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Oceanographic and atmospheric phenomena influence the abundance of whale sharks at Ningaloo Reef, Western Australia

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ABSTRACT

Seasonal observations of whale shark abundance recorded by ecotourist operators at Ningaloo Reef, Western Australia from 1999 to 2004 were compared with weekly regional and global oceanographic and atmospheric variables, including average sea surface temperatures, along-shelf wind shear, sea level and the Southern Oscillation Index (SOI). Estimates of these physical variables were derived from either ground-based data or from remote sensing instruments. A generalised linear mixed-effects modelling (GLMM) approach with random sampling and model simulation was used to determine the relationships between the number of whale sharks and all model variants of the environmental parameters, using information-theoretic weights of evidence to rank models. SOI and wind shear had the most support for explaining the deviance in weekly whale shark abundance at Ningaloo Reef during a season. The SOI and wind shear variables positively influenced whale shark abundance such that more sharks were sighted when the Southern Oscillation was stronger and along-shelf winds were increasingly prevalent. This may reflect changes in the strength of oceanographic processes such as the Leeuwin Current (in response to the Southern Oscillation) and wind/current driven upwelling which may affect the abundance of whale sharks transported to the region and/or the availability of their prey by driving productivity changes.

1. Introduction

Whale sharks (*Rhincodon typus*), the largest fishes in the ocean (attaining sizes>12 m in length), have a global tropical and warm-temperate distribution (Last and Stevens, 1994). In spite of their size and large range, little is understood about the influences of oceanographic and atmospheric processes on whale shark behaviour and life history (Colman, 1997). Our understanding of these animals is largely derived from observations during seasonal aggregations of sharks that occur at a few coastal locations (Clark and Nelson, 1997; Gunn et al., 1999; Heyman et al., 2001; Meekan et al., 2006; Rowat et al., 2007; Wilson et al., 2006).

Aggregations of whale sharks occur off Ningaloo Reef on the northern west coast of Australia between March and May each year (Gunn et al., 1999; Meekan et al., 2006; Taylor, 1996; Wilson et al., 2006). The occurrence of whale sharks in coastal waters is believed to coincide with productivity events that provide an ample supply of zooplanktonic/larval food (Clark and Nelson, 1997; Gunn et al., 1999; Heyman et al., 2001; Taylor, 1996; Taylor and Pearce, 1999; Wilson et al., 2001). Whale sharks use three main feeding behaviours to exploit these productivity pulses, namely: (1) passive or ram filter-feeding; (2) facultative suction feeding/vertical feeding; and (3) active feeding/ram-suction at the surface (Clark and Nelson, 1997; Graham et al., 2005; Gunn et al., 1999; Nelson and Eckert, 2007; Taylor, 2007) whereby each respective behaviour has been linked with increasing density of prey items (Nelson and Eckert, 2007). Although various studies have attributed the aggregations of whale sharks off Ningaloo Reef to feeding as opposed to reproduction (given that a major proportion of the observed whale sharks are sexually immature males — Meekan et al., 2006), few studies have attempted to verify how the abundance of whale sharks is influenced by other environmental conditions (Gunn et al., 1999; Wilson et al., 2001).

A variety of oceanographic and atmospheric variables are known to influence the spatio-temporal abundance of pelagic and migratory marine organisms. The relative importance of these variables to a particular organism will depend on the spatial scale at which these processes operate and the functional importance of this scale to the organism. El Niño-Southern Oscillation (ENSO) is a global atmospheric process that is described by the Southern Oscillation Index (SOI) as the

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mean sea-level pressure difference between the central Pacific (Tahiti) and the north-eastern Indian Ocean (Darwin). In years when the sea-level pressure is higher in Pacific than the Indian Ocean (La Niña), trade winds drive stronger currents and warmer sea temperatures along the north of Australia, positively influencing the southward flow of the Leeuwin Current along the west coast of Australia (Caputi et al., 1996; Pearce and Phillips, 1988). In a study by Wilson et al. (2001), annual whale shark aggregations at Ningaloo between 1993 and 1998 were moderately correlated with yearly SOI values, yet weakly correlated with local oceanographic variables such as sea level (SL) and sea surface temperature (SST). These authors concluded that inter-annual variation in the strength of the Leeuwin Current (related to the SOI rather than SL) had a greater influence on whale shark aggregations than local-scale processes, presumably due to the active-transport mechanism, or directional cues provided by the Leeuwin Current to whale sharks. However, results of the Wilson et al. (2001) study were potentially biased because of difficulties in correcting data for search effort and inconsistent sampling techniques, where both boat and plane-based counts were combined.

Here, we build on the work of Wilson et al. (2001) by analysing a more current time-series of whale shark observations from Ningaloo Reef spanning from 1999 to 2004. We use observation records collected exclusively from whale shark tour operator boats, include all available years of data (successive, continuous years) and analyse data at the scales of months and weeks to determine the relationship between abundance and atmospheric and oceanographic variations. We use data that have been corrected for sampling effort, a larger range of potentially influential environmental variables collected remotely and *in situ* and a statistical approach embracing multiple working hypotheses (Elliott and Brook, 2007) using generalised linear mixed-effects models (GLMMs) to determine how ocean and atmospheric processes may influence whale shark abundance. With these variations in data and analytical techniques we aim to estimate better the effect of physical oceanographic variables on whale shark abundance and understand and ultimately predict this relationship in the context of the Leeuwin Current (Pearce and Phillips, 1988).

2. Materials and methods

2.1. Whale shark abundance data

We accessed a relative abundance dataset spanning from 1999 to 2004 of whale shark observations from ecotourism vessels at Ningaloo Reef (Colman, 1997). The area surveyed for whale sharks by ecotourism operators encompassed the northern and southern sections of the Ningaloo Marine Park in the Indian Ocean on the Northwest Cape of Western Australia (21° 40′ S to 23° 30′ S and 113° 45′ E to 114° 15′ E), which spans approximately 260 km of coastline from north to south. The number of whale sharks encountered by each operator each day during the months of April and May (the peak of the whale shark season), the search time in hours:minutes and the GPS location were recorded in a standardised log sheet as a licensing requirement for operators by the West Australian Department of Environment and Conservation (DEC) (formerly, the Department of Conservation and Land Management). We attempted to standardise data for repeated counting of the same shark among different vessels by using a correction based on an assumed line-of-sight distance (search radius) for closely operating vessels (as determined by GPS coordinates).We divided the number (n) of whale sharks observed per period (i.e., week and month) by the daily search time for each vessel (effort) and then added these for each vessel to obtain a total standardised estimate of relative abundance. These data were used to calculate the average weekly and monthly abundance of whale sharks.

2.2. Oceanographic and atmospheric parameters

Daily and monthly SOI values were acquired from the Australian Bureau of Meteorology and weekly values were subsequently calculated using running mean sea-level pressure values (MSLP) between Tahiti and Darwin with the base period of 1932–1999. The temporal span of the SOI data was consistent with that of the whale shark abundance dataset.

Sea-level (SL) data were collected hourly from a tide gauge deployed at Milyering (21° 1.816′ S and 113° 55.316′ E) in the northern section of the Marine Park from 1998. The data were then corrected to remove the effects of tides and inertial signals using a low-pass filtering technique where values were smoothed (averaged) on a 30-hour basis. A 30-hour period was chosen to avoid leakage of high-frequency signals into the low-passed data. We used a filter that allowed a flat low-frequency response, sharp cut-off and low noise (see Thompson, 1983). Major tidal frequencies (M2, S2, N2, L2, K1, O1, and Q1) were also specified as zeros of the filter frequency response function to ensure tidal signal suppression (Burrage et al., 1991; Thompson, 1983). Weekly and monthly average SL values were calculated.

Wind shear (WS) was hypothesised to correlate with whale shark abundance because it is a good proxy for the strength and direction of wind along the shelf, and thus related indirectly to the strength of the Ningaloo Current, an inshore counter-current that is believed to be important for retaining planktonic biomass along Ningaloo Reef (Taylor and Pearce, 1999). Wind speed and direction data were collected half-hourly at a weather station at Milyering from 1997. These were used to calculate an along-shelf wind vector (V; see below), or wind shear parameter, that was a length vector calculated by combining wind direction and speed and rotating the data clockwise at 60°. Currents and winds were also rotated to along- and cross-shelf components.

Wind shear was calculated by decomposing wind speed and direction values into north–south (U) and east–west (V) vectors or components using the standard conversion between rotary and Cartesian reference systems:

$$U = \text{sine}\left(\frac{D\pi}{180}\right)S;\ V = \text{cosine}\left(\frac{D\pi}{180}\right)S$$

where direction (D) is in degrees. We used the V vector to denote wind shear given this aligned most accurately with the natural axis orientation of along-shelf currents at Ningaloo following rotation of the data clockwise by 60° (relative to true north). The same low-pass filtering technique used for SL (with 30-hour cut-off) was also used for wind shear and the resulting values averaged on weekly and monthly intervals.

Sea surface temperature (SST) is known to predict biologically important changes in fish abundance (Fiedler and Bernard, 1987; Iwasaki, 1970). SST data were calculated from daily and weekly composites of 4-km resolution NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite images of the Ningaloo region (21° S to 24° S and 112° E to 115° E). The 4 × 4 km pixel values in the composites were spatially averaged to calculate single daily and weekly SST values.

2.3. Analysis

Generalised linear mixed-effects models (GLMM) were used to explore relationships between oceanographic and atmospheric variables and whale shark abundance at Ningaloo Reef. Examination of the residuals for the saturated models determined the statistical family (i.e., Gaussian, gamma, etc.) and error distribution most appropriate for each analysis. In this case, a gamma error distribution with a log link function was most appropriate. The error structure of GLMM corrects for non-independence of statistical units (relative abundance estimates) due to shared temporal structure (months), and permits the 'random effects' variance explained at different levels of clustering (months) to be decomposed. All oceanographic and atmospheric variables were modelled as fixed effects.

Model comparison was based on Akaike's information criterion corrected for small samples (AIC_c), (Akaike, 1973; 1974; Burnham and Anderson, 2001; Lebreton et al., 1992). AIC_c values were ranked, with the most parsimonious model(s) having the lowest AIC_c values and highest model weights (Lebreton et al., 1992). From the set of *a priori* models we used a predictive model averaging procedure to determine the magnitude of the effect of some terms, keeping all other dependent variables constant (Burnham and Anderson, 2002). The weights of evidence ($w+_i$) for each variable were calculated by summing the model AIC_c weights (w_i) over all models in which each term appeared. However, the $w+_i$ values are relative, not absolute because they will be >0 even if the predictor has no contextual explanatory importance (Burnham and Anderson, 2002). To determine the predictors that were relevant to the data a baseline for comparing relative $w+_i$ across predictors was required. Following Burnham and Anderson (2002), we randomised the data for each predictor separately within the dataset, recalculated $w+_i$, and repeated this procedure 100 times for each predictor. The median of this new randomised $w+_i$ distribution for each predictor was taken as the baseline (null) value ($w+0$). For each term the relative weight of evidence ($\Delta w+$) was obtained by subtracting $w+0$ from $w+_i$. Predictors with $\Delta w+$ of zero or less have essentially no explanatory power. All statistical analyses were done using the *R* Package (Ver. 2.0.1) (R Development Core Team, 2004).

We included the environmental variables of SOI, SST, SL and WS (and all combinations of these) in the model set to determine how they influenced weekly whale shark abundance from 1999 to 2004. A Spearman's correlation matrix for the variables considered highlighted potentially collinear. Highly correlated ($r>0.8$) variables were not included in the same model. The percentage of deviance explained (% DE) was also calculated for each model as a measure of goodness-of-fit.

3. Results

3.1. Relative abundance

Within the annual period when whale sharks are known to occur at Ningaloo Reef (March to July), the highest abundances were observed towards the end of May in 2002 (Fig. 1A and B). In most years, weekly whale shark sightings were clustered between the beginning of April and the beginning of June, with few sighting occurring at the start of March or at the end of June.

3.2. Weekly environmental variables

SOI and sea level were moderately correlated (0.519, Table 1), as was SST and sea level (0.437) and wind shear and sea level (0.497). Despite several competing models (Table 2) only SOI and SL had sufficient evidence for explaining variance in whale shark abundance ($\Delta w+=$ 0.079 and 0.001, respectively). Both these variables were positively correlated with whale shark abundance (Fig. 2).The model that included SOI and WS was able to explain a larger amount of the deviance in the data compared to all other model combinations (Table 2). This suggested that SOI and WS had the best predictive capacity for explaining the weekly abundance of whale sharks at Ningaloo.

4. Discussion

Of the atmospheric and oceanographic variables that were hypothesised to influence whale shark abundance at Ningaloo Reef, only the SOI and WS appeared to be related to shark numbers. In the analysis, SOI was negatively correlated with weekly whale shark abundance. Surprisingly, sea level had little influence on whale shark abundance, despite its strong correlation with the strength of the Leeuwin Current and SOI (Pearce and Phillips, 1988).

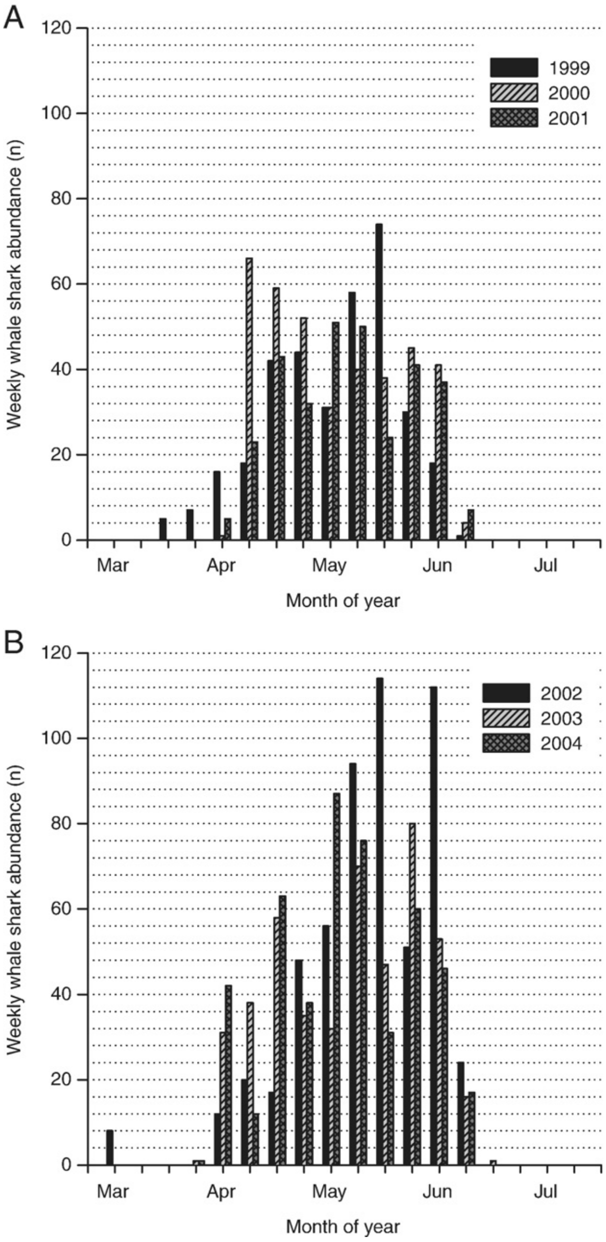

Fig. 1. The weekly abundance of whale sharks observed off Ningaloo Reef from March to July between years (A) 1999–2001, and (B) 2002–2004.

The results of our study partly support the findings of Wilson et al. (2001), who also suggested that SOI was an important factor influencing the abundance of whale sharks at Ningaloo Reef. The SOI is effectively a measure of ENSO, a large-scale climatic process that has two climatic phases: El Niño and La Niña. During the latter, strong Pacific trade winds and warmer sea temperatures (also known as the Walker circulation) in the ocean north of Australia increase the strength

Table 1
Correlation matrix between Southern Oscillation Index (SOI), sea surface temperature (SST), sea level (SL) and along-shelf wind shear (WS) from 1999 to 2004.

	SOI	SST	SL
SST	0.092	–	–
SL	0.519	0.437	–
WS	0.110	0.144	0.497

Table 2
Generalised linear mixed-effects models and their information-theoretic statistics based on the change in Akaike's information criterion corrected for small samples (ΔAIC_c) using Southern Oscillation Index (SOI), sea surface temperature (SST), sea level (SL) and wind shear (WS) to estimate trends in weekly whale shark abundance from 1999 to 2004.

Model (i)	%DE	ΔAIC_c	w_i
WS	19.216	0.000	0.307
SOI + WS	24.396	0.920	0.194
SST + WS	21.305	1.51	0.143
SL + WS	20.190	1.735	0.129
SOI + SST + WS	25.586	2.690	0.080

Notations; %DE = % deviance explained, w_i = AIC_c weight.

of a variety of ocean currents, notably the Indonesian Through-Flow and the East Gyral current and ultimately, the southerly-flowing Leeuwin Current (Rochford, 1962; 1984). The combined effects of wind shear and SOI are likely to be the main influencing factors driving the along-shelf current which produces localised re-suspension of nutrients and resultant productivity pulses.

A long-term (decadal) photo-identification study of whale sharks at Ningaloo Reef has shown that many sharks are resighted in successive years at this locality (Rowat et al., 2007; Bradshaw et al., 2008). Tagging studies using pop-up archival tags (PAT) show that following aggregations, whale sharks move northward from Ningaloo (Wilson et al., 2006). Tags that detach from whale sharks <4–5 months after deployment are typically found on the continental shelf to the north, while tags that detach after this time have been found in the open ocean beyond the continental shelf. Wilson et al. (2006) suggested that this indicates that whale sharks could be using the directional cues of the northward-flowing current systems such as the Ningaloo Current to migrate northwards along the shelf after visiting Ningaloo and then later move offshore to take advantage of the southward-flowing Leeuwin Current to return to the reef. This explanation assumes that whale sharks use currents a as transport mechanism and if true, it might be expected that in ENSO years when the Leeuwin Current is weaker, whale sharks should arrive at Ningaloo later in the season and possibly in fewer numbers if they were not transported as far down the coast.

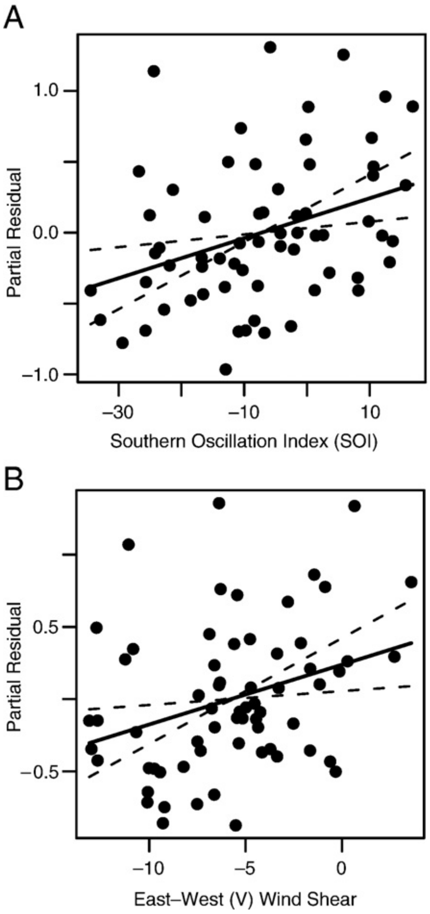

Fig. 2. Partial residual plot generated from the most parsimonious generalised linear model relating weekly whale shark abundance between 1999 and 2004 to the Southern Oscillation Index (SOI) and wind shear. The solid line is the fitted linear model. The dashed lines are the approximate 95% point-wise confidence intervals.

The influence of the ENSO climatic signal is not limited to physical effects on currents. Variation in the strength, timing and path of the Leeuwin Current due to ENSO has cascading effects on the types and abundances of marine organisms that occur on the Western Australian coastline (Caputi et al., 1996). For instance, recruitment of the western rock lobster (*Panulirus cygnus*) is positively influenced while recruitment of scallops (*Amusium balloti*) and pilchards (*Sardinops sagax neopilchardus*) are negatively influenced by the strength of the Leeuwin Current. These year-to-year differences probably reflect changes in the food chains and the availability of the appropriate prey for larval or young stages. For whale sharks, it is possible that La Niña climatic episodes influence abundance on Ningaloo Reef by favouring the oceanographic conditions necessary for increasing the availability of appropriate prey. While the strong Pacific trade winds characteristic of La Niña are important for driving the warm, southerly-flowing Leeuwin Current, the strength of this current also positively influences the flow of the cooler Ningaloo counter-current The Ningaloo Current predominates on the reef front from September to April, and is believed to influence coastal upwelling with prevailing South Westerly winds due to Ekman transport (Holloway, 2001; Holloway and Nye, 1985; Taylor and Pearce, 1999). This upwelling determines localised productivity events along the Ningaloo coast, which may attract whale sharks to the reef (Taylor and Pearce, 1999). In temperate regions there is some evidence that large-scale climatic phenomena influence the abundance of planktivorous sharks such as the basking shark (*Cetorhinus maximus*) by driving oceanographic events that alter productivity of coastal waters and ultimately the availability of zooplankton food for these animals. For example, abundances and distributions of basking sharks off the coast of southern England have been linked with the North Atlantic Oscillation (Sims and Quayle, 1998). Similarly, the El Niño/Southern Oscillation is thought to influence basking shark abundance off the coast of California (Squire, 1990).

It is difficult at present to determine how changes in the strength of current systems in response to the ENSO phenomenon may act to transport sharks to the region and/or indirectly affect their prey by driving productivity events at Ningaloo Reef. This issue is currently under investigation through the deployment of satellite tags so that whale shark migrations can be linked with oceanographic processes observed from remotely sensed data. Satellite measurements of chlorophyll *a* concentrations and other potentially important parameters (e.g., SST and salinity) can be overlaid on migration pathways to determine the extent to which whale shark aggregations are related to physical transport mechanisms and productivity of Ningaloo Reef.

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