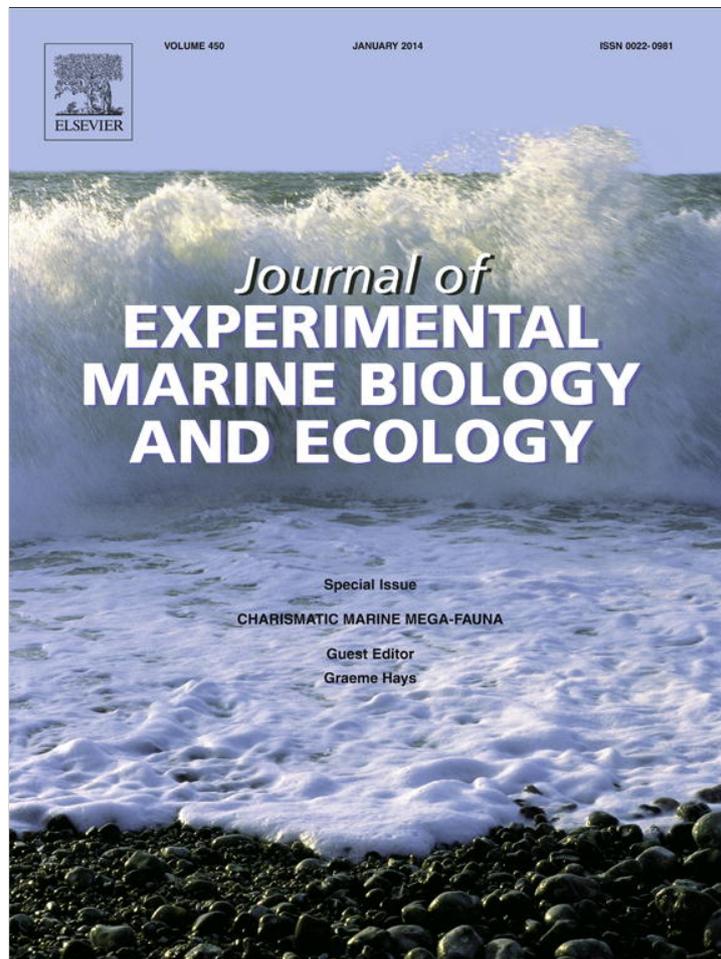


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Inter-ocean asynchrony in whale shark occurrence patterns

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ABSTRACT

The whale shark (*Rhincodon typus*, Smith, 1828) is a migratory species (classed as *Vulnerable* by the IUCN) with genetic and circumstantial evidence for inter-ocean connectivity. Given this migratory behaviour, population-wide occurrence trends can only be contextualized by examining the synchrony in occurrence patterns among locations where they occur. We present a two-step modelling approach of whale shark spatial and temporal probability of occurrence in the Atlantic and Pacific Oceans using generalized linear mixed-effects models. To test the hypothesis that the probability of whale shark occurrence is asynchronous across oceans, as expected if inter-ocean migration occurs, we used long-term datasets of whale shark sightings derived from tuna purse-seine logbooks covering most of the central-east Atlantic (1980–2010) and western Pacific (2000–2010). We predicted seasonal habitat suitability to produce maps in each area, and then evaluated the relative effect of time (*year*) on the probability of occurrence to test whether it changed over the study period. We also applied fast Fourier transforms to determine if any periodicity was apparent in whale shark occurrences in each ocean. After partialling out the effects of seasonal patterns in spatial distribution and sampling effort, we found no evidence for a temporal trend in whale shark occurrence in the Atlantic, but there was a weak trend of increasing probability of occurrence in the Pacific. The highest-ranked model for the latter included a spatial predictor of occurrence along with fishing effort, a linear term for time, and a random temporal effect (*year*), explaining 15% of deviance in whale shark probability of occurrence. Fast Fourier transforms revealed a prominent 15.5-year cycle in the Atlantic. The increase in the probability of occurrence in the Pacific is concurrent with a decrease previously detected in the Indian Ocean. Cyclic patterns driven by migratory behaviour would better explain temporal trends in whale shark occurrence at the oceanic scale. However, despite cycles partially explaining observations of fewer sharks in some years, overall reported sighting rate has been decreasing. As a result, we suggest that the current IUCN status of the species should be re-assessed, but more data are needed to examine the flow of individuals across oceans and to identify possible reasons for asynchronous occurrences.

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1. Introduction

Most of the readily measurable negative impacts of humans in marine ecosystems result from direct exploitation (Pauly et al., 1998; Worm et al., 2006) or related by-catch (Agardy, 2000; Hall et al., 2000). Climate change is also beginning to affect marine ecosystems (e.g., Sumaila et al., 2011) via temperature-driven range shifts and alteration of ocean chemistry (Dulvy et al., 2008; Parmesan, 2006; Perry et al., 2005; Wernberg et al., 2011). Reported declines in marine species increasingly challenge the idea that extinctions in the oceans are unlikely (Hendriks et al., 2006). Based mostly on a reduction in observed landings from targeted fisheries (Fowler et al., 2005), whale

sharks are currently listed as *Vulnerable* (i.e., facing a high risk of extinction in the wild) by the IUCN (www.iucnredlist.org).

Whale sharks (*Rhincodon typus*, Smith 1828) travel thousands of kilometres pelagically between near-shore aggregation sites (e.g., Rowat and Gore, 2007), and their sub-populations are assumed to be connected across the world's oceans (Castro et al., 2007; Sequeira et al., in press). This circumglobal migration raises concerns about the adequacy of current management measures (Rowat, 2007). These generally focus on confined areas of aggregation where tourism is locally important (Pierce et al., 2010; Quiros, 2007), and might therefore largely neglect negative impacts occurring elsewhere (Bradshaw, 2007). Whale shark-based eco-tourism has been developed based on the anticipation that individuals from local sub-populations return to the same location each year at approximately the same time (Taylor, 1996); however, evidence for declining relative abundance has been reported at some of these locations (Bradshaw et al., 2008; Theberge and Dearden, 2006). There is also quantitative support for a slight reduction in the

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probability of occurrence in the Indian Ocean during the last decade (Sequeira et al., 2013a).

Whale sharks are potentially affected by a range of human activities, including exploitation through direct commercial fisheries (the last fishing ban occurred in Taiwan only after 2007) (COA, 2007; but see Li et al., 2012), poaching (Riley et al., 2009), by-catch (Romanov, 2002), and habitat disturbance via tourism (Heyman et al., 2010) and shipping (Speed et al., 2008). With temperature being an important predictor of whale shark distribution (Sequeira et al., 2012) and local relative abundance (Sleeman et al., 2010a), anthropogenic climate disruption will possibly affect this species occurrence patterns (Sequeira et al., in press).

Changes in the abundance of whale sharks might be confounded by inter-decadal cycles in relative abundance (Sequeira et al., 2013a) possibly associated with broad-scale migration patterns. Because this species is highly mobile and populations are connected across oceans at least at the generational scale (Castro et al., 2007; Schmidt et al., 2009), temporal trends still can only be inferred by a combination of site-specific time series of relative abundance (e.g., sightings per unit effort) with inter-site comparisons of occurrence synchrony within ocean basins. Although this comparison is crucial to the understanding of temporal trends in whale shark occurrence, no study has so far quantified temporal sighting probability among known aggregation locations within the same ocean (as suggested by Sequeira et al., 2013a, in press).

Temporal trends in species occurrence are seldom dissociated from spatial processes. Although statistical models have been mostly used to assess and predict the spatial distribution of species (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Hirzel et al., 2002; Phillips et al., 2009) based on the ecological niche (Hutchinson, 1957), they can also be used to assess temporal trends (Gotelli et al., 2010). For example, species distribution models have indeed been used to estimate habitat suitability for highly migratory marine species (Elith and Leathwick, 2009; Oviedo and Solís, 2008; Praca and Gannier, 2007), as well as estimate their temporal trends (Sequeira et al., 2013a).

Access to fisheries' logbook data compiled by tuna purse-seiners from the Atlantic and Pacific Oceans gave us the opportunity to estimate broad-scale trends in whale shark occurrence to complement (and compare) the assessment made previously for the Indian Ocean (Sequeira et al., 2013a). Here we: (1) predict whale shark habitat suitability within the areas covered by the tuna fisheries in the Atlantic and Pacific, (2) test the hypothesis of temporal asynchrony in the probability of occurrence, and (3) assess possible cyclic patterns in occurrence. Our main objective is to assess the temporal variability in occurrence probability across most of the species' known geographical range by comparing their probabilities of occurrence in different oceans. We conclude with a discussion of our results with respect to the species' global threat status.

2. Material and methods

With the main objective to assess temporal trends in whale shark occurrence in the Atlantic and Pacific Oceans, and compare them with the results obtained previously for the Indian Ocean (Sequeira et al., 2012, 2013a), the models we develop here follow a similar approach. First, we developed habitat suitability models and used the resulting predictions as part of the input data in our temporal models of occurrence. Below we describe the biological and environmental data, the modelling methods including how we accounted for pitfalls in the opportunistically collected dataset (presence-only data and sampling bias), and the application of fast Fourier transforms to test for cyclic patterns in the probability of occurrence.

2.1. Whale shark and environmental data

We used whale shark occurrence data from the Atlantic and Pacific Oceans recorded in the logbooks of tuna purse-seiners. Because tuna and whale shark occurrence is often associated with these fisheries

(possibly because they forage on similar prey), nets deployed by tuna fishers frequently encircle (and subsequently release) whale sharks as well (Matsunaga et al., 2003). Hereafter, we use the term 'sightings' to describe logbook records of these whale shark-associated net sets. The datasets made available by the *Institut de Recherche pour le Développement* (France) and the Secretariat of the Pacific Community comprise most of the central area of the Atlantic (21°N–15°S and 34°W–14°E) and central western Pacific (15°N–15°S and 130°E–150°W) (Fig. 1). They include the date of sightings (month and year), longitude and latitude (0.01° precision), and information on sampling effort (number of days spent fishing per month) in each 1° grid cell in the Atlantic, and 5° grid cell in the Pacific (Fig. 1). No information on individual vessel, vessel nationality or trip units was available. The data spanned 1980 to 2010 in the Atlantic (total of 18,277 records provided by the French purse-seiners), and 2000 to 2010 in the western Pacific (total of 2272 records provided by only part of the fleets registered with the Secretariat of the Pacific Community, but these are representative of the fisheries in the area). To compare the possible synchrony of occurrence patterns within the Atlantic and Pacific with previous results obtained for the Indian Ocean (Sequeira et al., 2013a), and due to the generally low number of sightings in other seasons (Fig. S1), we used data for the months of April to June only. A total of 1018 and 167 sightings were reported in the Atlantic and Pacific oceans, respectively, during the months considered.

We assembled environmental data on daytime sea surface temperature (SST in °C) and chlorophyll *a* (Chl *a* in mg m⁻³) at a 9-km resolution derived from the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder version 5.0 and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellites, respectively. We used *ArcToolBox* functions (ArcGIS 9.3.1™ automated with *Python* scripts) to calculate mean and standard deviation of SST and mean Chl *a* per grid cell for all weekly composites between April and June for the time period of each ocean dataset. We also derived depth (m), slope (°) and distance to shore (km; using the *Near* tool in ArcGIS 9.3.1™ on an equidistant cylindrical coordinate system) from the General Bathymetry Chart of the Oceans (GEBCO, 2003). We then collated the full dataset at a common resolution of 9 km including six predictors: mean depth, slope, distance to shore, mean SST, SST standard deviation and mean Chl *a*. We did not include standard deviation of Chl *a* because in the models we previously developed for the Indian Ocean, this variable was excluded to avoid including highly correlated variables (Sequeira et al., 2012).

2.2. Models

We developed the modelling approach in two steps to (1) compare the ability of different combinations of the environmental variables to predict whale shark habitat suitability, and (2) assess evidence for a temporal trend in whale shark occurrence in each ocean using the spatial predictions of habitat suitability from step one. In both steps, we applied generalized linear mixed-effects models (GLMM) with a binomial error distribution and a logit link function to our presence-only data, and generated pseudo-absences for binomial estimation.

The process of generating pseudo-absences differed in each modelling step. In the first (spatial) step, we randomly generated 10 pseudo-absences per presence based on a spatially random distribution within the area covered by the fisheries (excluding all presence cells). In the second (spatio-temporal) step, we generated 100 pseudo-absences per presence based on both temporally and spatially random distributions, that is, randomly choosing a date within the temporal coverage of each dataset and then randomly assigning it to a grid cell within the area covered by the fisheries (for each ocean). In both steps, we generated the spatially random distributions with the *srsWOR* function (simple random sampling without replacement) from the {sampling} package in the *R* programming language (R Development Core Team, 2012). For the temporally random pseudo-absence distribution, we randomly selected a date within the temporal coverage of each dataset (April to

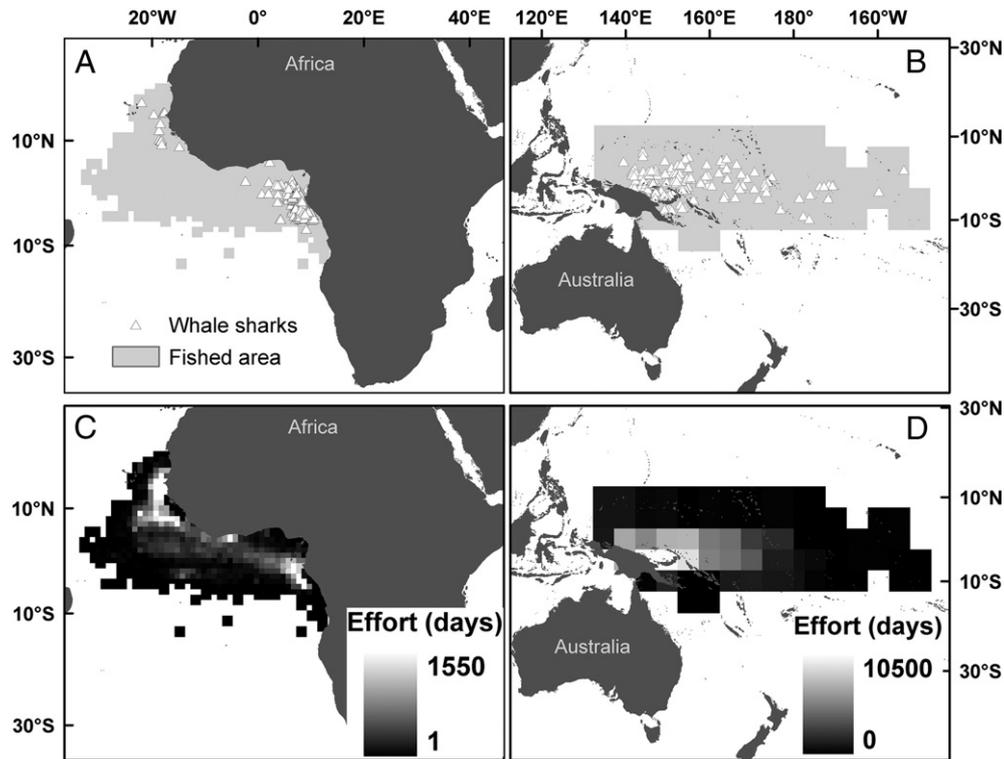


Fig. 1. Whale shark (*Rhincodon typus* Smith 1828) datasets recorded by tuna purse-seiners including location of net-sets in the Atlantic (1980–2010) (left) and the Pacific (2000–2010) (right). Top panel: area covered by the fisheries (grey), and location of whale shark sightings (blue dots). A total of 1030 sightings were recorded in the Atlantic (A), and 167 in the Pacific Ocean (between April and June) (B). Bottom panel: number of fishing days (effort) with a resolution of 1° for the Atlantic (C) and 5° for the Pacific Ocean (D).

June only) by using the *srswr* function (simple random sampling with replacement) from the same package in *R*. To assess the influence of the date and location associated with the selected pseudo-absences, we generated each set of pseudo-absences 100 times prior to incorporating them into the spatial models, and only 10 times for the temporal models (to keep computing time manageable).

In the first spatial step, we included as predictors the quadratic terms of SST and depth to account for a possibly higher suitability within a range of these variables (non-linear response). Here we used the *poly* function (with degree 2) from the *{stats}* package in *R*. We also included a code for each 1° grid cell as a spatial random effect to reduce spatial autocorrelation (Sequeira et al., 2013a). To account for the sampling bias associated with effort (i.e., related to the expectation of more whale shark sightings where fishing effort was higher), we included effort as an offset in all models.

In the second spatio-temporal step, to determine the probability of whale shark occurrence we used as predictors the spatial habitat suitability predicted in step 1, a zero-centred *effort* term (inter-annual variation around the mean not accounted for within the spatial predictor) (Sequeira et al., 2013a) and time, both as a fixed (*time*) and random effects (*year*) to ensure that the random structure contained only information that could not have been modelled with fixed effects (following Zuur et al., 2009). To account for a possible parabolic-like relationship between the probability of occurrence and time, we also added the quadratic term for *time* using the second-order *poly* function. Estimated probabilities of occurrence are based on the prevalence assumed by the presence/pseudo-absence data used (i.e., 0.01), assuming an even probability of detection across the dataset.

A generic way to write the logit-link GLMM is:

$$\text{logit}(\text{Presence}) = \alpha + \beta X_i + \gamma_i Z_i + \epsilon_i + \log(\text{fishing effort})$$

where *Presence* is the expected mean probability of sighting occurrence, *X* and *Z* represent the fixed and random effects (and their coefficients β

and γ), respectively (and as specified above), α is the intercept, and *i* corresponds to the number of observations among grid cells in the spatial models, and years in the temporal models.

We compared the models' relative strength of evidence by weighting each model's Akaike's information criterion corrected for small sample sizes (*wAIC_c*) (Burnham and Anderson, 2004), and calculating the percentage of deviance explained (%*De*) for each model as an index of goodness-of-fit. We calculated the 10-fold cross-validation error for the model with highest *wAIC_c* support and assessed the model's predictive power using Cohen's κ statistic (Cohen, 1960). To build the habitat suitability maps (as a result of the spatial modelling step), we used the multi-model weighted average (based on its weight of evidence; *wAIC_c*) to define the habitat suitability predictor in the spatio-temporal models. We also calculated the weight of evidence for each predictor used in the spatio-temporal models by summing the *wAIC_c* over all models in which each predictor appeared. This identifies the predictor with the highest predictive accuracy with respect to the response.

2.3. Fast Fourier transforms

Fast Fourier transforms decompose signals from time series into the sum of sinusoidal curves with different frequencies (Platt and Denman, 1975). To analyse possible cyclic variation in whale shark occurrences, we applied the fast Fourier transform function (FFT; following Moler, 2004) to the sighting time series after correcting for effort bias (i.e., by standardizing sightings per unit effort [SPUE] with an effort unit = 1 fishing day). We used MatLab version 7.12.0.635 (R2011a) (The Mathworks Inc., Natick, MA), and interpreted the results of the FFT by plotting the periodogram for the power of the signal (square of the absolute fast Fourier transform) against the frequency (inverse of time). A cycle is then defined by identifying the frequency with the strongest signal (power).

To examine cyclic trends apart from the known annual cycles (i.e., number of sightings is usually higher in particular seasons each year), we started by using data only for the season under consideration (Apr–Jun), and defining frequency as *year*. As an alternative test to include all sighting data available (all months), and therefore increase the length of the vector used in the function, we also ran FFT for the sightings per monthly effort (defining frequency as *month*). In this test, we used a running average including the six months before and after each month to eliminate the known annual periodicity. The strength of each resulting cycle (periodicity) is given by the power of the corresponding frequency in the periodogram.

3. Results

3.1. Spatial patterns

In the Atlantic Ocean, whale shark sightings occurred mostly off Gabon in equatorial eastern Africa, and at around 10°N between Senegal and Sierra Leone – these areas comprise most of the fishing effort (Fig. 1). Likewise in the western Pacific, more sightings were recorded within the area of highest fishing effort, even if sightings were spread out across the sampled area (Fig. 1).

Our spatial models (step 1) revealed higher habitat suitability mostly corresponding to the areas where more whale sharks were spotted in the Atlantic, and to the northeast of Indonesia/Papua New Guinea in the western Pacific also covering the area with more sightings (Figs. 1 and 2). The model with highest statistical support was the same for both oceans in step 1 ($wAIC_c = 0.83$ and 0.33 in the Atlantic and Pacific, respectively), and included all predictors except chlorophyll *a*. This model explained 50% of deviance in the Atlantic and only ~6% in the Pacific (Table 1). Results for the Pacific highlight the possibility that other important factors, not accounted for in our models, might affect whale shark occurrence in the area. During the months of April to June, habitat was more suitable in the Pacific (habitat suitability up to 0.7) than in the Atlantic (0.2) (Fig. 2); however, κ was higher in the Atlantic ($\kappa \sim 0.5$ compared to ~ 0.3 in the Pacific) (Table 1). According to Cohen (1960), the κ we obtained reflects a good performance for the models applied to the Atlantic and a poor performance for the models applied to the Pacific (possibly due to the low number of sightings in the latter area). The mean prediction error calculated through the 10-fold cross validation (CV_e) was low in both oceans (<0.1).

3.2. Temporal trends

The total number of whale sharks sighted annually in the Atlantic varied from 0 to 137 (Fig. 3A) between April and June. Sightings peaked (~120 individuals) in 1995, even though total fishing effort (sum of

Table 1

Summary of spatial generalized linear models (step 1) relating the probability of whale shark (*Rhincodon typus* Smith 1828) occurrence to ocean properties. Ocean properties – slope, depth, depth² and distance to shore (shore) – are referred to together as ‘physical variables’ ($phys_{var}$). Mean sea surface temperature (mSST) and its quadratic term (SST²), and sea surface temperature standard deviation are referred to together as ‘SST variables’ (SST_{var}). Mean chlorophyll *a* (mChl *a*) is the values measured in the Atlantic and west Pacific Oceans during April to June. Also shown are biased-corrected model evidence based on weights of Akaike’s information criterion corrected for small sample sizes ($wAIC_c$; only values ≥ 0.001 shown), percentage of deviance explained (%De), and the Cohen’s Kappa statistics (κ ; only values ≥ 0.1 shown) for each model performing better than the null model (including only an offset for effort and the spatial random effect) in each ocean.

Model	Atlantic Ocean			Pacific Ocean		
	$wAIC_c$	%De	κ	$wAIC_c$	%De	κ
<i>phys_{var} + SST_{var}</i>	0.83	50.4	0.7 ± 0.05	0.33	6.4	0.3 ± 0.08
<i>phys_{var} + mSST + SST²</i>	0.17	50.3	0.6 ± 0.06	0.33	6.1	0.3 ± 0.08
<i>mSST + SST² + mChl a</i>	–	–	–	0.28	5.4	0.3 ± 0.08
<i>phys_{var} + mChl a</i>	–	49.5	0.2 ± 0.02	0.03	5.4	0.3 ± 0.08
<i>mChl a</i>	–	47.0	–	0.01	4.3	0.2 ± 0.08
<i>mSST + SST²</i>	–	47.4	0.1 ± 0.01	0.004	4.3	0.3 ± 0.07
<i>phys_{var}</i>	–	48.3	0.4 ± 0.05	0.004	4.7	0.3 ± 0.08
<i>SST_{var}</i>	–	47.1	0.1 ± 0.01	0.003	4.4	0.3 ± 0.08
Shore	–	–	–	0.001	3.8	0.2 ± 0.07
Depth	–	–	–	0.001	3.6	0.2 ± 0.08
Depth ²	–	49.5	–	–	–	–
Slope	–	47.3	–	–	–	–

Bold italics represent the best ranked model for both oceans.

fishing days spent fishing in all 1-° grid cells) remained relatively constant between 1985 and 2000 at about 6000 fishing days ($5.8 \pm 2.6 \times 10^3$; Fig. 3C). During this peak, the number of occurrences was similar to the one recorded in the early 1980s (137 sightings) when effort was close to 10,000 days (Fig. 3). Between 2000 and 2010, effort dropped to ~2000 days in the Atlantic. In contrast, fishing effort increased steadily in the Pacific from 2000 (Fig. 3C). The number of sightings in the Pacific also increased with time, from around 10 sightings per year in the early 2000s to a maximum of 35 in 2010 (Fig. 3A).

The spatio-temporal model with highest statistical support differed between oceans (Table 2). In the Atlantic, the top-ranked model ($wAIC_c = 0.633$) included as predictors the habitat suitability derived from step 1, *effort* and *year* (as a random intercept). The models including the linear and quadratic terms for time resulted in similar log-likelihood (Table 2), and explained similar percentage of deviance (51.69 and 51.70%, respectively), but received lower support from $wAIC_c$ (0.234 and 0.133, respectively). In the Pacific, the highest-ranked model ($wAIC_c = 0.472$) also included the *time* predictor, although it only explained <15% of the deviance. The partial effect of time on the probability of whale shark occurrence during the months of April to June in the western Pacific increased from 0.003 to 0.012

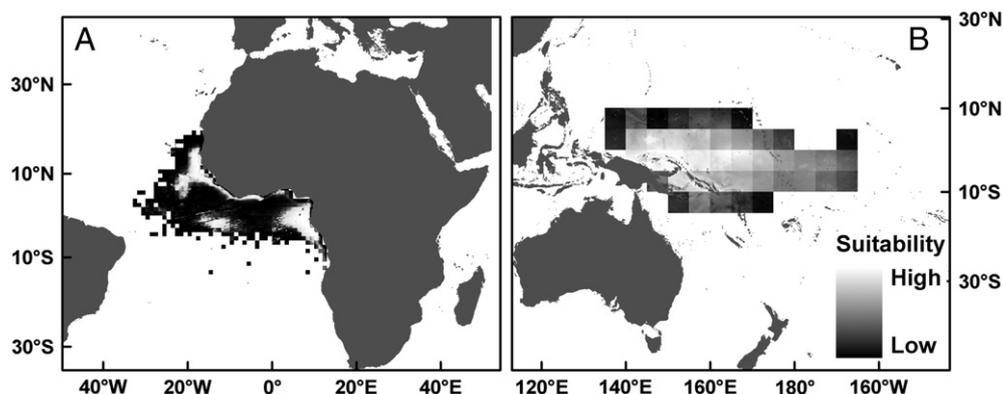


Fig. 2. Predicted habitat suitability of whale sharks (*Rhincodon typus* Smith 1828) in the Atlantic (A) and Pacific (B) Oceans during the months of April to June. Values for habitat suitability vary from 0 (low) to 0.2 and 0.7 (high) in the Atlantic and Pacific, respectively.

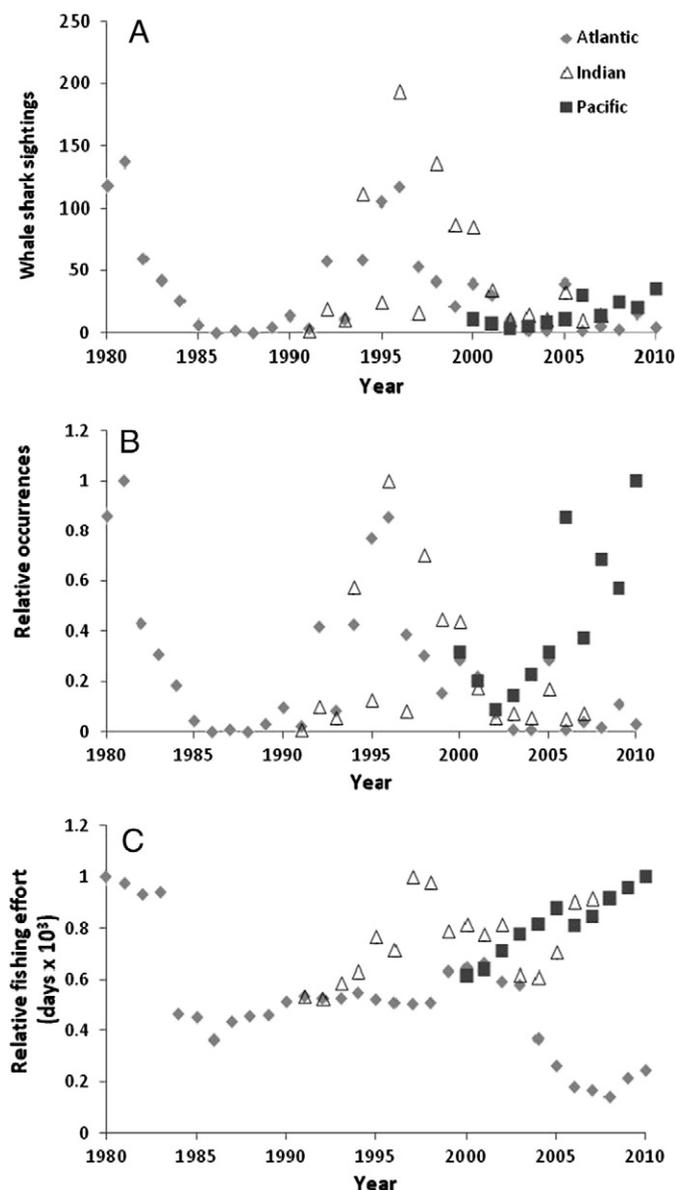


Fig. 3. Yearly variation in (A) number of whale sharks sighted, (B) relative whale shark occurrences (i.e., divided by maximum number of sightings in each ocean), and (C) days spent fishing. During the months of April to June in the Atlantic (1° resolution), Indian (5° resolution) (from Sequeira et al., 2013a; included here for comparison only), and western Pacific (5° resolution) Oceans.

between 2000 and 2010 (Fig. 4B). As for predictors, habitat suitability and effort received the highest weight (1 and 0.999, respectively) in the Atlantic Ocean, while in the Pacific we found the highest weight

for effort (weight of evidence = 1) followed by the linear term for time (time: 0.953) (Table 3).

3.3. Cyclicity

The fast Fourier transform applied to the time series of sightings per unit effort in the Atlantic (Fig. 5A, top) revealed a prominent peak at 15 years (Fig. 5A, centre), both with yearly and monthly frequencies. This periodicity also had the strongest signal when plotting the possible cycles present in the dataset (Fig. 5A, bottom); however, its relative magnitude was similar to other possible cycles present in the time series. In the Pacific, the power of any possible cycle was consistently low ($<10^{-3}$, Fig. 5B).

4. Discussion

Our predictions of habitat suitability for whale sharks and the spatially controlled temporal variation in occurrence are the first for this species both in the Atlantic and Pacific Oceans, and from the only datasets currently available at broad spatial scales. We found no evidence for linear or quadratic temporal trends in the Atlantic (although there was a suggestion of a ~15-year cycle), and there was a weak linear increase in the Pacific occurrence probability since 2000. This increase, from 0.003 to 0.012, indicates that the model predicts a four-fold increase of seeing a shark in the Pacific between 2000 and 2010 based on an average sighting (fishing) effort. The latter result contrasts with the decreasing trend detected in the Indian Ocean during the last decade (Sequeira et al., 2013a). If the temporal patterns we found reflect real patterns in whale shark occurrence, they show opposing trends in two adjoined ocean basins (Indian and Pacific). Moreover, the periodicity results for the Atlantic Ocean where the dataset available is the longest (30 years), even though weak, accord with the inter-decadal trend previously suggested for whale sharks in the Indian Ocean (Sequeira et al., 2013a).

Given these opposing trends for the Indian and Pacific Oceans, the evidence for inter-decadal occurrences (Sequeira et al., 2013a), the low genetic differentiation of world whale shark populations (Castro et al., 2007; Schmidt et al., 2009), and the implicit notion that whale sharks must travel among oceans at least occasionally (Hueter et al., 2008; Rowat and Gore, 2007), we hypothesize that occurrence might be asynchronously cyclical across oceans. Such a pattern would be consistent with the inter-ocean migratory behaviour we have previously hypothesized (Sequeira et al., in press). Similar distributional shifts, promoting asynchrony in occurrences, have also been suggested for other filter-feeding sharks (basking sharks *Cetorhinus maximus*) between the west coast of Ireland and the Norwegian Sea (Sims and Reid, 2002) – these were associated with spatial changes in foraging conditions. If whale sharks migrate between oceans (Sequeira et al., in press), as has been reported for other planktivores such as sea turtles (Luschi et al., 2006), such a cyclic pattern would explain both the interannual variation in sightings at the ocean-basin scale and the asynchrony in their occurrences in the Indian and Pacific Oceans.

Table 2

Summary of the spatio-temporal generalized linear mixed-effects models (step 2) relating probability of whale shark occurrence in the Atlantic and Pacific Oceans (from April to June) to: a spatial predictor derived from the spatial distribution models (*Hsuit*), effort (temporal variation in fishing effort), time (years), and a random effect for year. Shown for each model are the number of parameters (*k*), log-likelihood (LL), weights of Akaike's information criterion corrected for small sample sizes (*wAIC_c*) and the percentage of deviance explained (%*De*). Top-ranked models in each step are in bold and models are ordered by %*De* (according to which ranking was consistent between oceans). Models with *wAIC_c* < 0.05 are not shown.

Model	k	Atlantic Ocean			Pacific Ocean		
		LL	wAIC _c	%De	LL	wAIC _c	%De
Hsuit + effort + time + time² + (1 year)	7	−2790.90	0.133	51.70	−753.55	0.247	14.99
Hsuit + effort + time + (1 year)	6	−2791.34	0.234	51.69	−753.91	0.472	14.95
Effort + time + time ² + (1 year)	6	−	−	−	−755.67	0.081	14.75
Effort + time + (1 year)	5	−	−	−	−756.07	0.148	14.70
Hsuit + effort + (1 year)	5	−2791.34	0.633	51.69	−	−	−

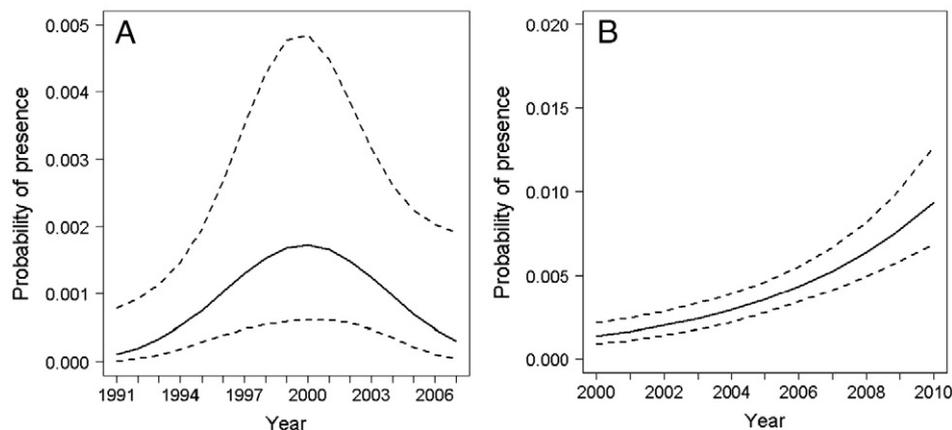


Fig. 4. Partial effect of time on the probability of whale shark presence during the months of April to June in (A) the western Indian Ocean (from Sequeira et al., 2013a; included here for comparison only), and (B) the western Pacific Ocean according to the model with highest information-theoretic support: $Presence \sim habitat\ suitability + effort + time + (1|year)$ (Table 2). Dashed lines indicate 95 % confidence intervals. Results are shown for 1991 to 2007 for the Indian Ocean and 2000 to 2010 for the Pacific Ocean.

Moreover, such large-group and multi-year migrations would still be consistent with the observed low genetic differentiation among populations (Castro et al., 2007; Schmidt et al., 2009). Migrations could be partly associated with changes in environmental conditions (Sleeman et al., 2010b; Wilson et al., 2001), or with sex/age or reproduction-related behaviour (Ramírez-Macías et al., 2007; Sequeira et al., in press). Reproduction-associated multi-year cycles have been observed in anadromous fish that shift habitat use for a few years while maturing (freshwater to saltwater), and return to hatching habitats for spawning (e.g., sockeye salmon *Oncorhynchus nerka*) (Dingle, 1996). Multi-year cycles have also been reported for fish catches in the western Indian Ocean (Jury et al., 2010), and for decadal cyclic cetacean strandings (Evans et al., 2005).

The quasi-15-year cycle suggested for the Atlantic Ocean occurrence time series corresponds to half of the dataset's temporal span. This cycle is therefore close to the highest frequency that can be detected by the fast Fourier method (Moler, 2004). Analogous studies reporting decadal cycles in marine species have used much longer datasets (Evans et al., 2005; Jury et al., 2010). Obtaining a longer time series for whale sharks in the Atlantic is required to reveal whether the 15-year cycle persists, and this should be reassessed as more data become available. The temporal extent of the western Pacific dataset spanned only a third of that of the Atlantic dataset, which potentially explains why no peaks were detected (power <math> < 10^{-3}</math>; Fig. 5).

The results from the spatial models (step 1) agreed well with the data in the Atlantic ($\kappa \sim 0.5$) where higher-resolution data (1-° grid cell) were available. Here, we predicted higher habitat suitability mostly close to shore around Gabon, Congo and Equatorial Guinea, and between Côte d'Ivoire and Mauritania. Due to the paucity of studies on whale sharks in the Atlantic (excluding the Gulf of Mexico and Caribbean Sea not covered by our data), we could not validate these

Table 3

Estimated weight of evidence for each temporal predictor used in the generalized linear mixed-effects models: *Hsuit*: predicted habitat suitability derived from the spatial distribution models, *effort*: temporal variation in fishing effort, and a linear (*time*) and quadratic (*time*²) term in years.

Ocean	Atlantic	Pacific
<i>Hsuit</i>	1	0.761
<i>Effort</i>	0.999	1
<i>Time</i>	0.367	0.953
<i>Time</i> ²	0.133	0.328

results. However, this high predicted suitability matches the areas where higher zooplankton biomass is expected (Strömberg et al., 2009), and higher relative foraging success has been observed in the subequatorial region between 5° and 10° N for other giant zooplanktivores such as the leatherback turtle (*Dermodochelys coriacea*) (Fossette et al., 2010). We also predicted higher suitability farther from shore around the Equator and between 15 and 20°W (Fig. 2, left panel). As an anecdotal validation, whale sharks occur close to this area in the Saint Peter Saint Paul archipelago, peaking in occurrence at the end of June (Hazin et al., 2008).

In the western Pacific, the predictions show mostly suitable habitat within the area covered by the fisheries, but despite the higher suitability (up to 0.7), model accuracy was poor ($\kappa \sim 0.3$). This low accuracy, together with the low percentage of deviance explained (~6%) might also affect the performance of the temporal models for the same area. For this reason, we advise caution when interpreting the results for the Pacific Ocean. Possible reasons for the poor performance include low-resolution data or unmeasured environmental covariates that could be better predictors, such as current or wind conditions (Wilson et al., 2001). During the season we considered (April to June), the number of sightings in the western Pacific (167) was about 6 times lower than in the Atlantic (1018; Fig. 1), which reduces the performance of the western Pacific model. Because the data available for this ocean represent only partial coverage, access to the full dataset (giving more sightings in this season) would likely improve model performance by refining the distinction between presence and absence locations. Nevertheless, the available data are representative of the total fisheries in the area, thus application of the same models to seasons when more sightings are recorded might improve results. However, to compare synchronous seasonal occurrences in the three major oceans, data covering the months of April to June were required (following from Sequeira et al., 2012). Due to the lack of independent studies reporting whale shark occurrence off Indonesia and Papua New Guinea, we could not externally validate this model's predictions.

The opportunistically collected datasets on which we relied had inherent complications and assumptions. For example, an underlying assumption of our models is that failure to report a whale shark presence (whether or not a shark was detected or reported) is evenly distributed across the sampling area and period. Access to higher-resolution data would likely improve the results (as exemplified by the Atlantic Ocean models), and could be achieved by better collaboration between researchers and fisheries-management organisations. Commercial-in-confidence restrictions on access to fisheries data (especially sensitive

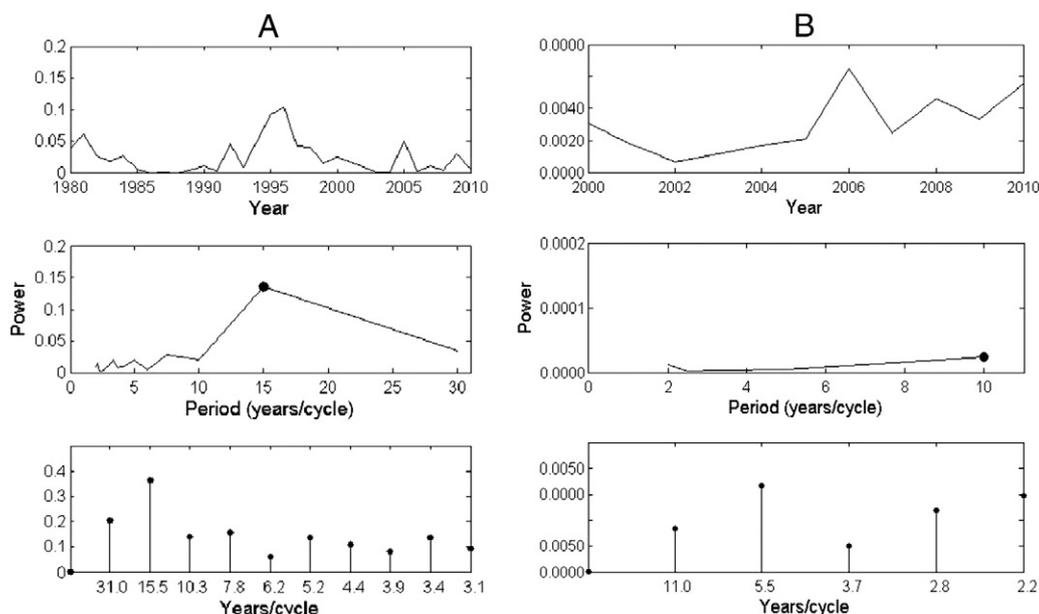


Fig. 5. Whale shark sightings per unit effort during the months of April to June in A) the Atlantic (1981–2010) and B) Pacific (2000–2010). Top: variation in sightings per unit effort with time; centre: strongest frequency observed; and bottom: cyclic description in whale shark sightings per unit effort as result of the fast Fourier transforms.

data such as fish catch) delay scientific research from providing more accurate models on fisheries impacts. Such collaborations could also lead to better data collection using the available resources. However, while data collected by fisheries might not be as precise as those derived from scientifically designed surveys, they are still essential sources of information given the logistic challenges of surveying widely distributed species over their entire range.

The generation of pseudo-absences was necessary to allow for the binomial estimation in the models. We previously assessed the differences associated with the method to generate pseudo-absences using similar datasets (Sequeira et al., 2012), and found that model performance was not reduced by using random pseudo-absence selection (see also Barbet-Massin et al., 2012). Barbet-Massin et al. (2012) also reported that model accuracy increases until the presence to pseudo-absence ratio (i.e., prevalence) reaches 0.1, and remains constant for lower ratios. Prevalence was 0.1 in our spatial assessment, and 0.01 in the temporal assessment (to allow enough points for the spatially explicit temporal analysis); therefore, we do not expect the presences:pseudo-absences ratio to have affected our prediction accuracy. Another important aspect is that both sightings and environmental variables correspond mostly to the ocean surface layer. Three-dimensional data at an adequate resolution for regional analyses are currently not available. Even though whale sharks spend most time at the surface (e.g., Rowat et al., 2007), they also dive frequently and so assessing how they explore their vertical habitat would be an important extension to our predictions. Other predictors such as currents could potentially also add some explanatory power as suggested by Sequeira et al. (2013c) when referring to whale shark occurrence in the Azores, Portugal.

Despite these limitations, we have demonstrated that whale shark occurrence is possibly asynchronously cyclical among ocean basins, which supports our notion of inter-ocean migration (Sequeira et al., in press). Despite this cyclicity possibly explaining declines observed in some years and locations, the total number of sightings has declined in the last decade (<50 per year in all oceans; Figs. 3a and S1). In the 1990s there were a total of about 500 sightings in the Atlantic Ocean (study months), while in the early 2000s, there were only around 150 (Fig. S1). We observed a similar pattern in the Indian Ocean (Sequeira et al., 2013a), with 600 sightings reported in the 1990s and ~200 in

following years (Figs. 3a and S1). The reduced sightings in the last decade agree with the recent accounts of declines from near-shore aggregations (Bradshaw et al., 2008). These results provide for the first time quantitative evidence that whale shark numbers are declining based on direct observations at a scale that largely encompasses the species' circumglobal range (Colman, 1997).

Whale sharks are currently listed as *Vulnerable* based on the Red List criteria $A2bd + 3d$ (Norman, 2005). Criterion $A2bd$ denotes a continuing, not understood or not reversible reduction of $\geq 30\%$ in population size over the last 10 years or three generations (whichever is the longer) based on “an index of abundance appropriate to the taxon” and “actual or potential levels of exploitation”. Criterion $3d$ denotes a projected or suspected $\geq 30\%$ reduction to be met within the next 10 years or three generations (whichever is the longer, up to a maximum of 100 years) based on “actual or potential levels of exploitation”. Targeted whale shark fisheries were mostly banned over 10 years ago (Sequeira et al., in press) (except in Taiwan, where the ban was imposed only after 2007) (COA, 2007) and according to the tuna fisheries datasets (Fig. S1), peak-month sightings have declined by about 50% in the last decade both in the Atlantic and Indian Oceans (there are no data available prior to 2000 for the Pacific Ocean). Considering the species' longevity of 60 to 100 years (Pauly, 2002), 10 years might correspond to only 10–20% of a single generation (Bradshaw et al., 2007). The observed decline in sightings is also occurring simultaneously in a large part of the species' known geographical range. This evidence, combined with their late age at maturity, and our poor understanding of the species' reproductive output, suggests that it is plausible that whale sharks are facing a higher risk of extinction than their current threat status indicates. Further, most whale sharks observed in aggregations worldwide are immature (Graham and Roberts, 2007; Heyman et al., 2001; Rowat et al., 2011; Wilson et al., 2001), and there is evidence that the average size of sharks is declining (Bradshaw et al., 2008). This mounting body of evidence calls for a re-assessment of their current status in the IUCN Red List. Adequate conservation measures are required to ensure the long term conservation of the species, as previously observed for sea turtles (Broderick et al., 2006; Hays, 2004).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2013.10.019>.

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Author contributions

AS planned the article, did the analysis, interpreted data, developed the models and wrote the manuscript; CM helped planning the article, and assisted with data interpretation and model development; LF and PJW assisted with data collection, extraction and interpretation; CJAB helped in model result interpretation and manuscript evaluation. All authors contributed to the writing of the manuscript. [SS]

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