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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.

1. Introduction

Most of the readily measureable 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 (Hutchison, 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 a 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