text{obs}}$ are total observed interactions in area s in year y .

To reflect variable observed mortality rates, we estimated the observable mortality v_y^{obs} within the model from the fraction of observed interactions that lead to mortality by year. The year effect was treated as a random effect, and for all effort beyond the observed purse-seine effort we drew samples of v^{obs} from the population distribution for v_y^{obs} . This assumes that mortality for the effort that was not covered by the observer programme should be within the range of mortality recorded in the portion of the effort that was covered by the ROP observer dataset.

2.3.1 Estimating population size

We required an estimate of population size N to derive q and R . It is possible to calculate effective population size from genetic studies (Castro et al. 2007, Schmidt et al. 2009), given a range of assumptions. However, such estimates of N remain highly uncertain (Vignaud et al. 2014). In particular, mutation rates for whale shark genetic markers are not reported, and it is therefore not possible to simply calculate effective population size from population genetic data. Nevertheless, a prior distribution for mutation rates can be derived, and applied to reported values of $N\mu$ from Vignaud et al. 2014 to obtain a distribution for possible values of N . Here we used mutation rates reported in Dudgeon et al. 2012 to constrain population size estimates ($\mu = 2-6 \cdot 10^{-9}$ substitutions per site per lineage per year).

Based on these rates and values for $N_{\text{eff}}\mu$ reported in Vignaud et al. 2014 for the Indo-Pacific Ocean population of whale sharks, we calculated a population size of between approximately 6 700 and 121 000 (95% confidence interval, CI) individuals. Although this estimate was highly variable, it was close to previous estimates based on the same mitochondrial control region marker (Castro et al. 2007). To ensure that our risk estimates reflected a conservative approach (i.e., to apply a precautionary approach), we simulated population size from a distribution whose probability density peaked towards the lower end of the calculated range. Specifically, we used a negative binomial distribution with a mean and scale parametrisation, using mean of 50 000 and a scale of 2. The 2.5th and 97.5th percentile of this distribution were at 6 045 and 139 427, respectively (Figure 3). Draws with less than 5 000 individuals were discarded as this low population size was considered to be contradicted by the number of individuals known from photo databases (Pierce & Norman 2016).

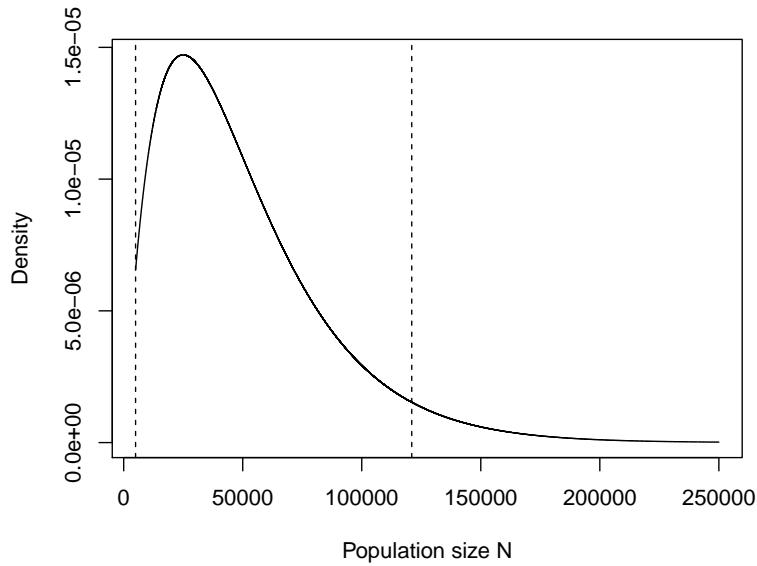


Figure 3: Histogram of the assumed uncertainty about the whale shark population size N . Dashed lines correspond to 5 000 individuals – the lower bound on population size – and 121 000, the 95 percentile of the estimate from population genetic data.

2.3.2 Estimating r_{\max}

Maximum population growth r_{\max} is difficult to determine empirically, but can be deduced from demographic data and life-history theory (Pardo et al. 2016, Pardo et al. 2018). Previous estimates of whale shark population growth r_{\max} are available (Pardo et al. 2016), but are only point estimates and do not reflect uncertainty about whale shark demography. We used theory presented in Pardo et al. 2016 and simulation methods of Pardo et al. 2018 to estimate a distribution for r_{\max} . This method used the Euler-Lotka formula to derive a formulation from which r_{\max} can be calculated. Analytical and computational detail is provided in the corresponding papers (Pardo et al. 2016, Pardo et al. 2018).

As inputs for the simulation of r_{\max} , we relied on demographic data (compiled by Clarke et al. 2015), using distributions spanning the range of reported values for parameters where estimates in published studies diverged, and heuristic arguments for parameters where only single estimates existed (all input parameters are shown in Figure 4, and the corresponding distribution in r_{\max} is shown in Figure 5). For example, it is often reported that whale sharks are the most fecund of shark species, but this statement appears to be based on a single pregnant female with 300 embryos that were at different developmental stages (Clarke et al. 2015). As the gestation period of this species is unknown, it is unclear over what timeframe these embryos would have been spawned, and the clutch size may be substantially different to 300. For this parameter, we used a distribution that had a peak at smaller clutch sizes, but also accounted for

the possibility of clutch sizes that were larger than 300. In addition, the inter-gestational period is unknown, with little information to guide any informed judgement. Here, we used a distribution specified as poisson(1)+1 to allow for the possibility that the inter-gestational period is two years or more.

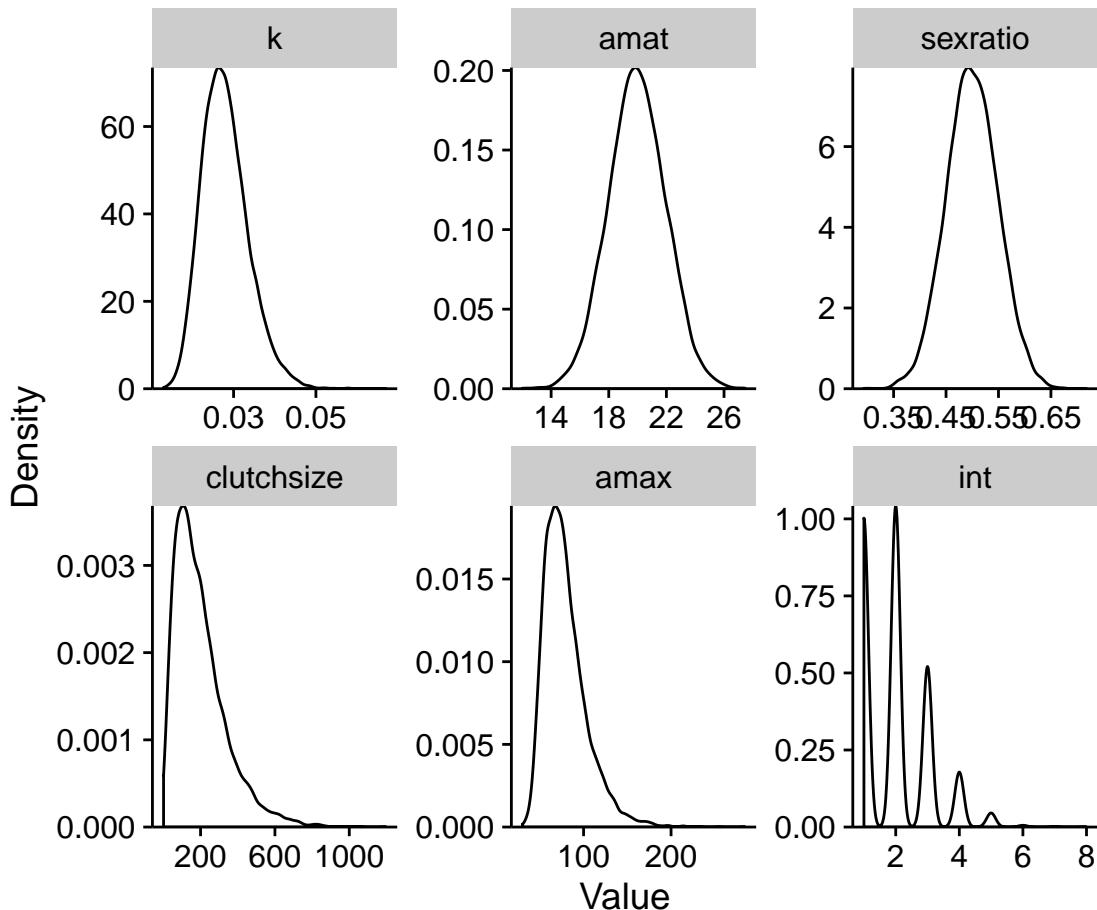


Figure 4: Input parameter distributions used to calculate r_{\max} for whale sharks based on Pardo et al. (2018). Parameters are: k , von Bertalanffy growth parameter; $amat$, age at maturity; $amax$, maximum age; int , inter-gestational period.

2.3.3 Delphi survey for post-release mortality v_{post}

While observable mortality is generally recorded in the fate code field for observed trips, post-release mortality for whale sharks is largely unknown and considered to vary with the release method and overall treatment of the animal (Clarke et al. 2015). This notion was supported by a recent tagging study that showed that adequate release methods lead to low medium-term mortality (i.e., tagged sharks showed zero mortality, but all tags detached prematurely after deep dives Escalle et al. 2017). At the same time, it is currently unknown how many fleets use “safe release” methods (i.e., release over cork line instead of tail-lifting individuals). In addition, as some

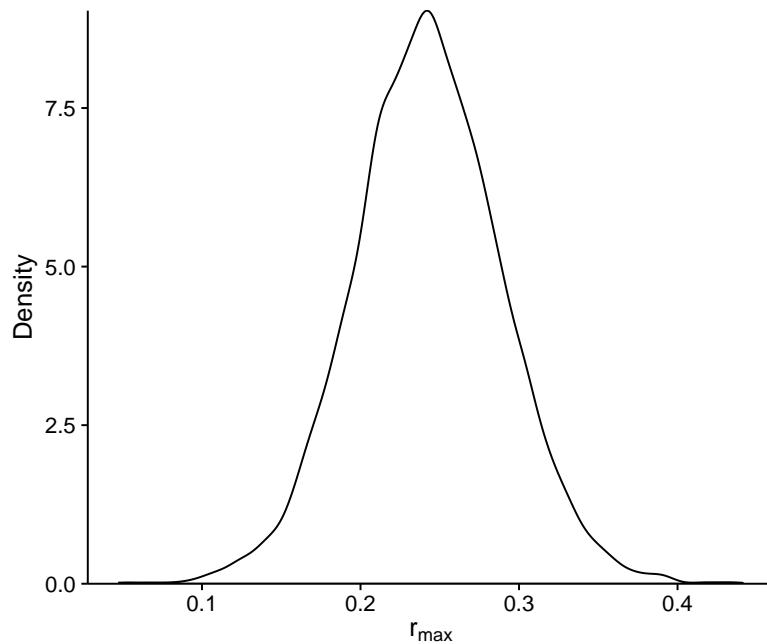


Figure 5: Maximum population growth r_{\max} for whale sharks calculated based on methods described in Pardo et al. (2018), and inputs shown in Figure 4.

interactions result in immediate mortality, we assumed that post-release mortality was also different from zero when it is summed across all fleets.

To gain an understanding of potential post-release mortality across Pacific Ocean purse-seine fleets, we conducted an e-Delphi survey, with the assistance of the International Seafood Sustainability Foundation (ISSF). Delphi surveys are used in data-poor situations, as they provide a structured approach for obtaining expert opinion in a systematic and transparent way (Linstone & Turoff 2002, MacMillan & Marshall 2006, Cole et al. 2013). The Delphi process is set up for experts to contribute information independently, and allows experts to participate in the survey remotely. The Delphi technique is based on an iterative process that facilitates contributions by participating experts and includes a feedback approach to build consensus, and obtain a measure of uncertainty.

The survey was designed as a two-stage online process, with a survey link mailed to potential respondents. We did not provide any auxiliary information to participants such as observer recording of whale shark condition. This is because we wanted to gain information based on experts experience of practiced release methods and potential effects only, and to avoid obtaining answers that are biased by the interpretation of particular results or datasets. Draft survey questions were assessed at the “Workshop on WCPFC Bycatch Mitigation Problem-Solving” in Noumea in May 2018. In response to feedback received from this workshop, the questionnaire was finalised for the expert elicitation exercise. The survey was set up to be anonymous to limit potential bias. The two-stage process was designed to enhance reflection among respondents, and to lead to a consensus that

can be used as an input for the v_{post} parameter. To facilitate consensus building in the second round, a summary of first round answers was shown to respondents before they were requested to consider their initial answer in view of responses from other survey participants and the overall consensus at that stage.

To obtain quantitative information to use in the risk assessment process, we queried three quantities from the respondents: the minimum, maximum and most likely post-release mortality rates from whale shark interactions with purse-seine fisheries. Procedures outlined in O'Hagan et al. (2006) were followed to elicit these quantities and relevant metadata (the full questionnaire for each round is available in Appendix C.1).

Expert answers were analysed using Bayesian methods to derive a consensus distribution for v_{post} . To obtain this distribution, we first assumed that respondents' answers about the minimum, maximum and most likely post-release mortality rates reflected the 0.001 and 0.999 quantiles and the mode of a skew-normal distribution (in logit space), respectively. The skew-normal distribution was fitted to individual answers using least-squares minimisation. We then used methods similar to those reported in a previous Delphi survey (Abraham et al. 2017) to elicit the consensus distribution from the individual answers: we assumed that the answer of respondent i about the most likely mortality value, $v_{\text{post}}^{\text{resp}_i}$, was drawn from a distribution with unknown true post-release mortality parameter $v_{\text{post}}^{\text{cons}}$ (the location parameter of the distribution) — this represents the consensus value, with uncertainty bound by the individual respondent's answers about their uncertainty (and its shape via the skew). We then estimated the consensus location using a vaguely informative, hierarchical prior. Simulations documented in a previous Delphi survey (Abraham et al. 2017) show that this method leads to a robust summary of expert answers into a coherent consensus distribution that reflects individual answers and their uncertainty (akin to a formal meta-analysis). The model is given by:

$$\text{logit}(v_{\text{post}}^{\text{resp}_i}) \sim \text{SN}(v_{\text{post}}^{\text{cons}}, \tau^{\text{resp}_i}, \alpha^{\text{resp}_i}), \quad (10)$$

$$v_{\text{post}}^{\text{cons}} \sim N(\mu_{v_{\text{post}}}, \sigma_{v_{\text{post}}}), \quad (11)$$

$$\mu_{v_{\text{post}}} \sim N(0, 2), \quad (12)$$

$$\sigma_{v_{\text{post}}} \sim N_{T0}(0, 2), \quad (13)$$

where $\text{SN}(\lambda, \tau, \alpha)$ is the skew-normal distribution with location λ , scale τ and skew α . N_{T0} is a normal distribution truncated at zero.

3. RESULTS

3.1 Data

3.1.1 Characterising interactions in the WCPO

Overall interaction estimates and interaction rates Total observer-reported interactions per year ranged from 31 in 2006 to 247 in 2014 (Table 1, Figure 6). Overall interaction rates per observed set declined from relatively high rates between 2006 and 2008 to a relatively stable mean interaction rate of approximately eight interactions per 1000 sets between 2009 and 2016 (Figure 6).

The AR1 data for the three years between 2014 to 2016 allowed cross-validation of the interaction rates estimated from ROP data. In 2015 and 2016, the total reported interactions in AR1 were higher than values documented in the ROP, but the calculated interaction rate (i.e., dividing by total effort) followed the same trend as observed interaction rates (Figure 6). AR1 data were approximately 1.5 interactions per 1000 sets lower than interactions rates from ROP data. As the AR1 data cover more effort and a larger area than the ROP, and not all interactions may be reported, this comparison is only an approximation, but it provides some indication that trends evident in the ROP data may apply across the wider WCPFC area.

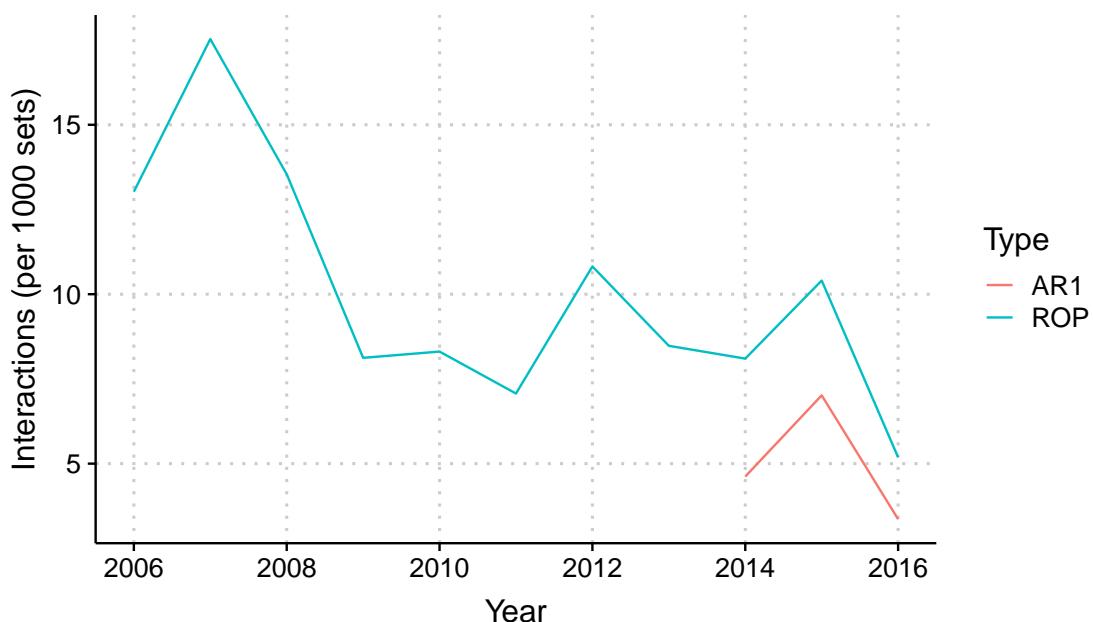


Figure 6: Whale shark interaction rates (per 1000 sets) with Western and Central Pacific Fisheries Commission purse-seine fisheries by year. Data were from the regional observer programme (ROP; blue) and annual reports (AR1; red).

Considering the estimated interaction rates for different types of set data, free-school sets may provide the least-biased estimate of abundance trends for whale sharks in the region with observer coverage as it may represent a somewhat random sample (see also Harley et al. 2013). There was a marked

peak in interaction rates estimated from un-associated sets in 2007 (Figure 7). Subsequently, the estimated interaction rates for these sets decreased, with small fluctuations since 2009. At the same time, there was no noticeable decline in interaction rates for sets identified as associated with whale sharks.

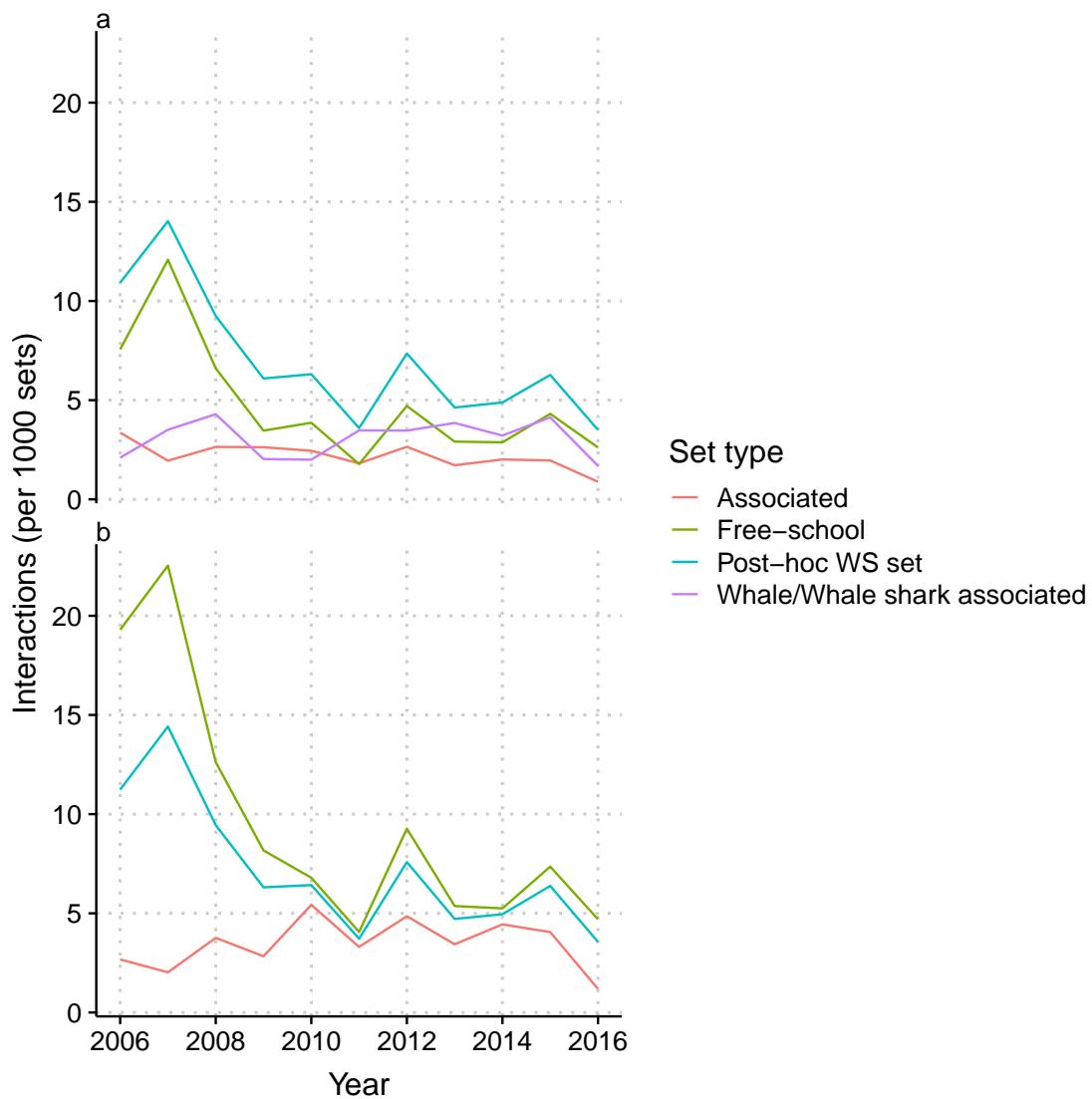


Figure 7: Observer-reported whale shark interactions with Western and Central Pacific Fisheries Commission purse-seine fisheries by set type. Number of total sets (i.e., the denominator for interaction rate) was calculated from (a) all sets by year, and (b) number of sets by set type. Sets associated with whales and with whale sharks were combined here as associations may have been mis-identified initially (note that rates for whale-associated sets were low compared with whale shark-associated sets). Interaction rates also include free-school sets (feeding on baitfish and unassociated), associated sets (excluding whale shark sets) and all set types (associated & unassociated) where whale shark were only recorded post-hoc (i.e., all non-whale/non-whale shark-associated sets).

Spatial distribution of interactions Both absolute interactions and interaction rate over all years in the retained dataset (2006 to 2016) were highest in western Pacific Ocean waters north of PNG (Figure 8). Interaction rates were relatively constant east of PNG along the equator, concentrated near areas of high purse-seine effort (Figure A-1). For both total interactions and interaction rates, there was considerable variability in spatial locations among years (Figures A-2, A-3).

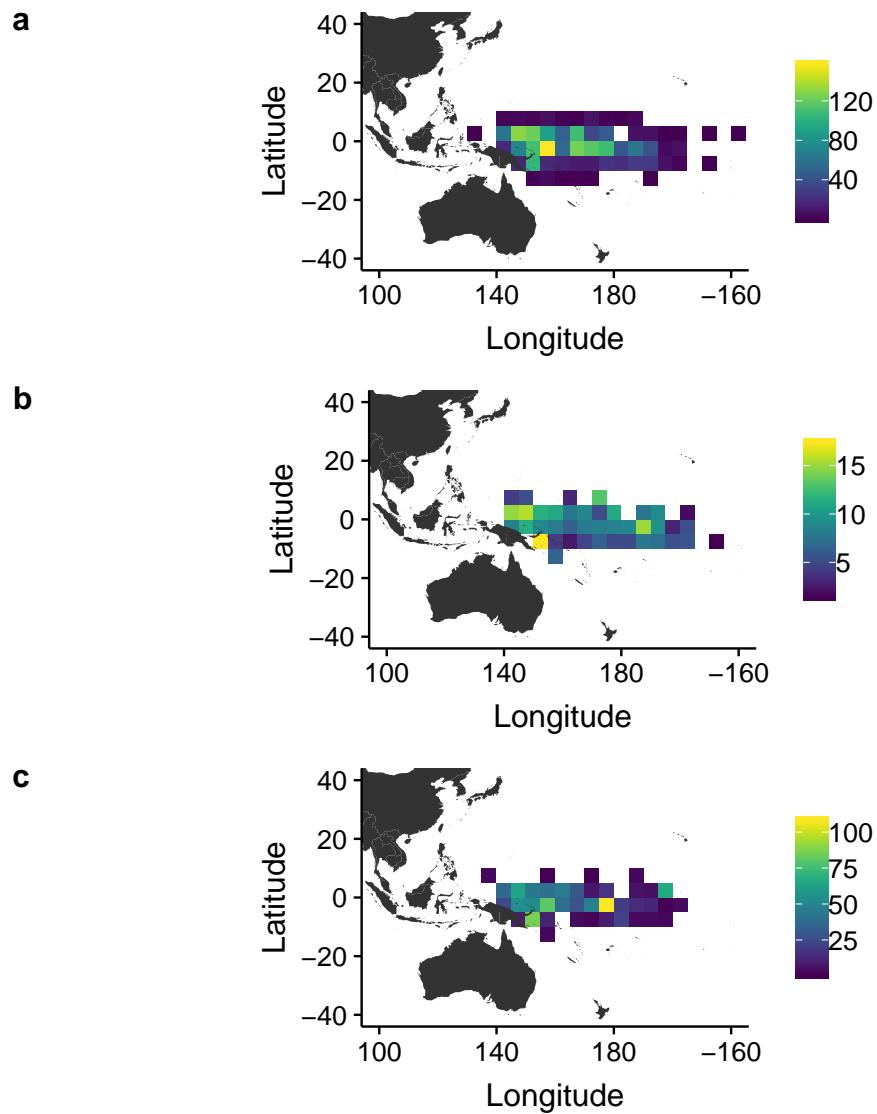


Figure 8: Spatial distribution of whale shark interactions with Western and Central Pacific Fisheries Commission purse-seine fisheries. Interactions shown are (a) total observer-recorded whale shark interactions, (b) observer-reported interaction rates, and (c) number of interactions from logsheet database reports on a 5x5-degree grid. Interactions in b) were only calculated for 5x5-degree cells with more than 500 observed sets across all years.

Observed outcome of interactions The majority of whale shark interactions resulted in the release of live individuals (Figure 9); however, the long-term post-release survival (“fate”) of whale sharks remained unknown. The rate of interactions that resulted in whale shark mortality was below one individual per 1000 sets, excepting in 2008 and 2009, when this interaction rate was 2.6 and one whale shark/s per 1000 sets, respectively. There was a slight trend of decreasing mortality from purse-seine interactions over time (Figure 9a, Table 3), but this trend may have been the result of an increased number of reports without fate codes; it was not evident when considering the proportion of labelled fates only.

Table 3: Summary of observed fate codes for whale shark interactions, plotted as interaction rate (top graph) and proportion of interactions (bottom graph) resulting in dead animals (i.e., observable mortality) versus interactions with unknown status, including all categories of released whale sharks (i.e., some of the released sharks may ultimately die from injury caused by interactions).

Year	Released			Known dead		
	Total int.	Rate (per 1000 sets)	Proportion	Total int.	Rate (per 1000 sets)	Proportion
2006	28	11.76	90.32	3	1.26	9.68
2007	43	16.75	95.56	2	0.78	4.44
2008	33	10.90	80.49	8	2.64	19.51
2009	60	7.17	88.24	8	0.96	11.76
2010	229	7.89	95.02	12	0.41	4.98
2011	181	6.84	96.79	6	0.23	3.21
2012	310	10.13	93.66	21	0.69	6.34
2013	291	8.06	95.10	15	0.42	4.90
2014	246	7.60	93.89	16	0.49	6.11
2015	269	9.58	92.12	23	0.82	7.88
2016	119	5.02	96.75	4	0.17	3.25

3.1.2 Comparison with EPO interactions

Relatively high interaction rates between 2006 and 2008 compared to later years for the WCPO tropical purse seine fisheries mirror similarly trends reported for the EPO (Román et al. 2018). The EPO analysis also found lower, stable interaction rates since 2008. However, while absolute interaction rates in the EPO from 2006–2008 closely matched those in the WCPO, interaction rates since 2008 are markedly lower ($\approx 0.1\%$ in the EPO compared with $\approx 0.5\%$ in the WCPO). In contrast to the relatively homogenous spatial structure of WCPO interactions, EPO interaction rates and total interactions were highest in relatively small areas near the Galapagos Islands and coastal Ecuador.

3.2 Standardising interaction rates

Here we present a preliminary analysis using GAMMs to estimate effects of environmental factors on whale shark interaction rates, as well as the strength of potential vessel level effects. We then move to a spatial GLMM fitted in a Bayesian framework in order to estimate habitat suitability in space and standardise interaction rates.

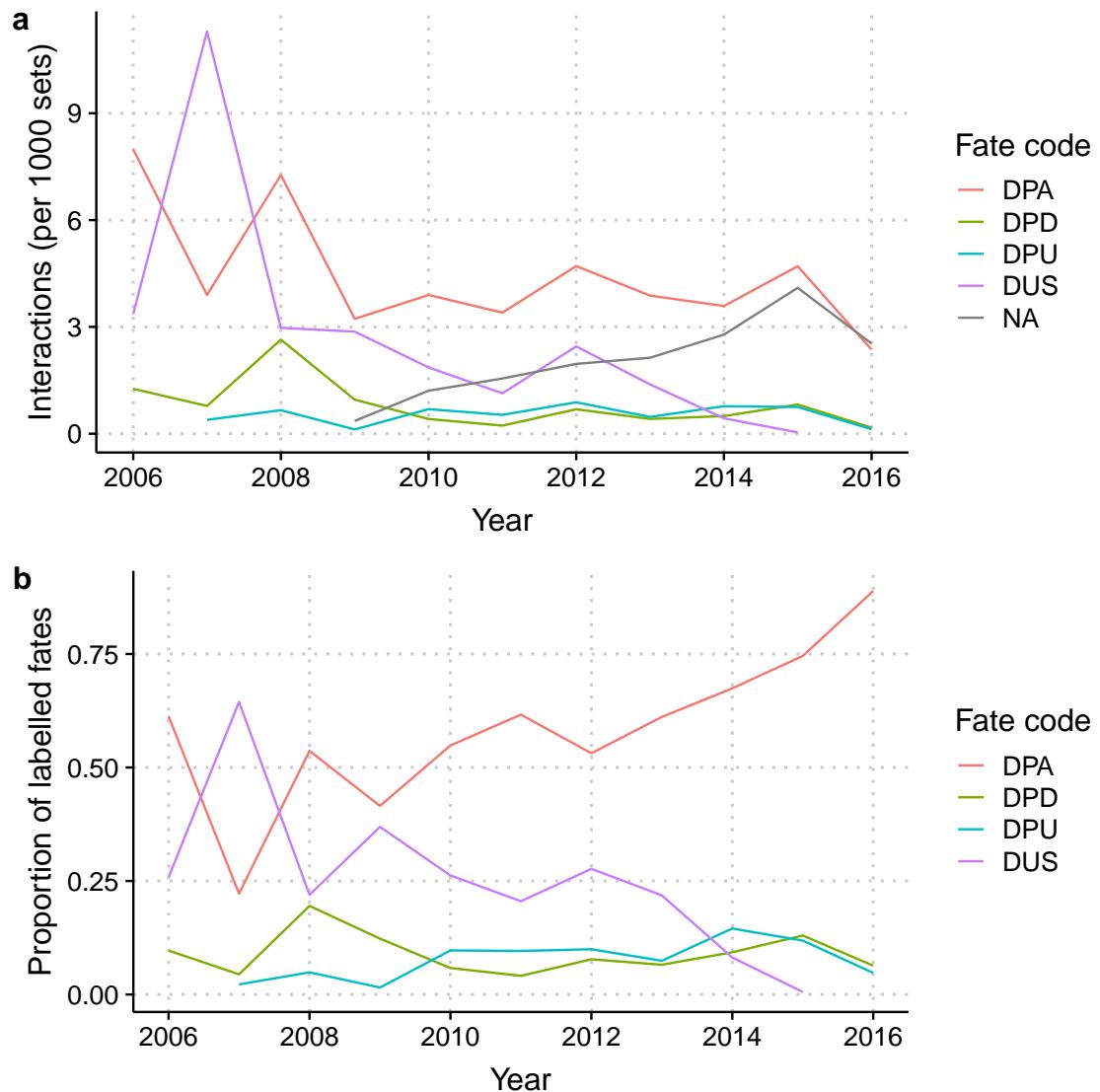


Figure 9: Observer-reported whale shark interactions with Western and Central Pacific Fisheries Commission purse-seine fisheries by fate code indicating the status of dead or released animals. Interactions are shown as (a) interaction rates (number of interactions per 1000 sets), and (b) proportion of all labelled fates (i.e., excluding interactions with un-documented fate codes). Fate codes included discarded protected species (DP), with their status recorded as alive (A), dead (D) and unknown (U); DUS refers to discarded, undesirable species; NA,

3.2.1 Initial standardisation: GAMMs

Initial exploration for the index standardisation model with smooth (thin-plate spline) effects for environmental predictors suggested highly non-linear effects. However, this non-linearity was largely characterised by high sinuosity of the estimated effects (Figure 10), which is difficult to reconcile with biological mechanisms. We therefore chose to work with a more constrained, but spatial GLMM with simple linear effects for all variables except SST for further analyses. The GAMM analysis also suggested that the

effect of vessel level effects, namely the vessel flag and observer programme, were somewhat minor drivers of interaction rates (Figure B-1).

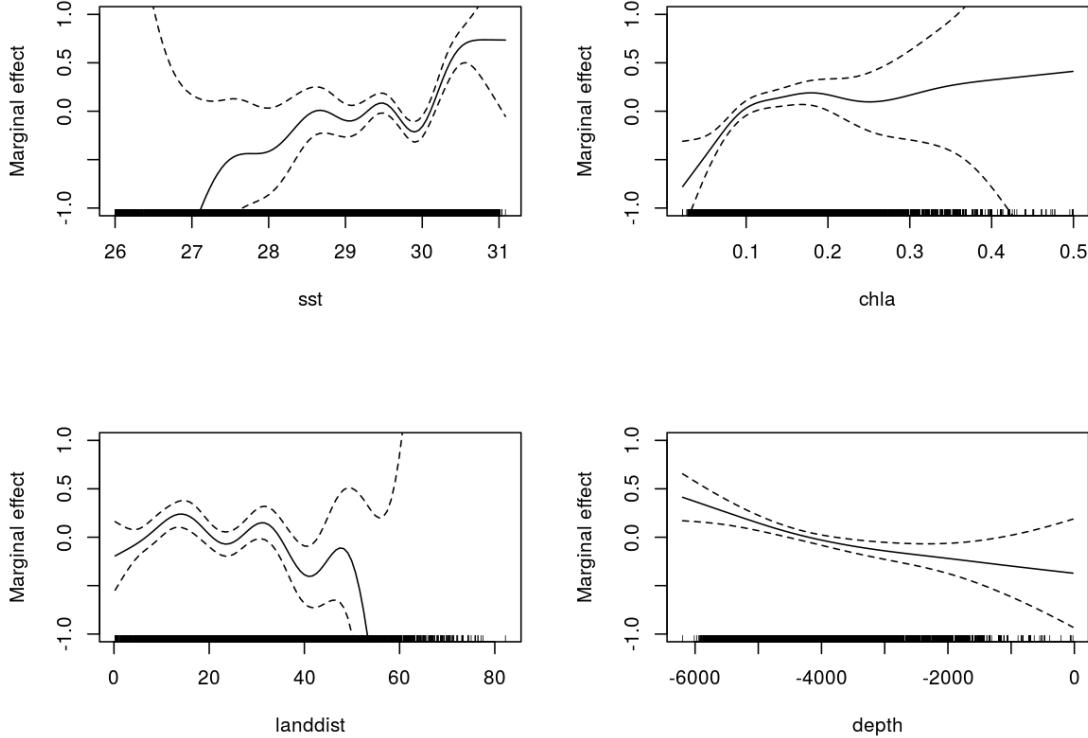


Figure 10: Estimate effect of potential environmental drivers on the number of interactions per 1000 sets, using all set types except whale and whale - shark associated sets.

3.2.2 Bayesian spatial effort standardisation

The Bayesian conditional auto-regressive GLMM recovered similar covariate effects compared to the GAMM (Figures B-3,B-5), and produced reasonable model fits (Figures B-4,B-6).

The analysis employed a thin-plate spline for the SST as it seemed unreasonable to expect linear extrapolations of temperature preference to hold beyond the dataset at hand. This is an important consideration when making predictions to regions beyond that of the tropical purse seine fishery. Environmental effects generally went in the expected direction, with a preference for warm waters and high productivity (Figure 11), as well a negative effect of distance-to-land and depth (Figure B-3). The model run for free-school sets only produced a pattern with higher incidence towards extreme temperatures in the dataset, and lower interaction rates estimated at intermediate temperatures (Figures 11e&f,B-5). Based on SST and interactive effects, it appeared that environmental covariates did not lead to biologically interpretable effects on free-school set interactions. For

instance, it would appear unreasonable to find large numbers of interactions in less productive waters at colder SSTs (c.f., Figure 11f). Across the three data scenarios, there was some residual, large scale spatial variation that could not be captured by the environmental covariates, and that was therefore ascribed to the latent auto-correlated grid effect (Figure 12).

The standardised index resulting from the environmental standardisation model reflected differences in the raw interaction rates in early years (2006–2008) between all sets and free-school sets alone (Figure 13). Nevertheless, over-all trends in the different subsets are qualitatively similar, and the environmental data provide little information explain the over-all changes in interaction rates among years. This is consistent with the GAMM model at the set level, which provided similarly little statistical adjustment of interaction rates (Figure B-2).

3.3 Integrated Bayesian risk assessment

3.3.1 Delphi survey results for v_{post}

We obtained 8 responses in round 1 of the Delphi survey, and 7 responses in round 2. There were 1 and 3 responses that were not valid for rounds 1 and 2, respectively. These responses did not contain an estimate of an interval, but rather had identical responses for minimal, maximal and most likely post-release mortality. The responses and elicited consensus distributions are shown in Figure 14, skew normal fits for individual answers are given in Figure C-1. The consensus distribution for both rounds was peaked at low rates — at $\approx 10\%$ for the second round — but it also reflected high uncertainty and higher values given by some respondents. Given that the survey was anonymous, we do not know to what degree the sample was representative of the over-all state of knowledge about this parameter. In the absence of any other data to parameterize v_{post} , we used the draws from the posterior consensus distribution directly as inputs in the risk assessment to reflect uncertainty in v_{post} .

3.3.2 Habitat predictions

Habitat predictions were based on our index standardisation model, with predictions based on the full linear predictor for a grid spanning the Indo-Pacific Ocean basins. Predictions were by year and quarter to capture seasonal variability in occurrence and overlap with the fishery. Although quarterly variation of predicted spatial habitat is relatively subtle, it captures seasonal increases in habitat suitability in the Northern hemisphere during boreal summer (Q3), as well as increased habitat suitability near the Galapagos and the northern South American coast during quarter one, when most interactions in this area occur (Figures 15, 16; Román et al. 2018). Between year variability in whale shark habitat was reasonably small, with large scale habitat suitability being consistently high towards the Indian- and Pacific Ocean basin boundaries.

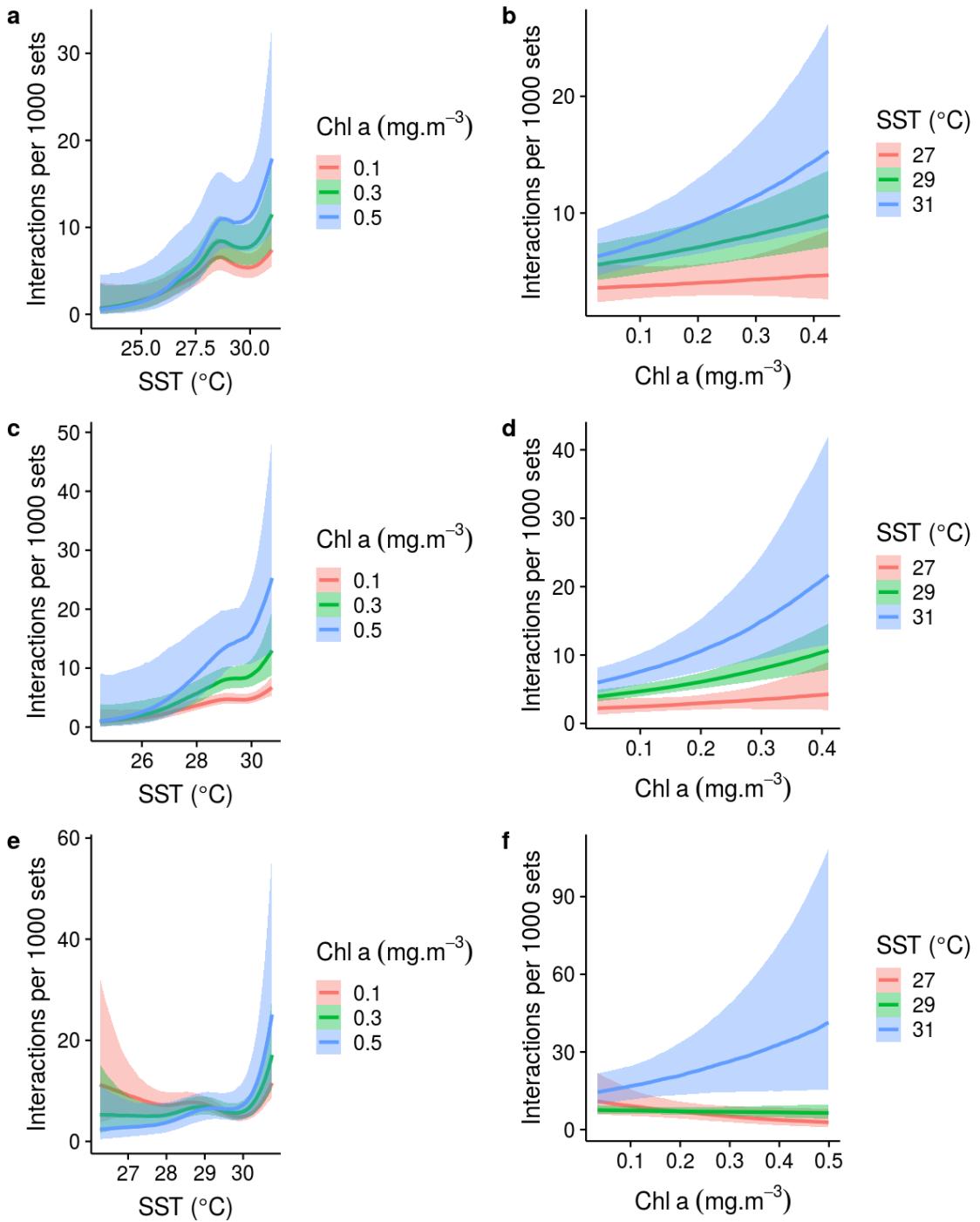
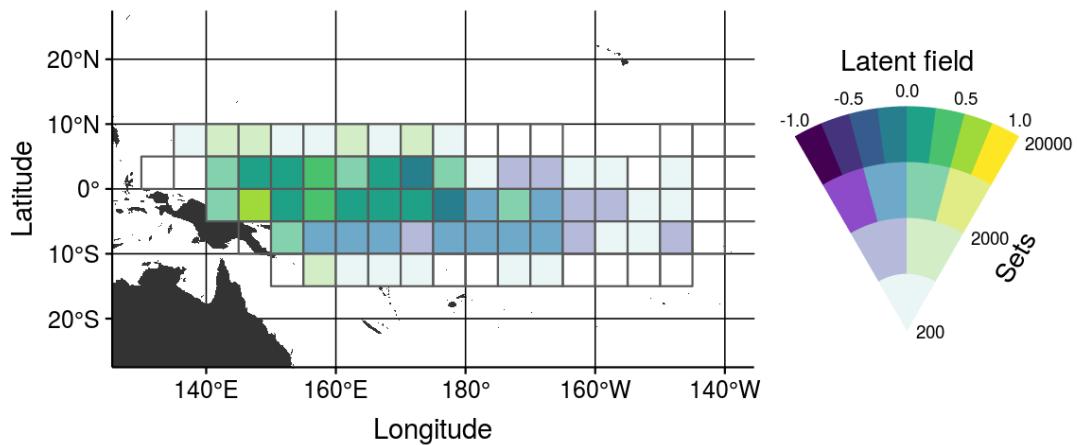


Figure 11: Estimate effect of SST (a,c,e) and chlorophyll a (b,d,f) on the number of interactions per 1000 sets, including interactive effects, for the complete observer dataset (a & b), the dataset without whale/whale-shark associated sets (c & d), and free-school sets only (e & f). The blue line shows the posterior median, intervals show the inter-quartile range of the posterior distribution.

a



b

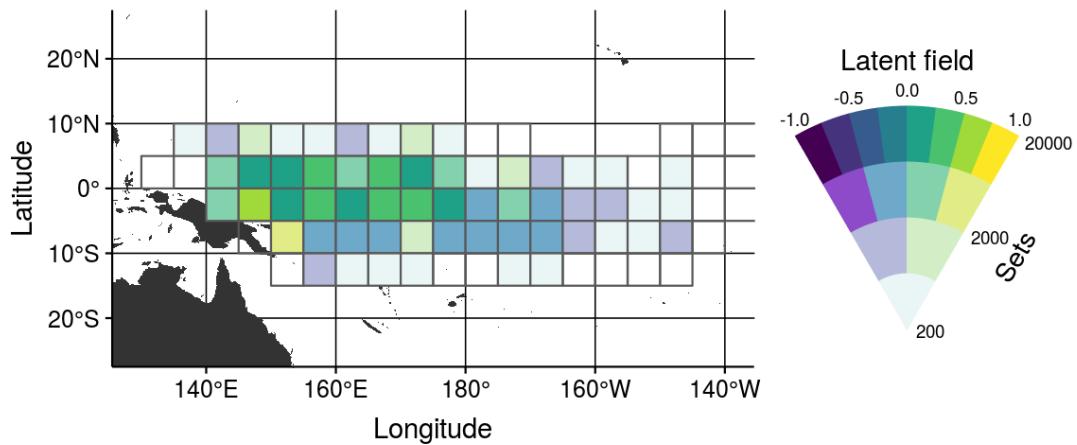


Figure 12: Latent, autocorrelated grid effect, representing un-explained spatial variation in the Bayesian CAR index standardisation model for a) datasets without whale- and whale shark associated sets, and b) free-school sets only.

3.3.3 Risk assessment

The estimated observable mortality v^{obs} was relatively stationary with little trend (Figure 17), while catchability q followed trends in interaction rates,

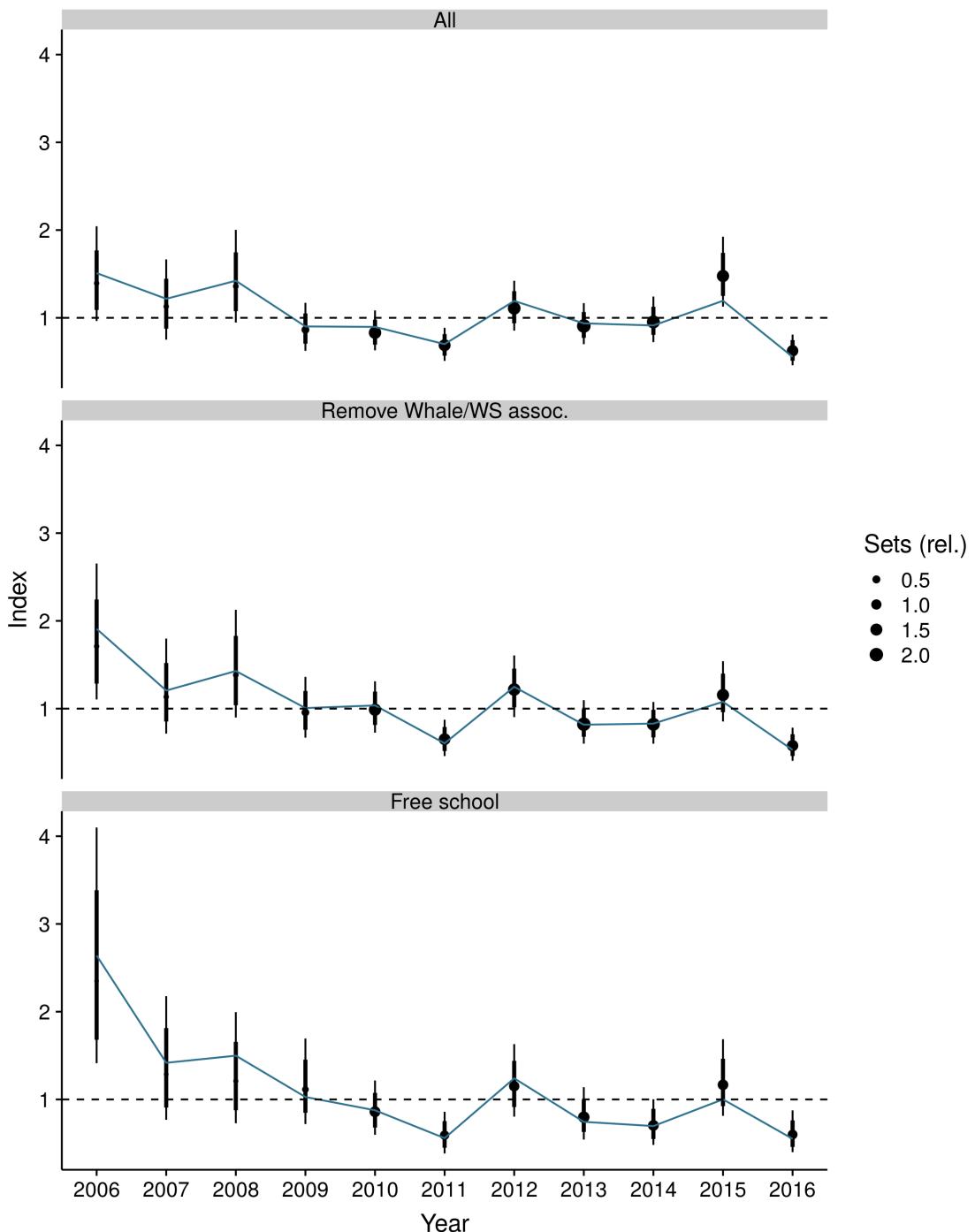


Figure 13: Estimated temporal index of interactions based on a) the full observer dataset, b) the full dataset without whale- and whale shark associated sets, and c) free-school sets only. The rationale behind the different effort subsets is given in section 2.2.2. The index is centered to have a geometric mean of one and is therefore unit-less.

accounting for unexplained variation in observed interactions as intended (Figure 13b).

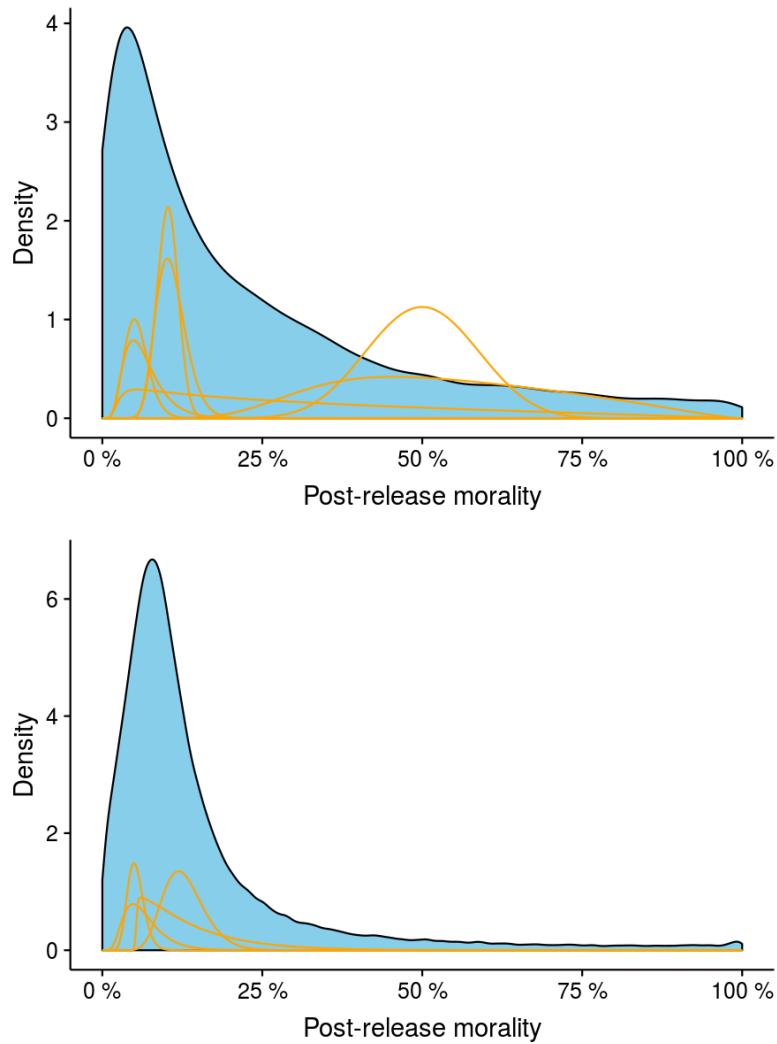


Figure 14: Estimated post-release mortality consensus distribution (blue) based on individual responses (orange) in round 1 (top) and round 2 (bottom).

We verified that our integrated risk model, using estimated mortality and q , could recover changes in observed whale-shark mortalities based on equation 7. Although our model predicts a smoother trend in observed mortalities (the reported mortality rate being different from estimated one), it estimates mortalities on the right order of magnitude across all years (Figure 18). *Philipp Neubauer: For 2012–2015, years with particularly high numbers of observed interaction mortalities, predictions somewhat under-estimate observed mortalities, with observations exceeding the 95% predictive interval in 2015. Risk estimates for 2012–2015 may therefore be biased low.* *Philipp Neubauer:* [The under-estimation was due to predictions being based on the datasets with whale-shark sets removed, but being compared to the full dataset. The revised version of Figure 18a compares total moralities from all sets with predictions generated from this dataset (i.e., using q estimated from this data rather than the subset with no whale shark sets.). This fix leads to an obvious improvement in model fit, but has only a very minor impact on estimated risk levels.]

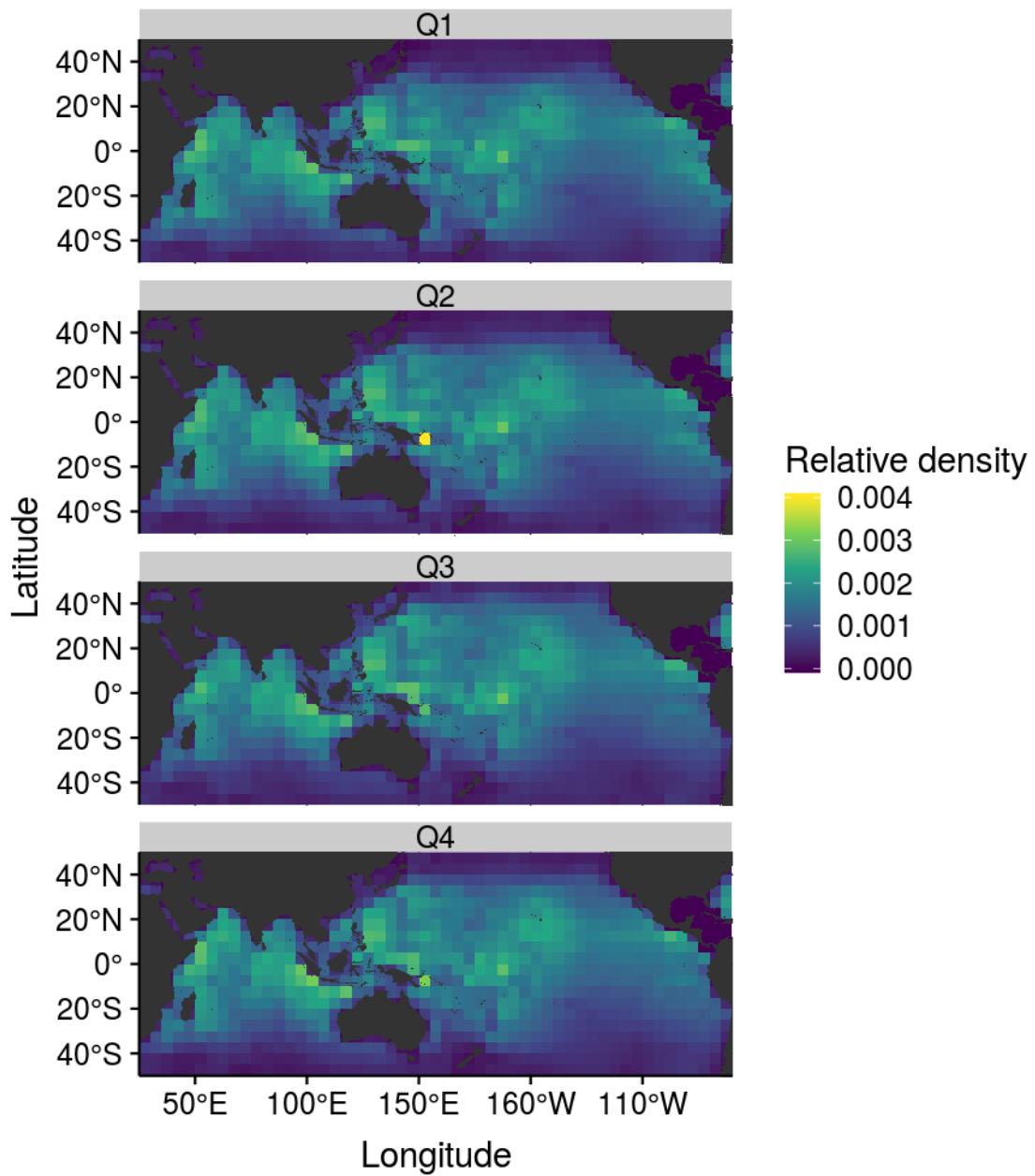


Figure 15: Predicted relative density of whale sharks across Indo-Pacific Ocean basins by quarter for 2006. 2006 was chosen for illustration as the year with highest observed interaction rates in the WCPO.

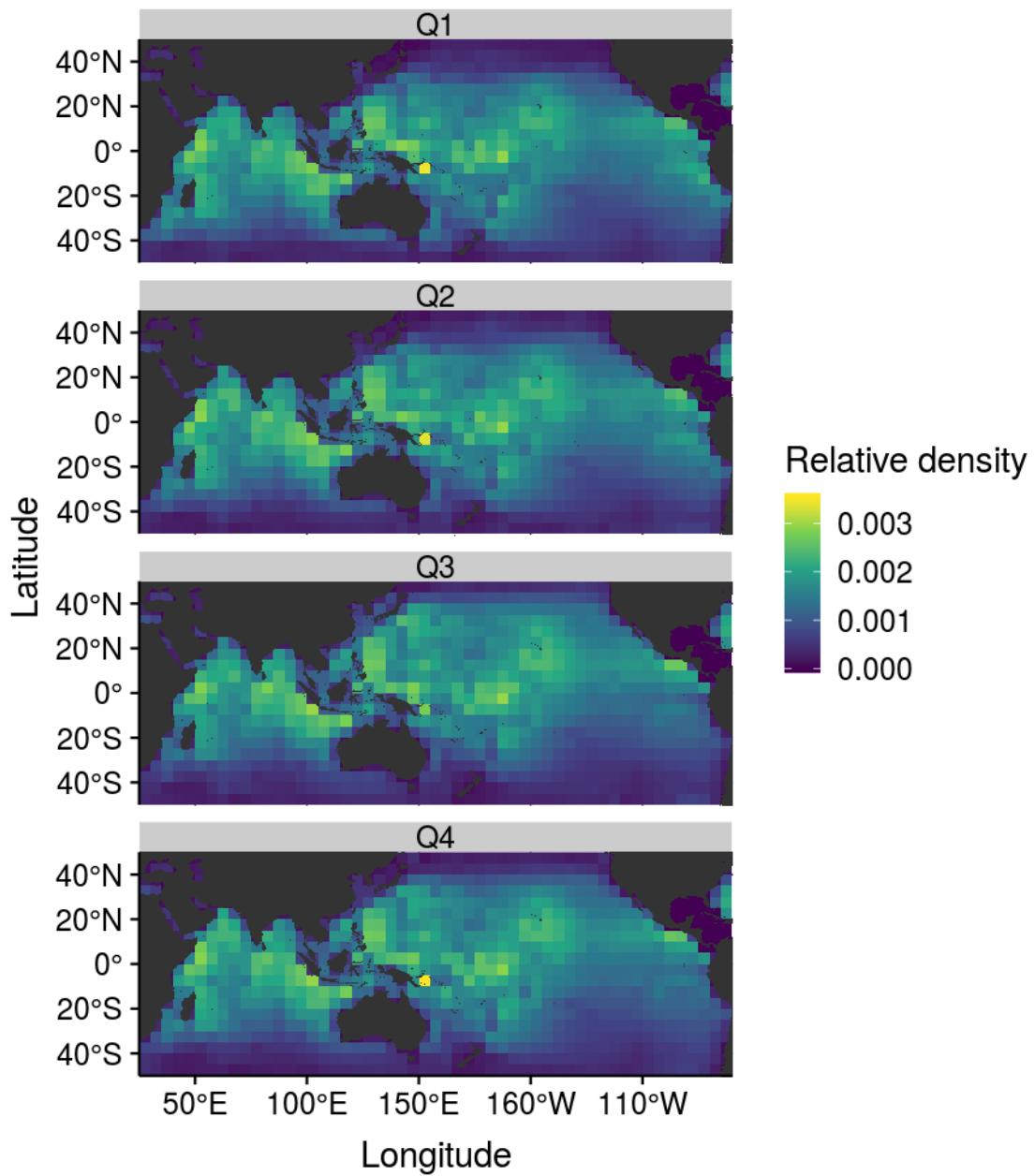


Figure 16: Predicted relative density of whale sharks across Indo-Pacific Ocean basins by quarter for 2013. 2013 was chosen for illustration as a year with relatively low interaction rates in the WCPO.

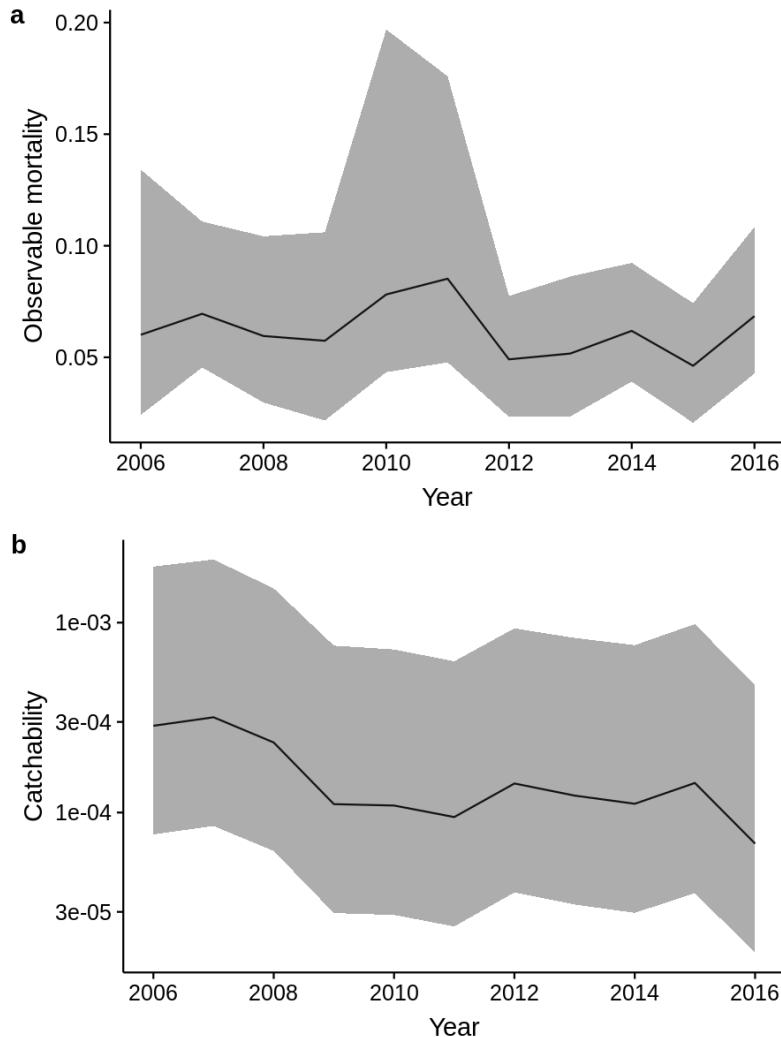


Figure 17: *Philip Neubauer*: a) Estimated trend in observable mortality and (b) catchability from the risk assessment model. [Panel b) fixed to reflect predictions for all mortalities, including whale-shark sets.]

Going from observable to total mortality, the high uncertainty in the elicited post-release mortality introduces a large amount of uncertainty in the predictions which vary over almost an order of magnitude, from 2 to 1421. This uncertainty translates into the risk ratio, which varies from near 0 (for the MSM definition of risk; Lim: 0; Crash 0) in most years, to 0.54 (Lim: 0.36; Crash 0.27) in years with elevated risk, such as 2007.

The temporal trends in predicted mortality and risk are somewhat minor, and given the reasonably stable habitat predictions among years, this trend is mainly driven by trends q and reported effort, mainly for the WCPO where reported effort has increased over the period considered here (Table 2). This trend is also reflected in the spatial distribution of the risk (note that this is extrapolated to the EPO from data for the WCPO only, as we did not have temporally resolved interaction data for the EPO). While in 2006 there were areas of high relative risk in the eastern boundary upwelling

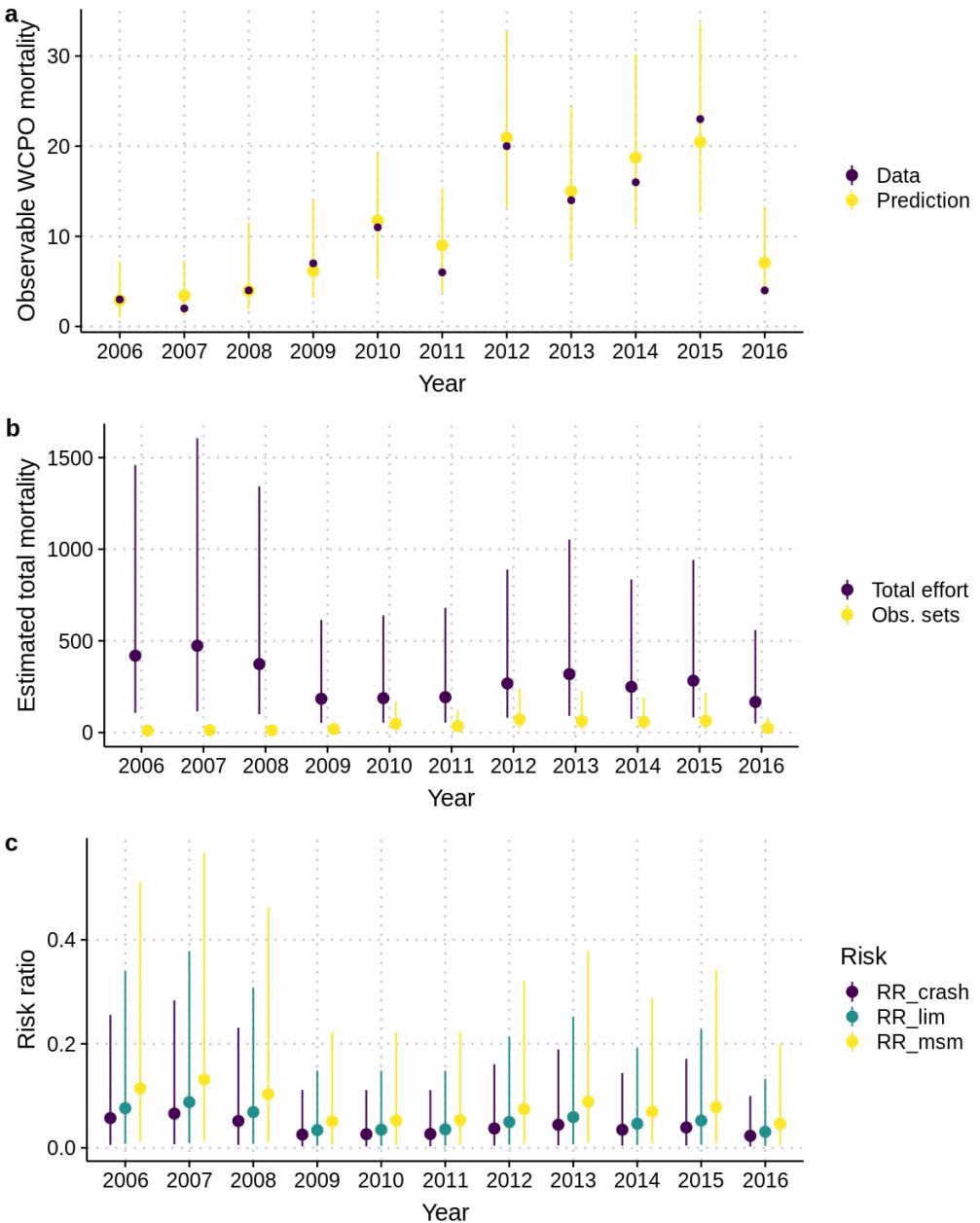


Figure 18: *Philipp Neubauer:* a) Predicted (yellow) and observer - reported (purple points) observable (i.e., without post - release mortality) whale shark mortalities across years, with 95% confidence intervals for mortalities. b) Predicted observable (yellow) and total (purple) mortality from 2006–2016, and c) associated risk that mortality exceeds either of three limit reference points (MSM: $0.5 \cdot r_{max}N$, Lime: $0.75 \cdot r_{max}N$, crash: $r_{max}N$). [Figure fixed to reflect predictions for all mortalities, including whale - shark sets.]

off Ecuador, by 2013 the areas contributing most to the over-all risk in the Pacific were mostly concentrated in areas of high effort in the equatorial West Pacific (Figures 15, 16). This is not due to a reduction in absolute risk in the EPO, but rather a shift in the relative risk due to effort trends (Table 2).

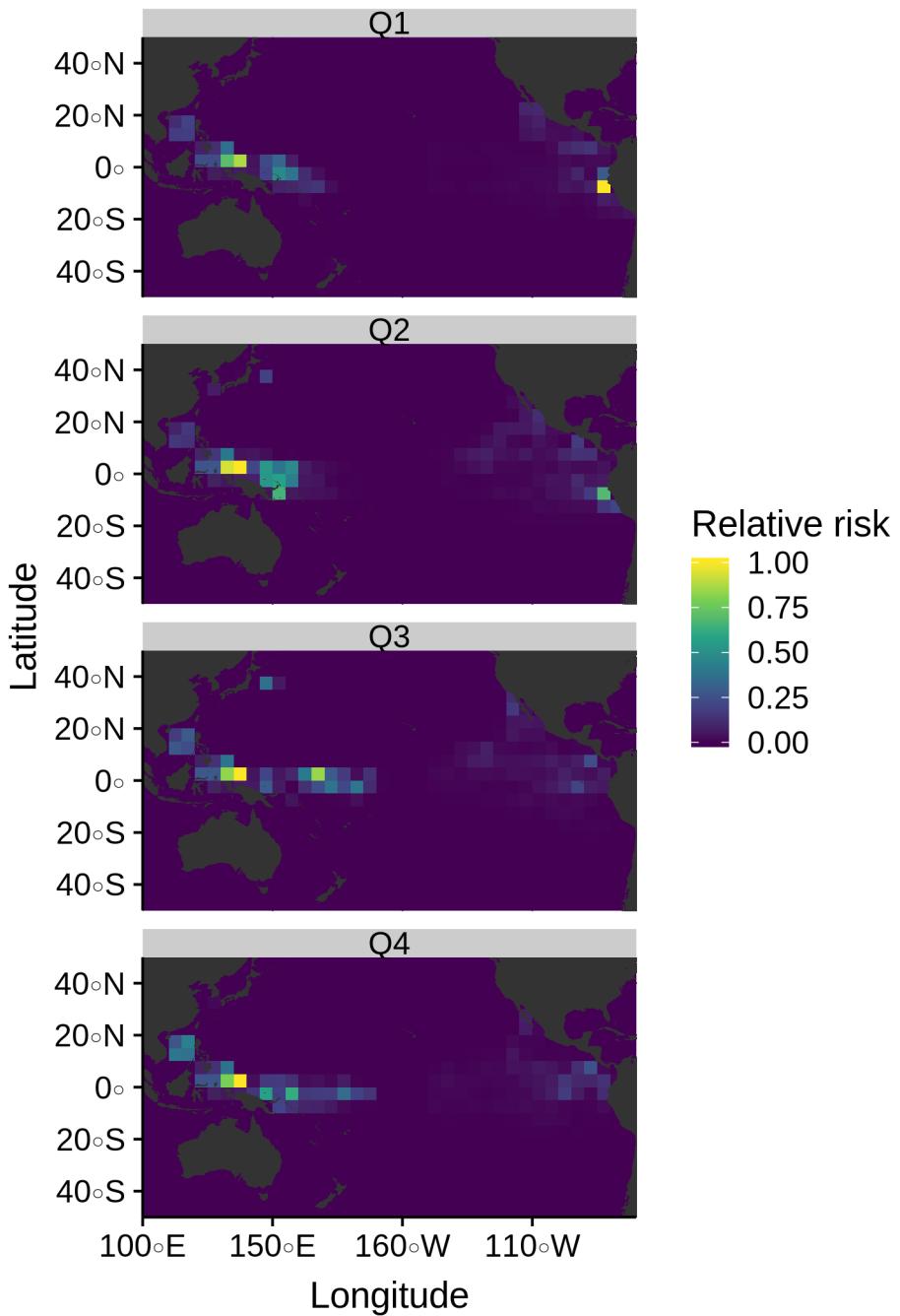


Figure 19: Predicted relative risk (scaled to maximum of 1) for whale sharks from Pacific purse-seine fisheries by quarter for 2006.

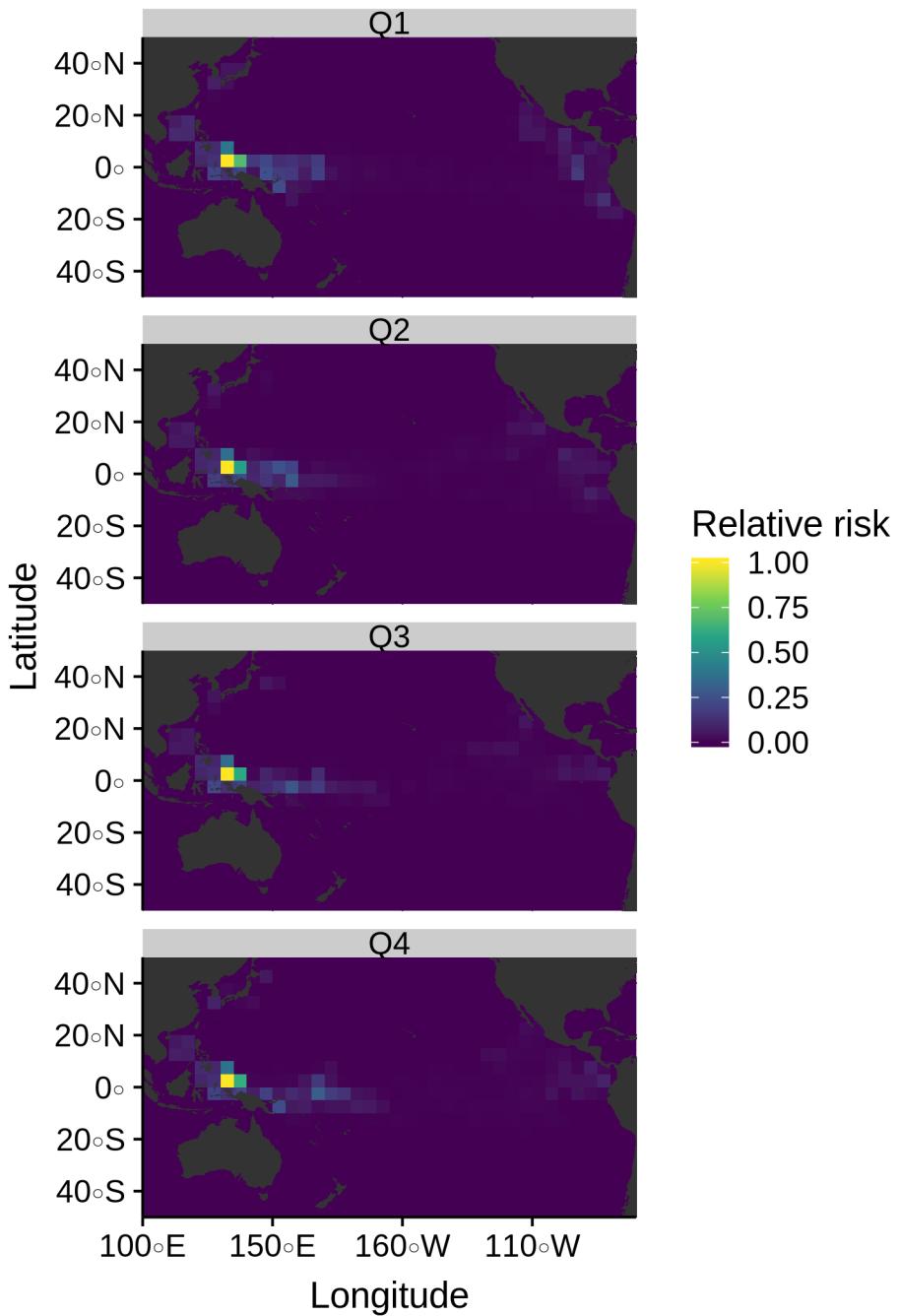


Figure 20: Predicted relative risk (scaled to maximum of 1) for whale sharks from Pacific purse-seine fisheries by quarter for 2013.

4. DISCUSSION

In this study, we attempted to provide a quantitative view of the trends and impacts of whale-shark interactions with Pacific purse seine fisheries. This analysis extends earlier studies detailing spatial and temporal trends in interaction rates in the WCPO (Harley et al. 2013, Clarke 2015) and EPO (Román et al. 2018). Following Harley et al. 2013, we attempted to standardise interaction rates recorded by WCPO observers to obtain an index of local abundance. We then used predicted relative abundance of whale sharks together with information about potential population size and life-history parameters to arrive at an estimate of risk for the Indo-Pacific whale shark population posed by mortality from interactions with Pacific purse-seine fisheries.

Harley et al. 2013 noted a declining trend in interactions of whale sharks with free-school purse-seine sets, and suggested a standardised analysis to confirm this potentially concerning trend. Our standardisation did not alter the qualitative trend of high interaction rates in early years of the observer programme (2006–2008), and lower rates more recently. Very similar rates and trends were observed in free-school sets in the EPO by Román et al. 2018, suggesting that this over-all trend is probably real and not just confined to the WCPO. However, it is noteworthy that in their analysis, Román et al. 2018 found low rates prior to this period. Given the life-history of whale sharks, it would appear unlikely that substantial changes in interaction rates over such short periods are due to over-all abundance changes. Rather, the interaction rates may reflect changes in overlap of the wider Indo-Pacific whale shark population with Pacific purse seine fisheries (i.e., in some years more whale-sharks may be present in the Pacific purse seine fishing grounds), or changes in “catchability” depending on unknown environmental conditions.

Interestingly, the interaction model for free-school sets did not estimate strong or coherent environmental effects on interaction rates. Coherent and nearly identical effects were only found for the full dataset and the data without whale/whale shark sets, suggesting that interactions with free-school sets may be driven by other variables, or on a spatial scale that is not resolved in our analysis. Whale sharks are known to dive deep (Escalle et al. 2017), and although it is thought that they mainly reside near the surface, they may spend more time in habitats other than productive surface waters in some years or areas. In addition, they have been found to occupy fronts of high productivity and temperature clines (Ryan et al. 2017, Afonso et al. 2014), the occurrence and location of which may not be resolved by the monthly-aggregated environmental predictors. As with all catch-per-unit-effort from purse-seine tuna fisheries (e.g., ISSF Foundation 2012), it is difficult to interpret differences in trends between free-school and associated sets. However, there is no *a priori* reasoning to exclude one or the other dataset from the analysis.

With the full dataset, we found effects of SST and productivity proxies that are in line with previously described effects of productivity and thermal habitat on whale-shark occurrence (Ryan et al. 2017, Afonso et al. 2014,

Sequeira et al. 2012). Making the assumption that estimated environmental effects on interactions in space reflect habitat preference, we were able to use large-scale environmental data to predict habitat across the potential range of the Indo-Pacific whale shark population. These predictions were generally in line with areas of known occurrence. For instance, predicted habitat in the EPO was highest in areas of coastal upwelling, such as the Galapagos Islands and the Ecuadorian eastern boundary upwelling system, where whale sharks are known to aggregate in frontal and upwelling systems (Ryan et al. 2017), presumably to exploit abundant food resources. In the WCPO, whale sharks are known to occur seasonally in higher-latitude waters off the coast of Japan (Matsunaga et al. 2003) and New Zealand — this pattern is also captured, if subtly, in seasonal prediction from the interaction rate model (Figures 15,16).

Our estimated map of Indo-Pacific habitat suitability has far more smooth gradients than those estimated in Sequeira et al. 2012 and Sequeira et al. 2014. The latter predictions were made using presence only data, and using pseudo absences to estimate occurrence probabilities (Barbet-Massin et al. 2012). To generate pseudo-absences, one needs to necessarily employ assumptions about where whale-sharks do not occur, which necessarily introduces information about occurrence rates. Inappropriate assumptions about pseudo-absences can lead to large bias in species distribution models, and there is no real way to check these assumptions except common sense. Our model employed true absences from all observed purse-seine sets to avoid having to generate pseudo absences. This leads to quite different predictions to those found in earlier species distribution models for whale-sharks, which assign very low habitat suitability in the Pacific relative to the Indian and Atlantic Oceans. These models also assigned very low habitat suitability in areas of known aggregations (e.g., in the Central American Caribbean).

We used the predicted habitat suitability to derive the overlap of the predicted whale-shark distribution and Pacific purse seine effort, and calculated risk levels for the Indo-Pacific population of whale sharks using life-history parameters. *Philipp Neubauer: Although mortality levels were estimated to be relatively constant between 2006 and 2016, and we employed variable q and mortality parameters among years to capture temporal variability, our model still underestimated mortality in some years. This is likely due to smooth environmental gradients which underlie our predictions, and which cannot predict areas of high local whale shark densities (aggregations). Aggregations may occur on patches of prey smaller than the resolution of our oceanographic habitat variables. As a result, our model cannot predict occasional high capture rates in space, and future iterations of this work could incorporate different distributional assumptions in the risk assessment model to explicitly account for this over-dispersion.*

Estimated risk levels are very uncertain for whale-sharks due to a general paucity of data on fundamental life-history parameters such as growth, fecundity and breeding intervals (Clarke et al. 2015). We attempted to reflect this uncertainty in our inputs for calculating both r_{max} and N , in a manner that is consistent with a precautionary approach, placing more weight on areas of parameter space that might lead to lower population resilience (lower r_{max}), and conservative estimates of population size.

Another major unknown, the post-release mortality rate of whale-sharks interacting with purse-seine fisheries, was elicited using a Delphi survey. There was some disagreement among experts, even after the second round of questions. Most respondents estimated low post-release mortality (i.e., < 25%), but there were answers that suggested much higher post release mortality. We also note that the two second round answers that were invalid also gave high estimates. Regardless of the answer, many respondents noted that the release method probably has the largest impact on post-release mortality. Post release mortality is therefore most sensitive to the proportion of the fleet that practice safe release methods. In terms of the elicited risk, this parameter has a large influence, leading to order of magnitude differences in risk, from low risk at all reference points, to potentially impactful levels, especially once one considers other potential sources of uncertainty and vulnerability.

Although our framework aims to account for sources of uncertainty explicitly by propagating all sources of uncertainty through to risk estimates, there are aspects of risk that we cannot account for explicitly at this stage. For instance, there is some evidence for population structure in space and differential habitat use (Pierce & Norman 2016). In some areas, such as the relatively cool but rich waters off the Galapagos Islands, a single sex dominates aggregations (Acuña-Marrero et al. 2014, Norman & Stevens 2007). There is also some evidence for differential habitat use among adults and juveniles (Ketchum et al. 2013, Ramírez-Macías et al. 2017). If risk from fishery interaction, either through higher catchability or higher mortality, is disproportionately associated with a particular demographically isolated sub-population, sex or ontogenetic stage, then the true risk for the larger population may be under-estimated by a model that considers that the whole population is equally vulnerable.

Lastly, it is important to note that although the risk estimated here does not appear to be at a potential threshold (i.e., a risk ratio of ≥ 1), this risk is associated with Pacific purse-seine fisheries only - any additional mortality from India ocean purse seine fisheries as well as any other interactions and directed fisheries will serve to increase the risk. Risk from Pacific fisheries alone is at a level where minimising unnecessary mortality due to inappropriate handling will serve to ensure that the risk from Pacific purse-seine fisheries is minimised.

We note that there were several data limitations that could be overcome by directed studies and/or extending the current interaction dataset beyond the WCPO in future studies. First, environmental conditions in the WCPO are relatively homogeneous compared to those found near upwelling zones in the EPO. Having similar temporally- and spatially resolved interaction data from the EPO could therefore significantly increase our ability to predict whale shark habitat. Similarly, extending the interaction and effort dataset to the Indian Ocean would mean that we could address risk from all known purse seine activity to the Indo-Pacific whale shark population. The greatest source of uncertainty in our risk estimates comes from the expert-elicited post-release mortality factor. Although post-release mortality studies have

been conducted in the Atlantic Ocean, these have been limited to a few sharks, and have used best practice release methods. Implementing larger tagging studies to estimate post-release mortality in whale sharks across the range of release practicals currently practiced in Pacific fisheries could provide a more nuanced picture of post-release mortality, and could substantially reduce our uncertainty about risk to the population.

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APPENDIX A: Data appendix

A.1 Total and observed effort

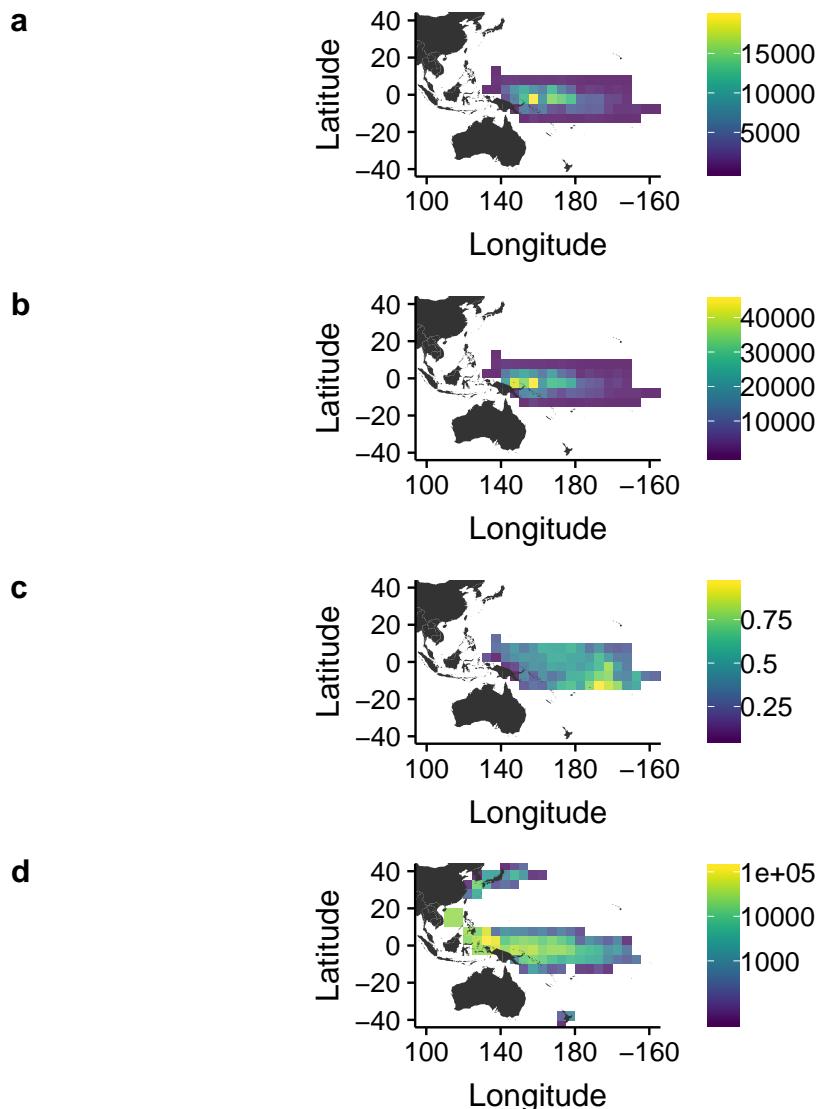


Figure A-1: Observed effort (a; number of sets), b) total effort (sets) and c) observer coverage of the set - level effort and d) Catch Effort Information System (CES) reported effort (in days) in the tropical purse seine fishery over all years from 2006–2016.

A.2 Yearly interaction totals and rates

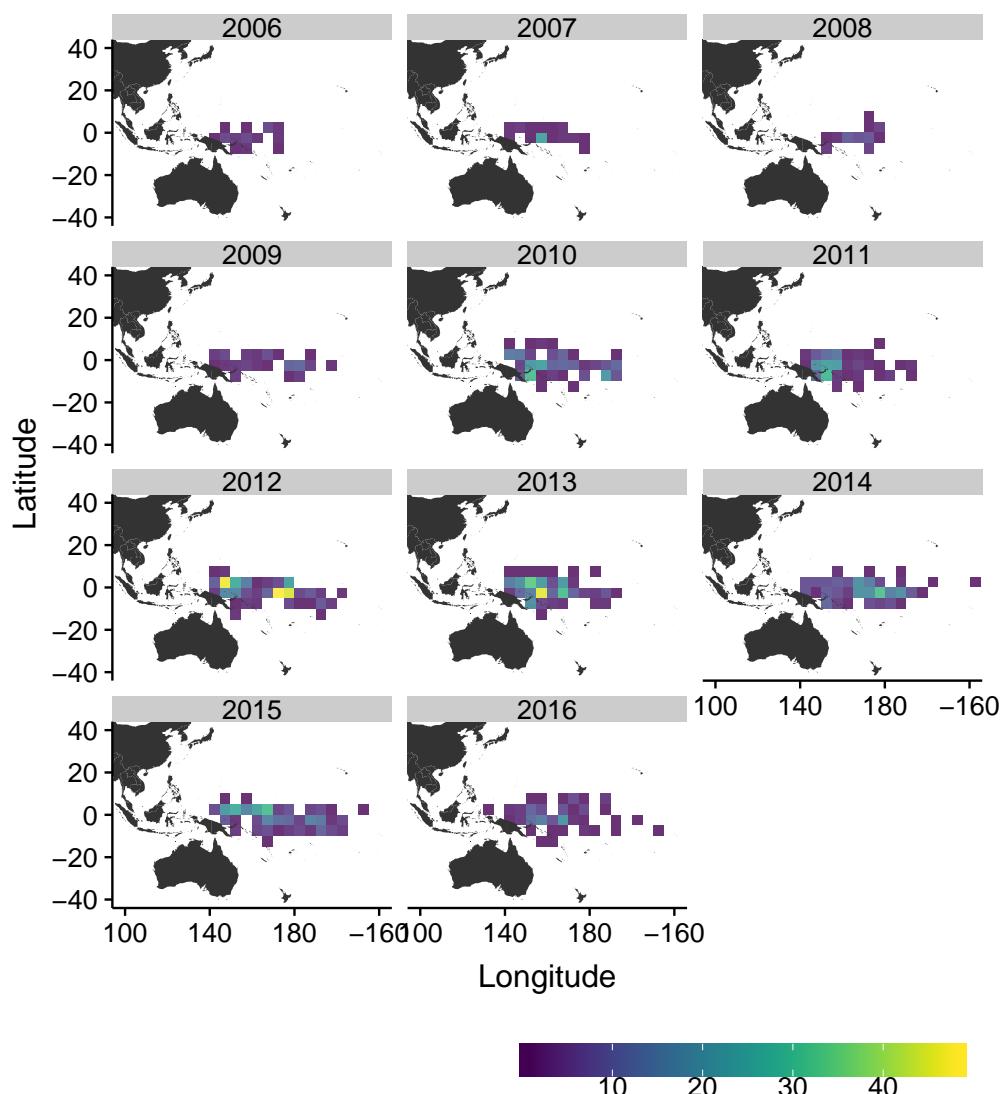


Figure A-2: Total observer-recorded whale shark interactions by year on a five-degree grid.

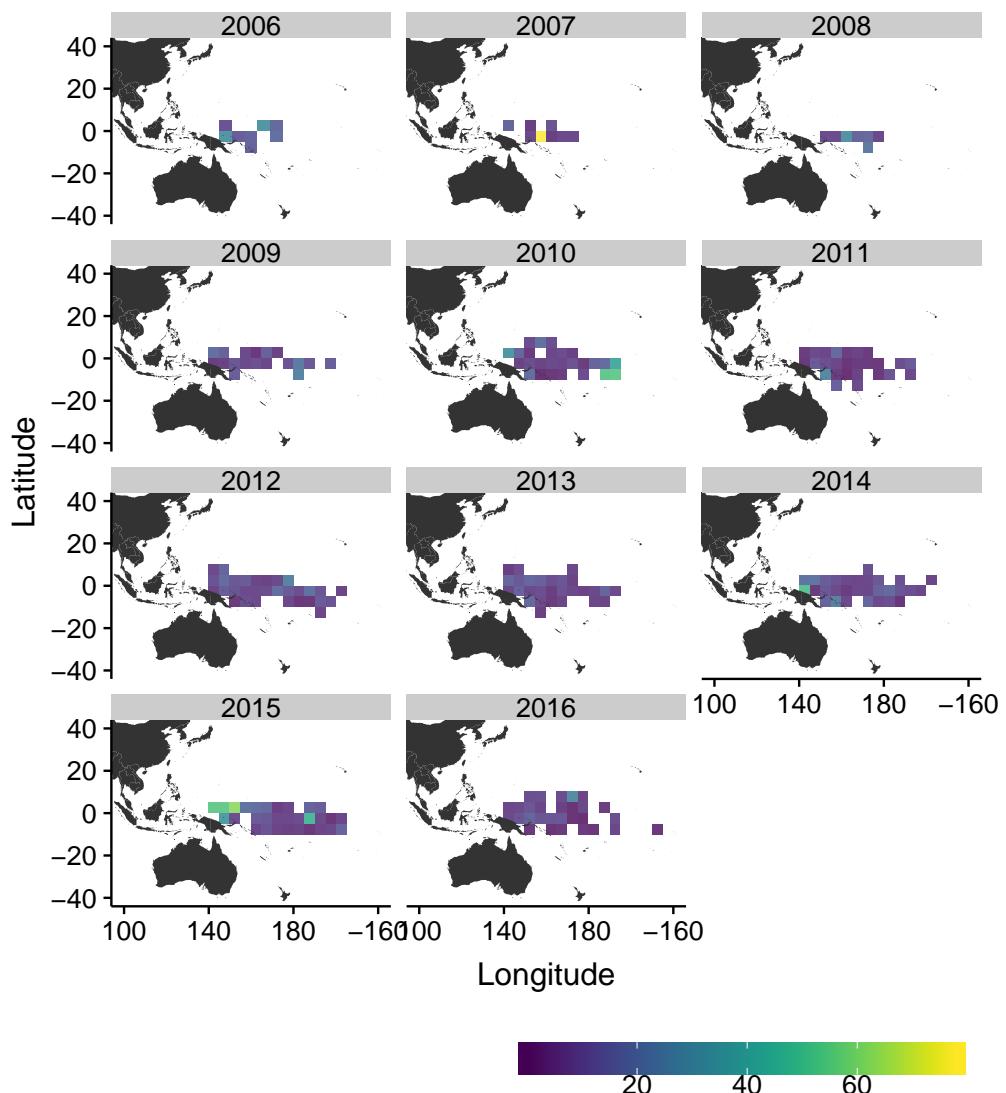


Figure A-3: Observer-recorded whale shark interaction rates (per 1000 sets) by year on a five-degree grid

APPENDIX B: Index standardisation appendix

B.1 GAMM figures

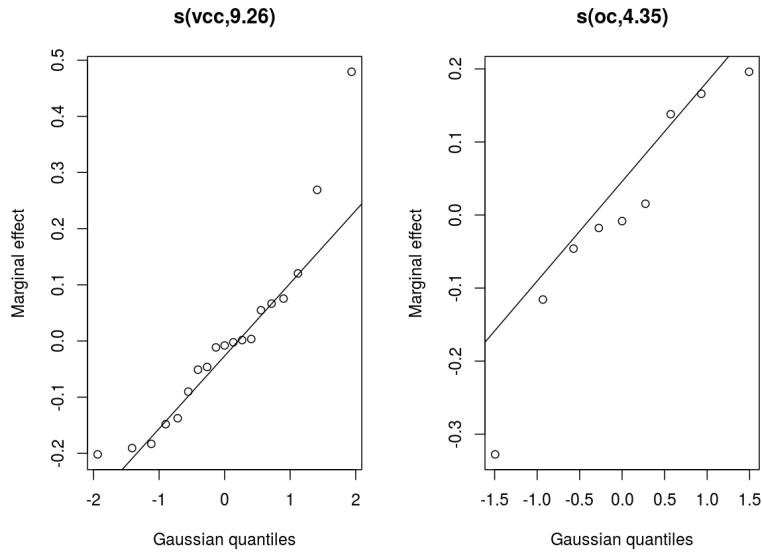


Figure B-1: Estimate effect of vessel flag and observer programme on interaction rates in WCPO tropical purse seine fisheries, using all set types except whale and whale-shark associated sets. Note, relative effect size can be inferred by comparing against the y-axes in Figure 10.

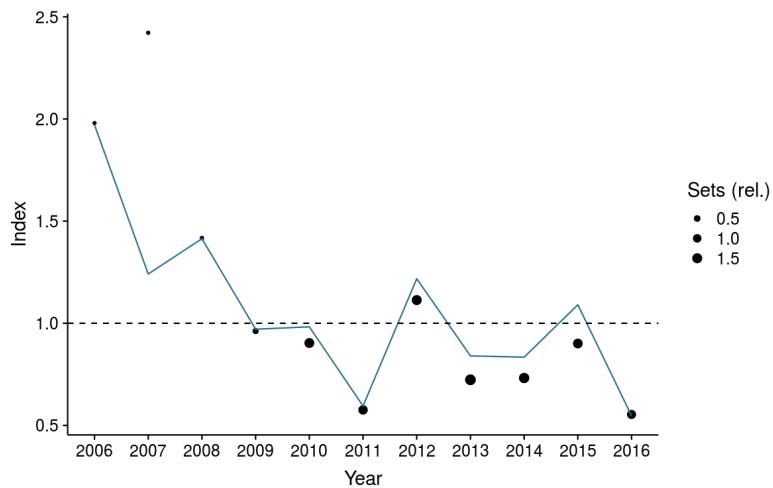


Figure B-2: Standardised interaction index from the GAMM model, using all set types except whale and whale-shark associated sets.

B.2 Bayesian CAR GLMM figures

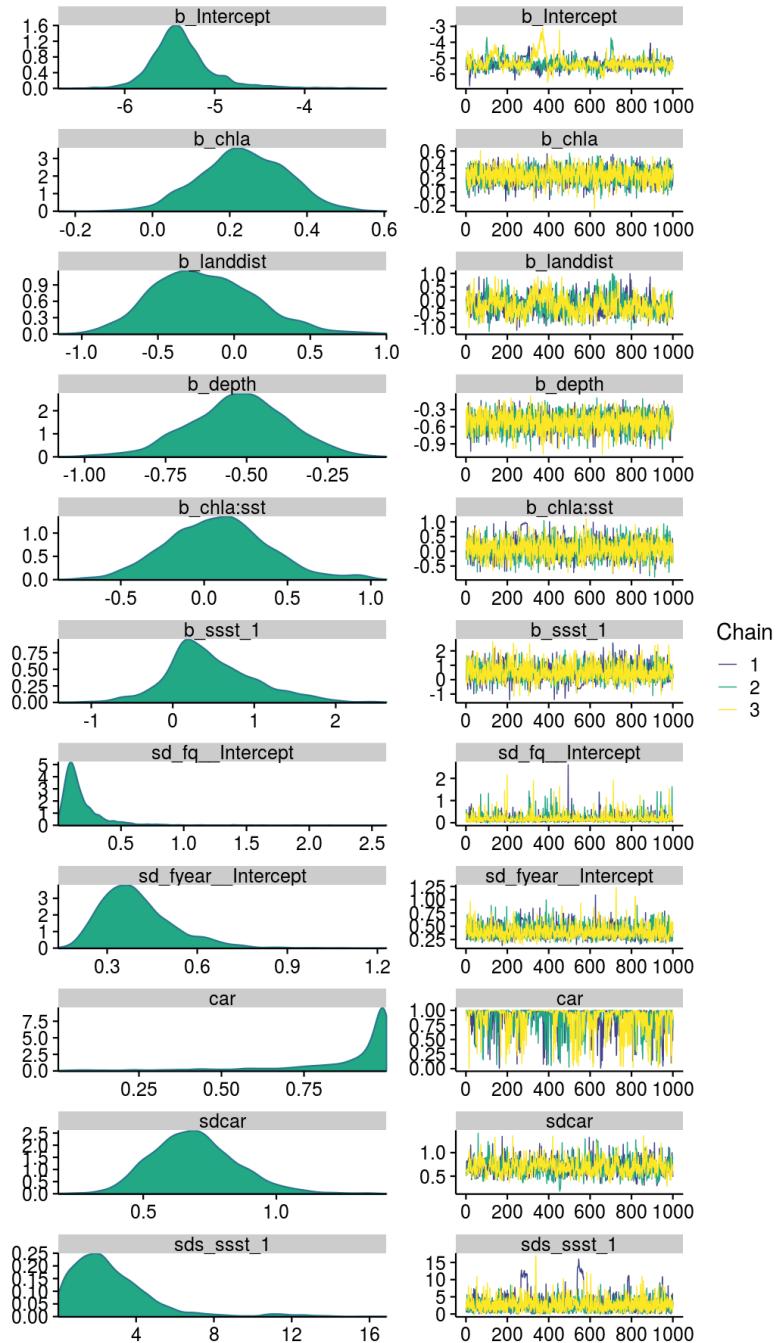


Figure B-3: Estimated model parameters and MCMC chains for the index standardisation model with all observed sets except for whale and whale-shark associated sets.

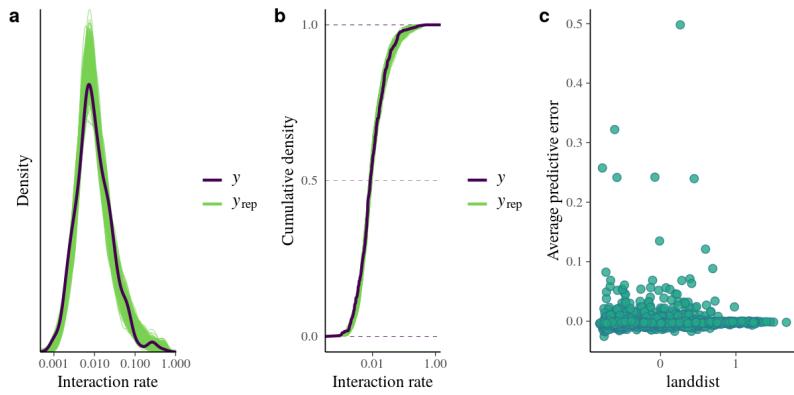


Figure B-4: Model fit for the index standardisation model with all observed sets except for whale and whale-shark associated sets (a & b) as judged from MCMC draws from the posterior predictive distribution; and c) model residuals with respect to (standardised) distance from land.

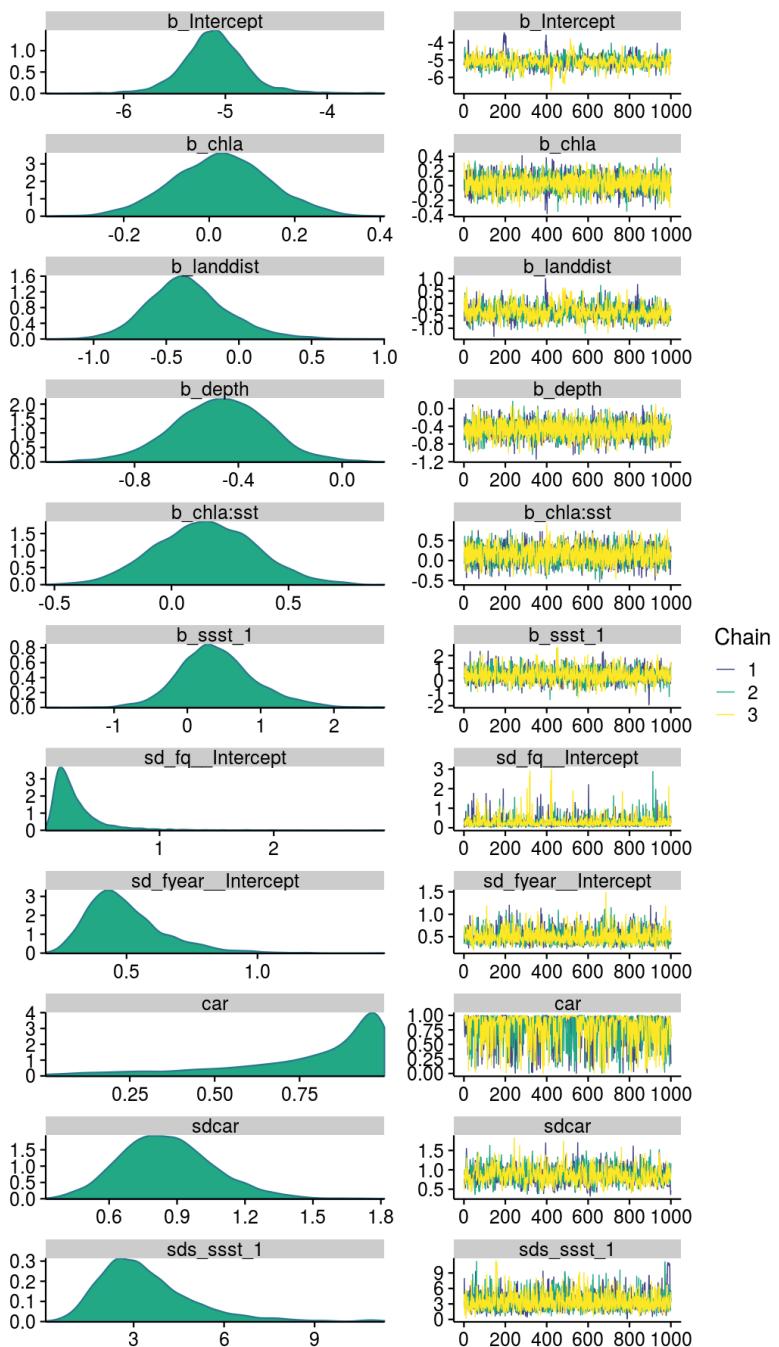


Figure B-5: Estimated model parameters and MCMC chains for the index standardisation model for free school sets only.

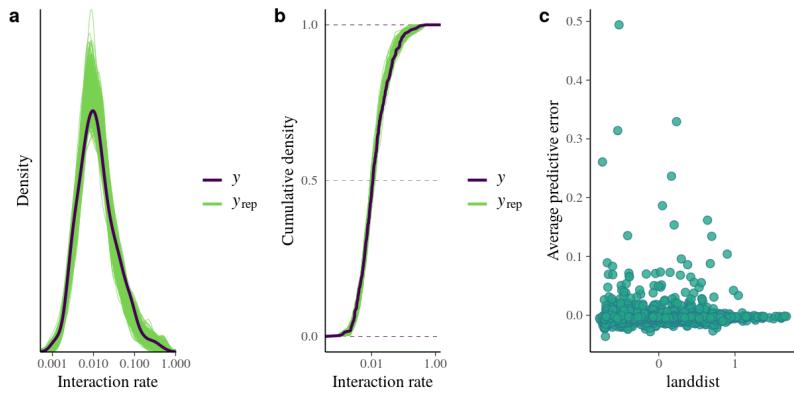


Figure B-6: Model fit for the index standardisation model for free school sets only (a & b) as judged from MCMC draws from the posterior predictive distribution; and c) model residuals with respect to (standardised) distance from land.

APPENDIX C: Risk assessment appendix

C.1 Delphi questions

1. How confident do you feel about answering questions relating to whale shark post-release mortality in Pacific purse-seine fisheries?

Please note that this survey is sent to a range of potential respondents. If you do not have any specific domain knowledge about Pacific purse seine fisheries and their interactions with whale sharks from experience or data, please answer zero here - you can still finish the survey if you like, or simply close this browser or tab if you feel you are not in a position to answer questions about whale shark post-release mortality in Pacific purse-seine fisheries.

2. Have you ever witnessed a whale shark being released from a purse seine vessel (in person, video footage or photos)?
3. Have you been on board a purse seiner where other large bycatch was released?
4. Do you know of, or recommend, any special guidelines for whale shark release from purse seine fishing gear?
5. If you answered yes for the previous question, could you briefly elaborate on special release guidelines?

6. Think of all factors that might lead to the survival of whale sharks released from purse seines. With these factors in mind, what would be your estimate of the minimum chance (in percent [%]) that a whale shark who is released alive from the net would subsequently die of its injuries?

Please pick a number between 0-100%, and type this number (without typing the percent [%] sign) on the line below. Note this ONLY includes whale sharks that are released alive, NOT whale sharks that are landed dead or were released dead.

7. Think of all factors that might lead to mortality of whale sharks released from purse seines. With these factors in mind, what is the maximum chance (in percent [%]) that any given whale shark who is released alive from the net would subsequently die of its injuries?
8. What would be your best estimate of the chance (in percent [%]) that a whale shark who is released alive from the net would subsequently die of its injuries?
9. Please let us know if you have any additional comments on whale-shark post-release mortality.
10. I am a/am affiliated with:
 - Observer/Observer programme manager
 - Fisher

- NGO
- Manager
- Scientist

C.2 Delphi results

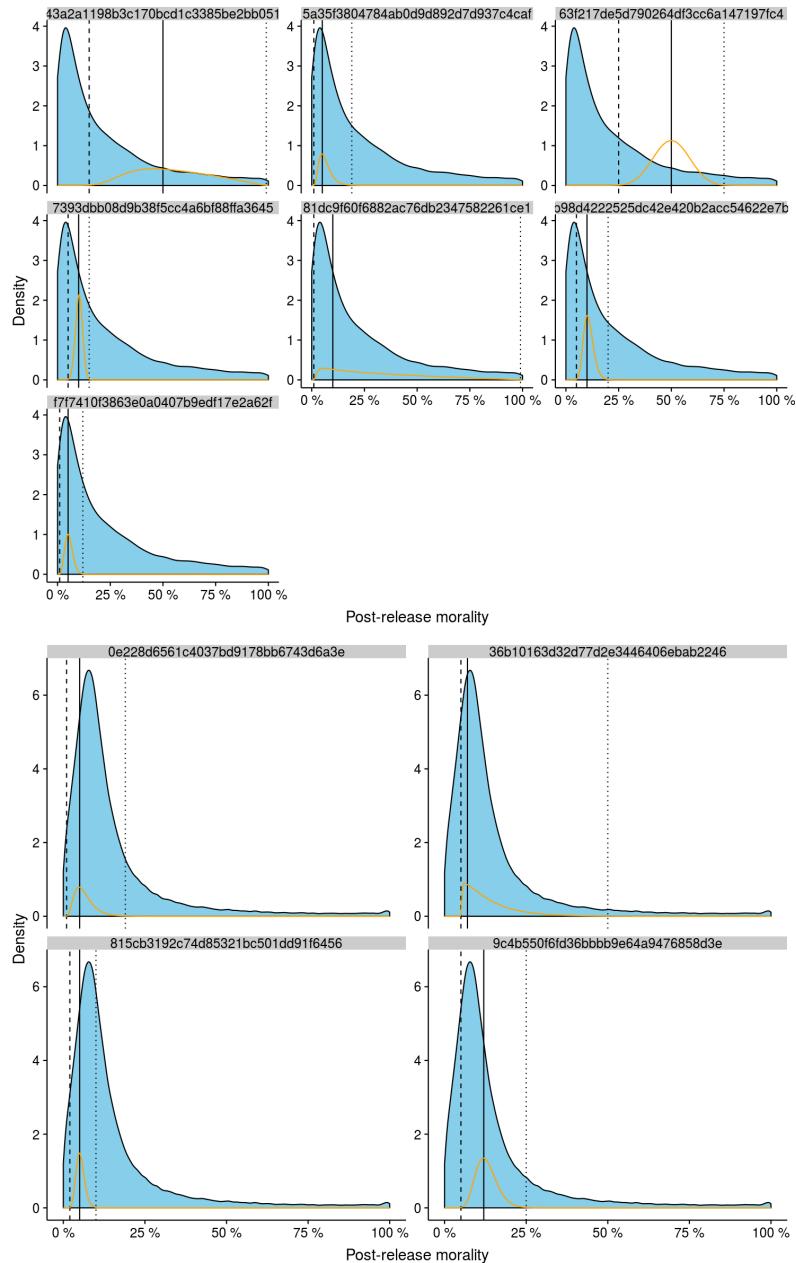


Figure C-1: Estimated post-release mortality consensus distribution (blue) based on individual responses (orange) in round 1 (top) and round 2 (bottom). Vertical lines show individual responses for the minimum (dashed-), maximum (dotted-) and most likely (solid line) post-release mortality.

C.3 Delphi results for meta-data questions

How confident do you feel about answering questions relating to whale shark post-release mortality in *Pacific purse-seine fisheries*?

9 out of 9 people answered this question

Average: 2.00



Not confident

Somewhat confident

Very confident



Have you ever witnessed a whale shark being released from a purse seine vessel (in person, video footage or photos)?

9 out of 9 people answered this question



Have you been on board a purse seiner where other large bycatch was released?

9 out of 9 people answered this question



Do you know of, or recommend, any special guidelines for whale shark release from purse seine fishing gear?

9 out of 9 people answered this question



I am a/am affiliated with:

5 out of 9 people answered this question

