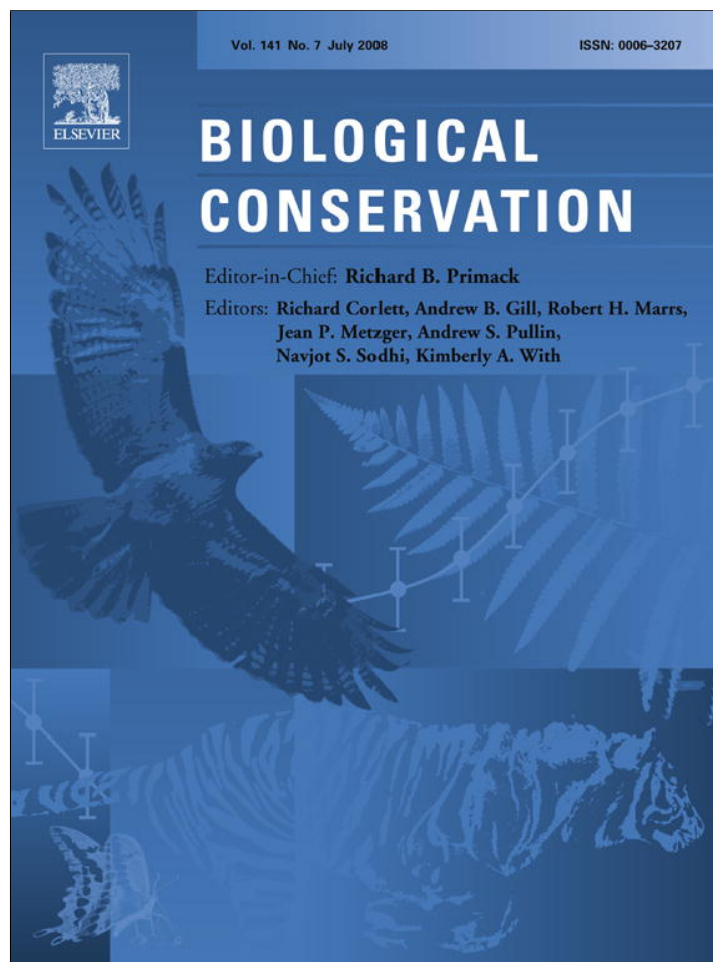


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Decline in whale shark size and abundance at Ningaloo Reef over the past decade: The world's largest fish is getting smaller

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ABSTRACT

Over-exploitation of whale sharks threatens the future of these wide-ranging pelagic fish. A long-term continuous record (4436 sightings) from a large aggregation (300–500 resident individuals) of whale sharks at Ningaloo Reef, Western Australia shows that mean shark length declined linearly by nearly 2.0 m and relative abundance measured from ecotourism sightings (corrected for variation in search effort and environmental stochasticity) has fallen by approximately 40% over the last decade. This population-level result confirms previous predictions of population decline based on projection models parameterised using mark-recapture estimates of survival. The majority of these changes are driven by reductions in the number of large individuals in the population. Phenomenological time series models support a deterministic (extrinsic) decline in large females, although there was some evidence for density dependence in large males. These reductions have occurred despite the total protection of whale sharks in Australian waters. As this species is highly migratory, the rapid change in population composition over a decade (<1 whale shark generation) supports the hypothesis of unsustainable mortality in other parts of their range (e.g., overfishing), rather than the alternative of long-term abiotic or biotic shifts in the environment. As such, effective conservation of whale sharks will require international protection, and collaborative tagging studies to identify and monitor migratory pathways.

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1. Introduction

The effects of overfishing reach far beyond the relatively predictable reduction of yields (Food and Agriculture Organisation of the United Nations, 2006); overfishing of marine species can also disrupt important biological processes by removing particular size classes (Walker, 1998), thereby changing an exploited population's age structure, individual maturation times and growth rates (Myers et al., 1995; Jennings and Kaiser, 1998; Jennings et al., 1998; Dulvy et al., 2003; Reynolds et al., 2005). Changes to demographic rates and the evolutionary patterns induced by size-selective fishing can increase extinction risk in harvested species (Jennings et al., 1998; Jennings et al., 1999; Conover and Munch, 2002; Reynolds et al., 2005), so measuring changes in size structure is an important step in identifying whether over-exploitation has occurred (Shin et al., 2005; Greenstreet and Rogers, 2006).

Many large pelagic species such as tunas, billfishes and sharks that are targeted directly or are taken as bycatch in industrial fisheries have experienced substantial declines over the last century (Baum et al., 2003; Sibert et al., 2006; Myers et al., 2007). For sharks in particular, high harvest rates mainly from bycatch have resulted in rapid population declines (Baum et al., 2003; Robbins et al., 2006; Sibert et al., 2006; Myers et al., 2007), although the dynamics of the interacting drivers of decline make predictions of extinction risk difficult (Walker, 1998; Stevens et al., 2000; Baum et al., 2005; Burgess et al., 2005a; Burgess et al., 2005b; Robbins et al., 2006). Additionally, these population crashes have occurred in spite of the perceived lower extinction risk of broad-ranging and wide-dispersing species (Terborgh and Winter, 1980).

Although harvested to an unquantified extent (Chen et al., 1997; Chen and Phipps, 2002), the world's largest fish, the whale shark (*Rhincodon typus* Smith, 1828), also appears to have declined throughout much of its range (CITES, 2002; Theberge and Dearden, 2006; Bradshaw et al., 2007). These wide-ranging (Eckert et al., 2002; Wilson et al., 2006; Bradshaw, 2007; Castro et al., 2007) filter feeders are distributed throughout the world's tropical and warm temperate seas and are classed as *Vulnerable* under IUCN Red List criteria and listed by the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES) in *Appendix II* (i.e., "species not necessarily threatened with extinction, but in which trade must be controlled in order to avoid utilization incompatible with their survival") (CITES, 2002). Like most shark species, whale shark have slow growth rates, late maturity and extended longevity (Frisk et al., 2001; Bradshaw et al., 2007; Graham and Roberts, 2007), and such traits are likely to limit annual recruitment and increase susceptibility to over-exploitation by humans (Smith et al., 1998; Bradshaw et al., 2007). The high degree of connectivity among aggregations at broad spatial scales (Castro et al., 2007; Graham and Roberts, 2007) suggests that unsustainable fishing mortality at one locality will affect unexploited aggregations at another (Bradshaw, 2007).

In the late 1980s, aggregations of whale sharks were reported in coastal waters at a few locations in Australia, South-east Asia and the Caribbean (Taylor, 1996; Heyman et al., 2001). Since this time, the predictability of seasonal aggregations has fostered the development of a profitable ecotourism

industry (Meekan et al., 2006; Graham and Roberts, 2007). Ecotourism at Ningaloo Reef, Western Australia, one of the world's largest whale shark aggregations, began in the early 1990s and since 1995, location, sex and length data have been recorded for most individuals encountered (Meekan et al., 2006). This industry uses light aircraft to locate the sharks in surface waters and to direct vessels into their path so that paying tourists are able to swim with the slow-moving sharks (Davis et al., 1997). Whale sharks come to Ningaloo Reef from March to June, where they are found in shallow water (<100 m) along the front of the fringing coral reef (Taylor, 1996). These continuous records now span a decade, providing a large sightings dataset that offers insight into this aggregation's demography and population status.

Based on the anecdotal and catch evidence that the whale shark population has experienced (largely unmeasured) exploitation in the Indian Ocean basin (Chen et al., 1997; Chen and Phipps, 2002), we hypothesised that evidence for over-exploitation would be revealed by an observed decline in larger (older) individuals (Stergiou, 2002). Previous work using photo-identification of 159 known individuals at Ningaloo Reef has provided some support for this hypothesis, with an observed increase in the proportion of small (<6.7 m total length) sharks (Meekan et al., 2006). Here we used a much larger and independently collected dataset to test for a continuous reduction in average shark size (total length). There are three main mechanisms that may drive changes in body size of harvested populations: (1) abiotic factors affecting growth and development (e.g., large-scale climate or regime shifts); (2) biotic changes such as density-modified growth rates and (3) changes to demography and genetic composition via harvesting (Ratner and Lande, 2001). We therefore explicitly examined the form of the decline (linear, logistic or quadratic) to test for the presence of a new mean size equilibrium. We hypothesised that a rapid, deterministic mortality source of a particular size class (e.g., size-biased harvest) might induce a gradual decline in mean size followed by a tapering toward a new equilibrium size as larger individuals were systematically removed from the population. By comparison, sustained linear decline without tapering may indicate a shift by fishers to target progressively smaller individuals as larger individuals are depleted from the population (cf. Pauly et al., 1998).

A natural corollary of over-exploitation is the prediction that overall abundance of the population decreases (Food and Agriculture Organisation of the United Nations, 2006); as such, we tested the hypothesis that the number of whale sharks seen at Ningaloo Reef has changed since monitoring began. This hypothesis is based on previous capture-mark-recapture model estimates of survival and matrix projections that inferred long-term decline of whale sharks visiting Ningaloo Reef (Bradshaw et al., 2007). Using the large operator-collected dataset, we tested the hypothesis of a decline directly using relative abundance data corrected for sampling effort and environmental stochasticity because whale shark abundance is known to fluctuate annually relative to local oceanographic conditions (Wilson et al., 2001).

Our final aim was to gain insight into the relative contribution of demographic and environmental processes driving the population trends. We hypothesised that abundance time series from a declining population will demonstrate more

support for an exponential model describing the relationship between the rate of change and population density compared to a stable population fluctuating around carrying capacity (see Brook and Bradshaw, 2006). As such, we predicted that the exploited whale shark abundance time series will show little support for density regulation, and we test this explicitly by contrasting phenomenological density-dependent and density-independent models applied to the relative abundance time series. Although we focus on a single iconic species, our intent is to provide marine conservation biologists with a general approach for examining potential causes of decline in long-lived marine predators when detailed demographic data are rare and relative abundance time-series data are readily available.

2. Materials and methods

2.1. Tourist operator-collected data

Numbers of whale sharks at Ningaloo Reef peak in the months of April and May (Davis et al., 1997; Wilson et al., 2001). Because sighting effort occurs sporadically outside of the peak months, our analysis was restricted to the peak period. Tour operators collected information on estimated total length (TL, visual estimation from the spotter plane and vessel; corroborated by in-water measurements) (Meekan et al., 2006) and sex (via the identification of claspers on males) (Taylor, 1994) for each shark observed. Licenses for tourist boat access to sharks are restricted by the Western Australian Department of Environment and Conservation (WA-DEC). This means that the same vessels tend to operate from year to year (Davis et al., 1997). There is however, turnover in crew, which should negate the possibility that any observed trends in size distribution are merely the result of year-by-year improvement in an operator's assessment skill and capacity. Supporting this, the same observed trends were consistent in data collected by licensees operating only from Coral Bay or Tantabiddi >100 km away (B.M. Fitzpatrick, unpubl. data). Recently, WA-DEC implemented a training course that all employees of the whale shark tourism operations are required to attend, and records indicate that no single boat skipper, dive master or crew member has remained during the entire sample interval. In fact, most employees remain for an average of two years only. Additionally, spotting-plane pilots typically provide the first estimate of whale shark size, and pilots turnover at a similar rate to boat crews (B.M. Fitzpatrick, unpubl. data).

Spotter planes are generally shared between two or more tourist vessels with patrons sharing the same shark. Length estimates of the same shark are a combined effort between a plane pilot, one or more boat skippers, and in-water shark spotters, all with varying experience. Such repeat observations of the same shark were identified in different ship logs and removed from the dataset. Length estimates of surfaced sharks are typically made by pilots and corroborated by comparison to known-length vessels in the water; further validation is provided by in-water measurements compared to known-length snorkelers. Length measurements are only entered into the database once pilots and multiple operators

agree. As quantified corroboration, direct in-water measurements of sharks compared favourably to pilot and vessel-operator estimates of total length (Norman, 1999).

There is little evidence that the presence of snorkelers influences whale shark behaviour. The interaction of tourists and vessels with sharks is tightly controlled by a code of conduct enforced by DEC (Davis et al., 1997). This ensures that patrons do not approach within 3 m of the shark while snorkelling, and vessels must remain a minimum of 30 m from the shark for a maximum of 90 minutes (Davis et al., 1997). Studies of whale sharks at Ningaloo Reef could find no detectable changes in behaviour of sharks in the presence of snorkelers (Norman, 1999) that might bias our results.

2.2. Reduction in total length over time

To test the hypothesis of a continuous decline in mean shark size and to examine the form of this trend, four linear and non-linear models of mean annual TL (over all individuals for which a TL estimate was made) against year were contrasted. Models represented four hypotheses: (1) no temporal trend (intercept: $TL \sim 1$), (2) linear decline (linear: $TL \sim \text{year}$), (3) curvilinear decline (quadratic: $TL \sim \text{year} + \text{year}^2$), and (4) sigmoidal decline (logistic: $TL \sim a/b \cdot e^{\text{year}}$, where a and b are constants). Non-linear models were used in addition to linear models because distinct processes affecting mean size in a population may introduce different trends in size over time (see Introduction).

We used Akaike's Information Criterion corrected for small sample size (AIC_c) as an index of Kullback–Leibler (K–L) information loss to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002). One could also employ other methods to compare models such as the dimension-consistent Bayesian Information Criterion (BIC); however, BIC may only be preferable when sample sizes are approximately ≥ 20 data per parameter estimate (Burnham and Anderson, 2004; Link and Barker, 2006). The relative likelihoods of candidate models were calculated using AIC_c (Burnham and Anderson, 2002), with the weight ($wAIC_c$) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. For each model considered, we also calculated the percentage deviance explained (%DE) as a measure of goodness-of-fit. Information-theoretic evidence ratios (ER, an index of the likelihood of one model over another, calculated as the $wAIC_c$ of one model \div $wAIC_c$ of another model) (Burnham and Anderson, 2002) were used to contrast specific model pairs.

The above analysis only examines the trend in mean total length over time. To incorporate uncertainty due to year, month and vessel into the test for a decline in mean total length, we also applied a series of five *a priori* general linear models (GLM) with Gaussian error distributions and identity link functions, where individual TL was set as the response and the terms year/month were treated as a nested term and individual factors made up the various model combinations. The term month was included in some models to account for possible phenology changes (e.g., temporal changes in arrival patterns during the peak season) that may vary with strength of the El Niño–Southern Oscillation events each year (Wilson et al., 2001, and see below). We also

considered a second set of models replacing month with day of year as a covariate to investigate whether more variance in total length could be explained. Models were contrasted using the Bayesian Information Criterion (BIC) given the large sample size ($n = 1814$) and our desire to distinguish main from tapering effects (Burnham and Anderson, 2004; Link and Barker, 2006). We also considered a second set of 8 models that included the sex effect (with a reduced overall sample size given that not all individuals could be sexed reliably; $n = 1333$). To test further the hypothesis that systematic changes in observers may have biased observed size trends, we constructed a series of linear mixed-effects models (GLMM) using the `lmer` command in the `lme4` library of the R Package (R Development Core Team, 2004), coding year as a fixed covariate and vessel as a random factor.

2.3. Relative shark abundance and climate variation

Relative shark abundance was calculated by summing the total number of sharks seen for the months of April and May and dividing these values by the total search time for all observing vessels for these two months over each year of the study (SPUE = sightings per unit effort). The monthly interval was chosen to match available environmental data for sightability bias correction (see below). Search time was calculated only over the peak interval and not the entire year. The database was corrected so that a shark was only recorded once per day even though it may have been sighted by several tourist operators during that day. The majority of this 'effort' (>90%) is devoted to searching for sharks rather than transiting to one once it has been identified by another vessel. There is therefore little chance that extra time spent transiting between a single shark visited by several vessels would impart any important bias to indices of search effort. However, it was still possible that the same shark was seen on subsequent days (i.e., individual sharks were not marked). Tagged whale sharks remain near the Ningaloo coast for several weeks after tagging (Wilson et al., 2006), so repeated sampling of some sharks was probable. However, this problem is unlikely to affect overall size and abundance trends unless there was some systematic change in residence times that we could not record. Furthermore, given that individual sharks are unlikely to remain at Ningaloo Reef for more than a few weeks (at most), monthly comparisons of relative abundance should account for gross changes in abundance more appropriately than examining the trends at finer temporal scales.

Climate variation is thought to affect whale shark relative abundance at Ningaloo Reef (Wilson et al., 2001). Critically, however, the relationship between whale shark abundance and El Niño-Southern Oscillation (ENSO) variation established by Wilson et al. (2001) did not correct relative abundance estimates for variation in search effort. The oceanography around Ningaloo Reef is dominated by the Leeuwin Current (LC), which forms from the Indonesian Through-Flow system to the north (Morrow and Birol, 1998). The LC flows south along the shelf break bringing warm, nutrient-poor water to the coast of Western Australia (Pearce and Griffiths, 1991). Between the LC and the coast, cooler water upwells from depth to form the Ningaloo Current, which flows along the edge of Ningaloo Reef towards the north (Morrow and Birol, 1998).

The relative strengths of these current systems are strongly influenced by El Niño-Southern Oscillation (ENSO) events (Pearce and Phillips, 1988). During El Niño years, the LC is weak and water temperatures along the coast of Western Australia are relatively cool, while in La Niña years the current is stronger and water temperatures are higher. This variability in current flow is known to influence recruitment to many commercial fisheries in Western Australia (Lenanton et al., 1991; Caputi et al., 1996).

To correct the relative abundance data (sightings per unit effort – SPUE) for this annual climate variation, we used maximum likelihood estimation (MLE) to fit a linear regression between mean SPUE to the mean April and May Southern Oscillation Index (SOI) (calculated from a two-month running mean smoother). We then detrended the SPUE time series based on this relationship (subtracting fitted values from observed SPUE). Temporal comparisons of detrended SPUE assume, of course, that SPUE reflects relative changes in total abundance.

Photo-identification data of 159 known individuals suggest that that whale sharks at Ningaloo Reef have changed in age/size composition since monitoring began (Meekan et al., 2006). To expand on this preliminary work and to test the hypothesis with the much larger tourist operator dataset, we examined the SOI-detrended SPUE trends for four size-sex classes based on the median TL (6 m) observed over all sharks: small (<6 m) or large (≥ 6 m), and male or female (median TL was not calculated for each sex separately due to the weak sex effect; see Results). We deliberately avoided using a putative size at maturity as the threshold for dividing 'small' and 'large' sharks, given the uncertainty associated with this value (Bradshaw et al., 2007). Our aim here was primarily to ensure representative samples in each size category, to test the hypothesis that different size categories of whale sharks (based on the median threshold) demonstrate different temporal trends in abundance.

2.4. Evidence of intrinsic and extrinsic control in SPUE rate of change

In addition to testing for a decline in the raw temporal trends in SOI-detrended SPUE, we examined the relative evidence for intrinsic (including both births and temporary immigration) and extrinsic (e.g., deterministic drivers such as over-harvest) control of the detrended relative abundance data. Our hypothesis in this case was that evidence for an exogenous (i.e., environmental or anthropogenic) driver of the decline, as revealed by the SPUE data, would be supported if density-independent models of the relationship between population rate of change (r) and relative abundance (SPUE) had stronger information-theoretic evidence than density-dependent models (an approach used for many other taxa to determine the relative contribution of extrinsic versus intrinsic control of population size – de Little et al., 2007; Chamaillé-Jammes et al., 2008; Yang et al., 2008). This hypothesis is based on the assumption that deterministic declines caused by harvest do not fluctuate with respect to stock density; this is a fundamental tenet of fisheries management based on catch-per-unit-effort (CPUE) data (Walters, 1995; Walters and

Martell, 2004, but see also [Maunder et al., 2006](#) for the limitations of CPUE data interpretation).

We adopted a multiple-working hypotheses approach based on information-theoretic multi-model inference ([Burnham and Anderson, 2002](#)) by applying two variants of the generalised θ -logistic population growth model ([Turchin, 2003](#)) to the detrended SPUE series (averaged by year): (1) Gompertz-logistic growth

$$\log\left(\frac{\text{SPUE}_{t+1}}{\text{SPUE}_t}\right) = r = r_m \left[1 - \left(\frac{\log(\text{SPUE}_t)}{\log(K)} \right)^\theta \right] + \varepsilon_t$$

where SPUE_t = SOI-detrended relative abundance time t , r = realised population growth rate, r_m = maximal intrinsic population growth rate, K = carrying capacity, θ is a shape parameter set to 1, and ε_t has a mean of zero and a variance (σ^2) that reflects environmental variability in r ; and (2) exponential growth (where $\theta = -\infty$, and r_m and σ are estimated). We used MLE to fit model parameters via linear regression, and models were contrasted using AIC_c as described above.

Table 1 – Four models applied to the relationship between mean total length (TL) and year for whale sharks from Ningaloo Reef between 1995 and 2004

Model	k	LL	ΔAIC_c	$w\text{AIC}_c$	%DE
Linear	3	3.49	0.00	0.71	91.49
Logistic	3	2.20	2.57	0.20	89.00
Quadratic	4	4.53	3.93	0.09	93.08
Intercept	1	-8.83	20.35	<0.01	0.00

Models are ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c). Shown for each model are the number of parameters (k), the maximum log-likelihood (LL), the difference in AIC_c for each model from the top-ranked model (ΔAIC_c), AIC_c weight ($w\text{AIC}_c$), and the percent deviance explained (%DE) in the response variable (TL).

All detrended SPUE were first standardised according to the expression $y' = y + 1.1 \max(\text{abs}(y))$ to remove negative values that can be problematic for ML estimation.

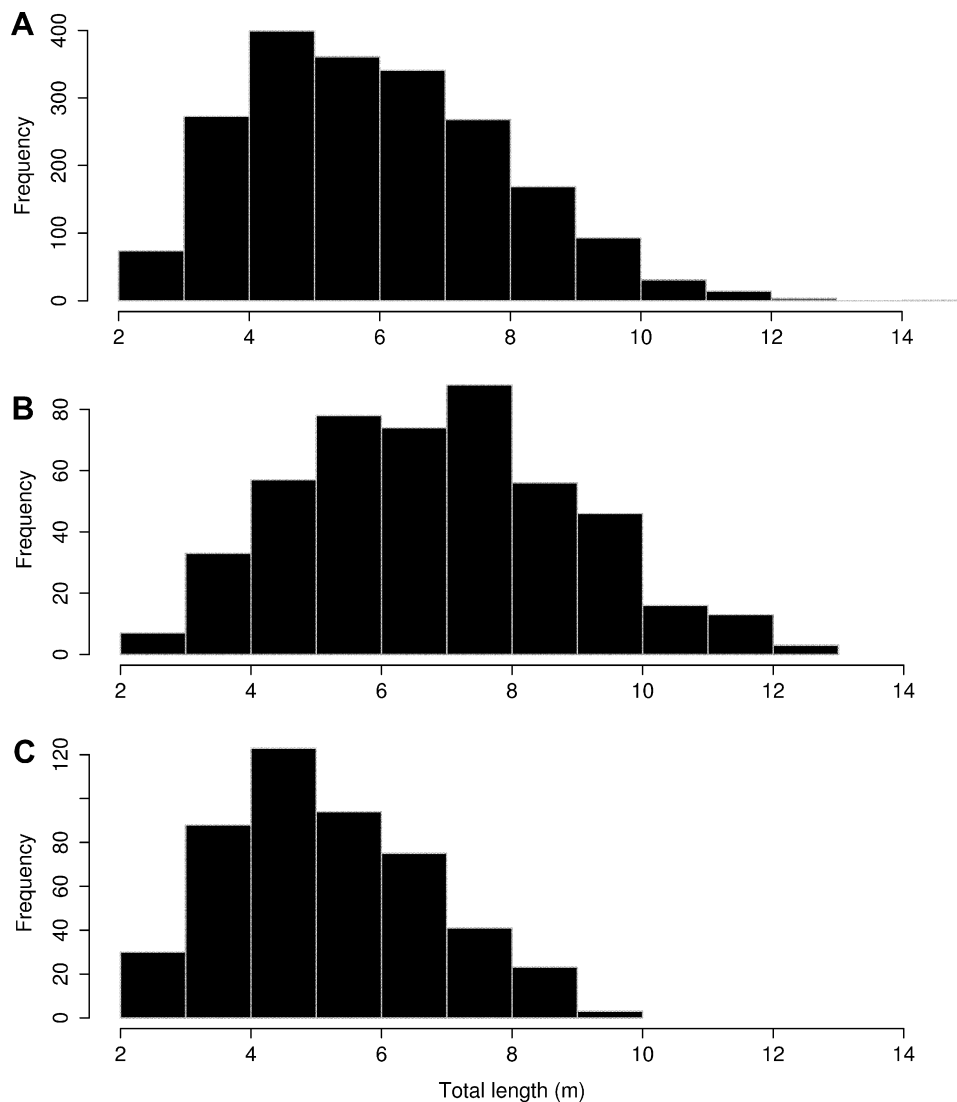


Fig. 1 – Estimated total length (TL in m) distribution for whale sharks seen at Ningaloo from (A) 1995–2004, (B) only 1995–1996 and (C) only 2003–2004. There is a noticeable loss of larger individuals in the more recent distribution.

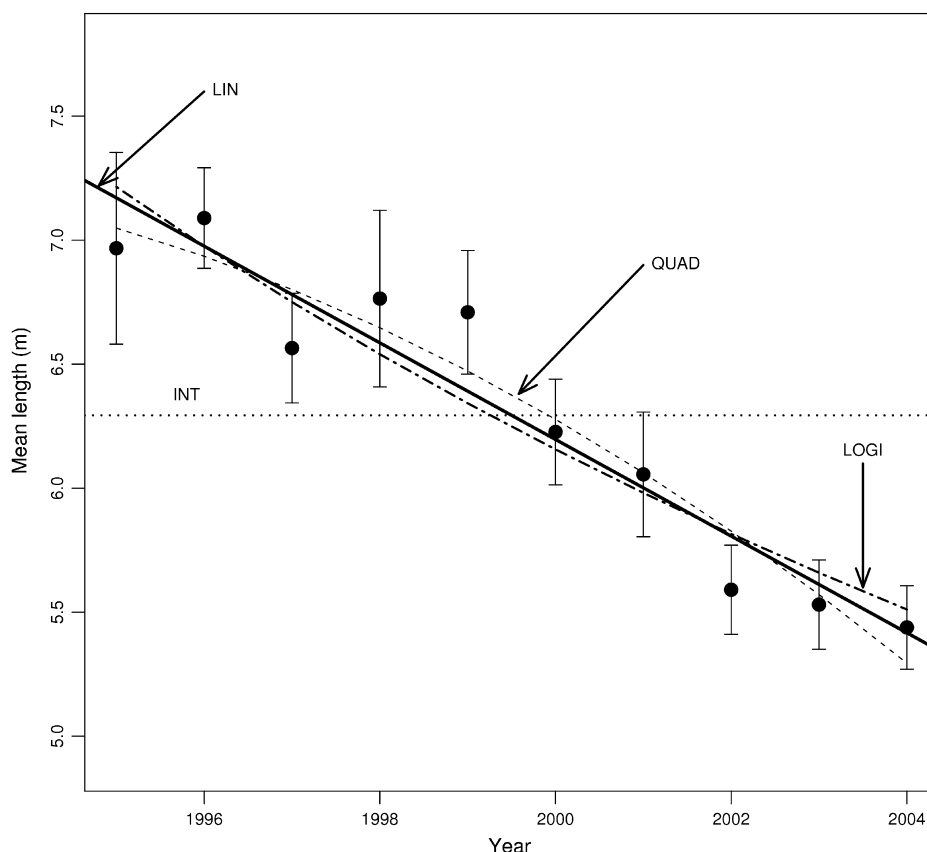


Fig. 2 – Mean length ($\pm 95\%$ bootstrapped confidence intervals based on 10,000 iterations to account for non-normal data in some years) of all whale sharks observed at Ningaloo Reef from 1995 to 2004. Information-theoretic model rankings indicated highest support for a linear decline (LIN) against the quadratic (QUAD) and logistic (LOGI) models. Relative to any of these models of decline, the intercept model (INT), characterising a stable population, had no support.

Table 2 – Comparison of general linear models (GLM) examining the relationship between total length (TL) and temporal variables for whale sharks at Ningaloo Reef from 1995 to 2004

Model	k	LL	Δ BIC	wBIC	%DE
<i>(A) Year and month only</i>					
TL ~ year/month	4	-3646.06	0.00	0.72	9.99
TL ~ year	3	-3650.87	2.12	0.25	9.51
TL ~ 1	2	-3741.51	175.90	<0.01	0.00
TL ~ month	3	-3741.47	183.32	<0.01	<0.01
<i>(B) Year, month and sex</i>					
TL ~ sex + year	4	-2676.01	0.00	0.51	11.33
TL ~ sex + year/month	5	-2672.44	0.07	0.49	11.80
TL ~ sex + year/month + year/month * sex	7	-2671.63	12.84	<0.01	11.91
TL ~ year	3	-2686.35	13.49	<0.01	9.94
TL ~ sex	3	-2749.52	139.83	<0.01	0.99

(A) TL versus year and month, and (B) Five top-ranked GLMs examining the relationship between year, month and sex and TL. Models are ranked according to the Bayesian Information Criterion (BIC). Shown for each model are the number of parameters (k), the maximum log-likelihood (LL), the difference in BIC for each model from the top-ranked model (Δ BIC), BIC weight (wBIC), and the percent deviance explained (%DE) in the response variable (TL).

Table 3 – Comparison of general linear models (GLM) examining the relationship between total length (TL) and temporal variables for whale sharks at Ningaloo Reef from 1995 to 2004

Model	k	LL	Δ BIC	wBIC	%DE
<i>(A) Year and day-of-year only</i>					
TL ~ year	3	-3650.87	0.00	0.74	9.51
TL ~ year/doy	4	-3648.18	2.12	0.26	9.78
TL ~ 1	2	-3741.51	173.78	<0.01	0.00
TL ~ doy	3	-3740.55	179.35	<0.01	0.11
<i>(B) Year, day-of-year and sex</i>					
TL ~ sex + year	4	-2676.01	0.00	0.91	11.33
TL ~ sex + year/doy	5	-2674.69	4.56	0.09	11.51
TL ~ sex + year/doy + year/doy * sex	7	-2671.90	13.37	<0.01	11.87
TL ~ year	3	-2686.35	13.49	<0.01	9.94
TL ~ sex	3	-2749.52	139.83	<0.01	0.99

A. TL versus year and day of year (doy), and B. Five top-ranked GLMs examining the relationship between year, doy and sex and TL. Models are ranked according to the Bayesian Information Criterion (BIC). Shown for each model are the number of parameters (k), the maximum log-likelihood (LL), the difference in BIC for each model from the top-ranked model (Δ BIC), BIC weight (wBIC), and the percent deviance explained (%DE) in the response variable (TL).

3. Results

A total of 4436 sightings provided 2411 unique (per day) sightings of whale sharks from 1995 to 2004, of which 1333 records had estimates of TL and sex. The overall length-frequency distribution was moderately right-skewed (Fig. 1A) as is expected for a largely juvenile aggregation (Meekan et al., 2006; Bradshaw et al., 2007). Comparing the length-frequency distribution from 1995 to 1996 (Fig. 1B) to that from 2003 to 2004 (Fig. 1C) shows a marked shift of the frequency distribution to one dominated by smaller (<6 m TL) individuals with few large representatives (Fig. 1C). This can also be shown as a temporal trend; the annual mean estimates of TL showed a strong linear decline with year, explaining over 91% of the deviance (%DE) (Table 1; Fig. 2). In 1995, whale sharks averaged 7.0 m TL (95% 10,000 iterations bootstrapped confidence interval: 6.5–7.4 m), but by 2004, sharks averaged only 5.4 m (5.2–5.6 m; Fig. 2). There was moderate support for the logistic model (Akaike's Information Criterion weight [$wAIC_c$] = 0.20); however, the increase in %DE using the logistic against the linear was minor (<3%; Table 1). This implies that the decline

is being driven by the faster disappearance of the remaining largest individuals – a result consistent with hypothesis that an anthropogenic source of mortality is driving the decline. Using all data (i.e., not just annual means), we found strong support for a nested year/month effect on TL, but nearly no support for a month effect alone on %DE (Table 2). Including the sex term in the reduced dataset improved model fit slightly (Table 2), but the relatively small improvement in the % deviance explained (1.8%) suggested that its effect was negligible (i.e., no major size differences between males and females). Replacing the month factor for the day of year covariate changed the model rankings only marginally and overall %DE was similar (Table 3). The linear mixed-effects models (GLMMs) used to account for potential trends within vessels demonstrated that the model $TL \sim year/month$ remained the most highly ranked ($wBIC = 0.58$), indicating a decline in TL even after accounting for any observer bias (i.e., bias accounted for by partitioning the variance among vessels in the random effect).

Total numbers of sharks observed from year to year varied by nearly an order of magnitude, with peaks in the 1996 and

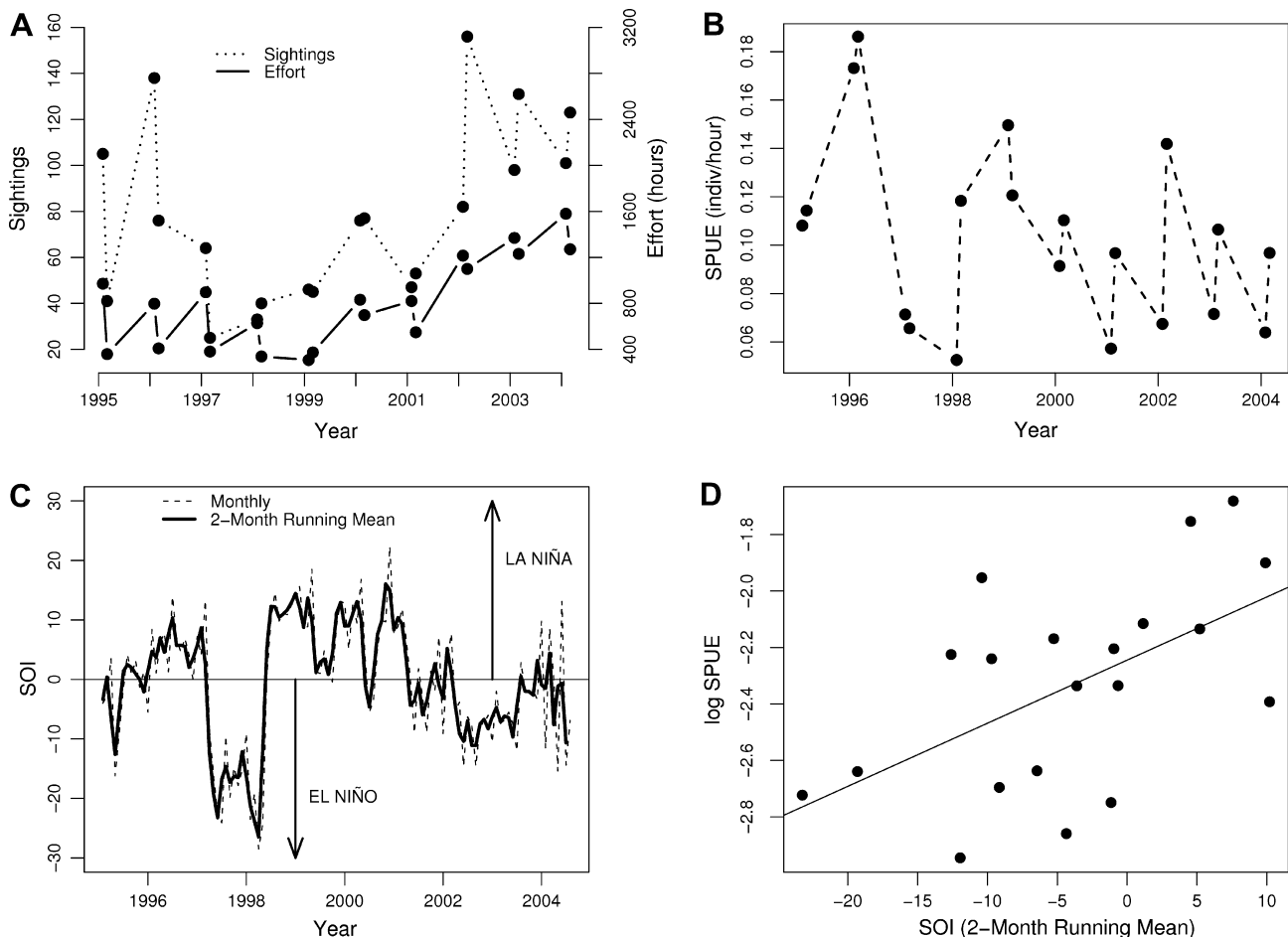


Fig. 3 – (A) Total number of sharks seen at Ningaloo Reef in April and May from 1995 to 2004 after removing individuals seen more than once per day, and total vessel search time (h) as an index of effort; **(B)** Relative abundance corrected for effort (sightings per unit effort = SPUE); **(C)** Monthly and two-monthly running mean of the Southern Oscillation Index (SOI) from 1995 to 2004. High positive values are indicative of La Niña conditions, whereas low negative values signal El Niño events; **(D)** Linear relationship between the two-monthly running mean of SOI and log SPUE for all individuals combined (information-theoretic evidence ratio [ER] = 10.6 times more support than the no-change model; $R^2 = 0.28$).

2002 seasons, and lows in 1998 (Fig. 3A). Search effort (number of search hours by vessels) was also variable (Fig. 3A) and tended to increase through time. The sightings per unit effort (SPUE) appeared to decline through time, albeit with substantial annual variation (Fig. 3B). The relationship between SPUE and the SOI was strongly supported (AIC_c evidence ratio [ER] = 10.6; $R^2 = 0.28$; Fig. 3D), such that during years characterised by cooler El Niño events (low SOI; Fig. 2C), relatively fewer sharks were seen by tourist operators. This provides clarity on the earlier work demonstrating a possible relationship between whale shark abundance and ENSO-related climatic variation (Wilson et al., 2001). SOI-detrended SPUE for all sharks combined demonstrated a gradual decline from 1995 to 2004 (ER = 2.4; $R^2 = 0.16$) – tourist operators saw approximately 40% fewer sharks per hour of searching in 2004 than in 1995. This population-level result confirms life history-based predictions of decline at Ningaloo Reef (Bradshaw et al., 2007). There was no discernible reduction in SOI-detrended SPUE for small individuals (small males: ER = 0.4; $R^2 < 0.01$; small females: ER = 0.3; $R^2 < 0.01$; Fig. 4A, C), but both large male (ER = 6.0; $R^2 = 0.25$; Fig. 4B) and large female (ER = 39.8; $R^2 = 0.38$; Fig. 4D) SPUE declined substantially over the study interval, suggesting that the overall decline is driven mainly by a loss of larger individuals rather than a change in the number of smaller individuals (cf. Figs. 1 and 2).

The relative contribution of intrinsic versus extrinsic control in the various age–sex classes provides insight into the possible mechanisms driving the observed decline. For all individuals combined ($\bar{r} = -0.015$, $\hat{\sigma}^2 = 0.24$), the Gompertz-logistic (GL) versus exponential (EX) model ranking was equivocal (little support for the GL versus EX models: ER = 1.2; Table 4; and mean r and estimated variance were $\bar{r} = -0.08$, $\hat{\sigma}^2 = 0.27$, respectively); however, there was moderate support for a density-dependent GL relationship (ER = 2.7; Table 4) for large males (Fig. 5), suggesting a possible negative feedback control. Large female SPUE had higher relative support for the EX model (ER = 2.8; Table 4), reinforcing the hypothesis of a deterministic reduction ($\bar{r} = -0.03$, $\hat{\sigma}^2 = 0.16$) in the large females.

4. Discussion

Our results are derived from one of the largest-ever databases compiled for whale sharks. They provide empirical confirmation at the population level of the vital rate predictions of Bradshaw et al. (2007), who argued that apparent survival probability combined with plausible reproductive rates predict a declining population. While it is possible that the observed trends in mean size and relative abundance could be driven by permanent emigration of larger animals away from Ningaloo rather than an increased mortality rate,

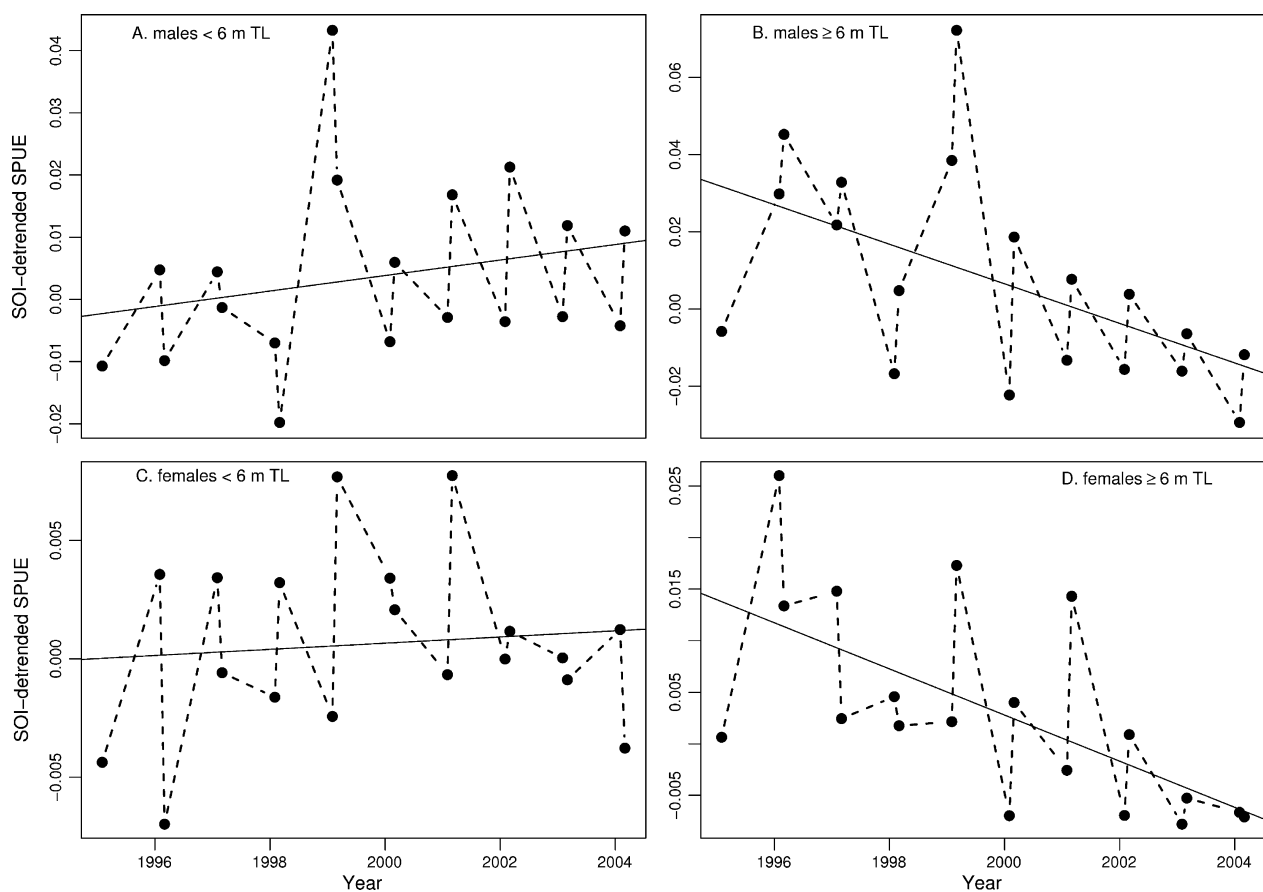


Fig. 4 – Southern Oscillation Index (SOI)-detrended whale shark sightings per unit effort (SPUE) for (A) small (<6 m total length) males (evidence ratio [ER] = 0.4; $R^2 < 0.01$), (B) large (≥ 6 m TL) males (ER = 6.0; $R^2 = 0.25$), (C) small females (ER = 0.3; $R^2 < 0.01$) and (D) large females (ER = 39.8; $R^2 = 0.38$).

Table 4 – Comparison of two population dynamical models (Gompertz-logistic and exponential) describing the relationship between rate of change in Southern Oscillation Index (SOI)-detrended whale shark sightings per unit effort (SPUE) for (A) all individuals combined, (B) large (≥ 6 m total length) males only and (C) large females only. Models are ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c)

Model	k	LL	ΔAIC_c	$wAIC_c$
(A) All individuals				
Gompertz	3	-3.75	0.00	0.54
exponential	2	-6.31	0.31	0.46
(B) Large males only				
Gompertz	3	-2.43	0.00	0.73
exponential	2	-5.81	1.97	0.27
(C) Large females only				
exponential	2	-3.88	0.00	0.74
Gompertz	3	-2.51	2.06	0.26

Shown for each model are the number of parameters (k), the maximum log-likelihood (LL), the difference in AIC_c for each model from the top-ranked model (ΔAIC_c), and AIC_c weight ($wAIC_c$).

photo-identification data suggest that the Ningaloo aggregation is comprised of mainly non-transient individuals (Meekan et al., 2006). In other words, individuals residing at Ningaloo for a few weeks or months per year return regularly over time, at least at the decadal scale. This supports the conclusion that current survival rates are insufficient to maintain population stability or increase (Bradshaw et al., 2007).

The pronounced linear reduction in mean size we report here provides a robust empirical confirmation of previous results (based on a much reduced sample) that larger individuals are being lost from the Ningaloo Reef aggregation (Meekan et al., 2006). The rapid reduction in mean size we observed over a decade and the greater support for a linear model without tapering support the hypothesis of a rapid, deterministic mortality source such as harvesting. The latter evidence for exponential decline does also rely to some extent on the degree of measurement error associated with the SPUE time series. We could not assess the magnitude of potential measurement error, so we provide the caveat that if it is high in the whale shark CPUE time series, estimates of r and their relationship to relative abundance may be biased. However, high measurement (observation) error tends to overinflate

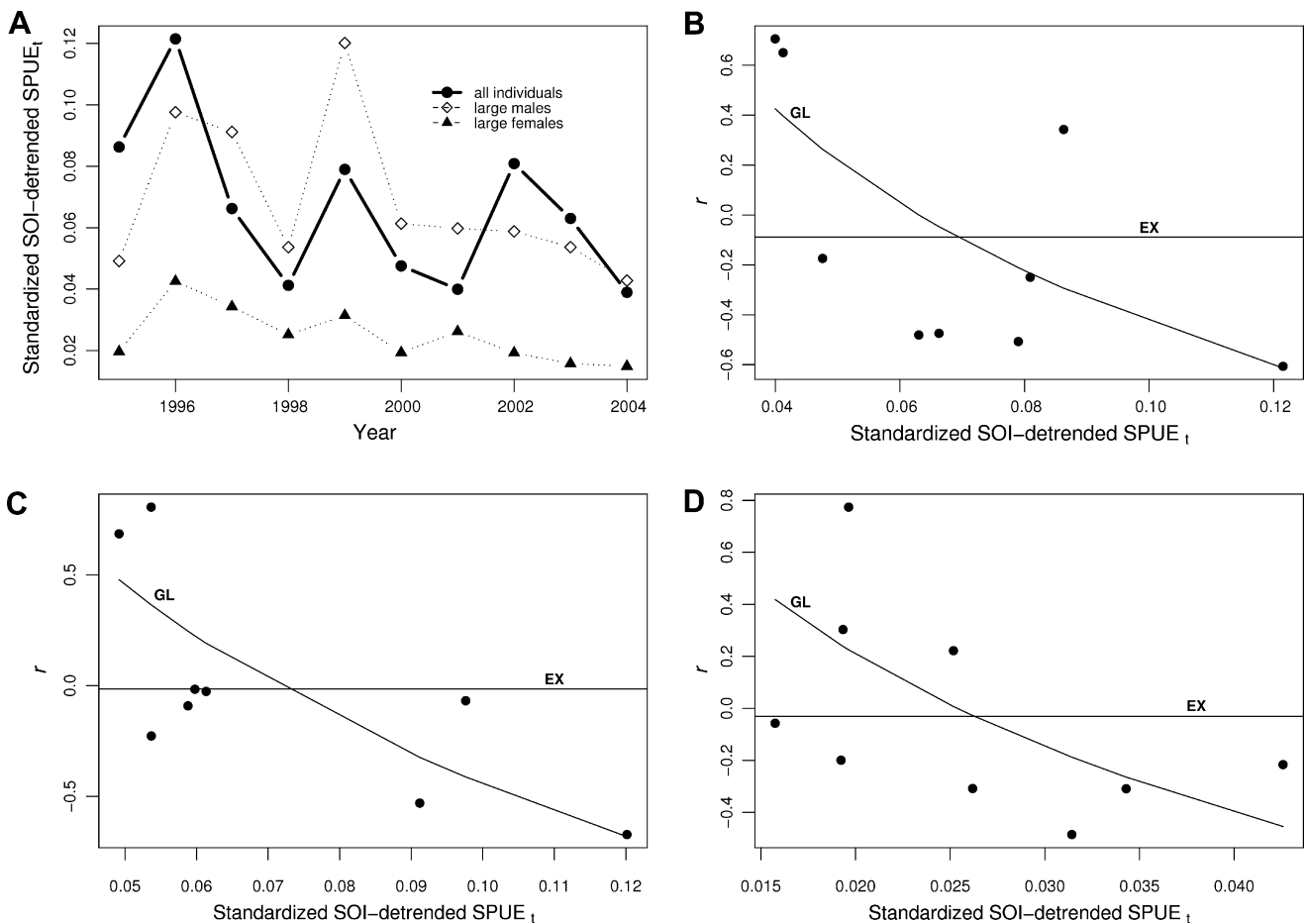


Fig. 5 – (A) SOI-detrended SPUE versus year for all individuals combined, large (≥ 6 m total length) males only, and large females only; (B) SOI-detrended SPUE rate of change and standardised SPUE according to the Gompertz-logistic (GL) and exponential (EX) dynamical models; (C) The same relationship for large males only. (D) The same relationship for large females only. Model results are presented in Table 4.

the evidence for density-feedback models (Freckleton et al., 2006), so the support of the exponential model suggests any possible bias was low. Another potential source of error is that trending populations can mask some of the evidence for endogenous mechanisms (Brook and Bradshaw, 2006), especially if the time series does not represent a large variation in densities (Strong, 1986). However, none of the SPUE declines measured were precipitous (r varied from -0.015 to -0.03 for large males and females, respectively), so we expect little undue bias. Although alternative hypotheses, such as an increase in ship-strike (Speed et al., 2008) or entanglement rates, or genetic changes and re-equilibration of population density to shifting climate patterns, cannot be rejected given the relatively short time series available, the long generation time of whale sharks (>14 years; Bradshaw et al., 2007) suggests that genetic and abiotic factors would likely drive a much more gradual body size trend than the one we observed over a single decade. Furthermore, recent evidence that the incidence of scarring in whale sharks does not correlate well with relative mortality rates (Speed et al., 2008) suggests that non-targeted sources of anthropogenic mortality are unlikely to account for the large changes observed.

In Australia, whale sharks are protected by government legislation and are not fished or caught incidentally (Davis et al., 1997). However, satellite tracking and genetic data have shown that this species has a propensity to migrate large distances (i.e., in the order of 1000s of kilometres; Eckert et al., 2002; Wilson et al., 2006; Bradshaw, 2007; Castro et al., 2007), implying that the geographical range of Ningaloo whale sharks is large and potentially encompasses much of Southeast Asia and the Indian Ocean. These lines of evidence – decline in relative abundance driven mainly by the disappearance of large individuals in less than a single whale shark generation, lack of evidence for a re-equilibration in mean body size, and long-distance migratory capacity – all lend support to the view that unsustainable mortality sources are occurring outside of Australia's jurisdiction. The most likely candidate is the whale shark fishery of Southeast Asia (IUCN-SSC Shark Specialist Group, 2002). The commercial harvest of whale sharks principally supplies markets in Taiwan, where fins (preferably from large individuals) are used for soup and the flesh is sold for human consumption (Chen and Phipps, 2002). Demand has driven increased fishing effort at aggregation sites throughout the Indian Ocean and Asia (Chen et al., 1997; Pravin, 2000), although Taiwan recently announced its decision to halt commercial harvest of the species. Although many countries now have prohibited or reduced commercial harvest in recent years, there is little enforcement of regulation and it seems likely that considerable illegal and legal exploitation of whale sharks still continues throughout much of Asia (Fowler, 2000).

5. Conclusions and conservation remarks

Our hypothesis that the trend observed is driven largely by over-harvesting throughout the species' range within Southeast Asia and the Indian Ocean is also consistent with declines in abundance and change in the size composition of other exploited animal populations worldwide (Ricker, 1981;

Pauly et al., 1998; Stokes and Law, 2000; Tenhumberg et al., 2004). The support for the alternative hypothesis, that the decline results from an ocean-wide regime shift or climate change, is comparatively weak. Indeed, the long time series (relative to generation length) normally required to detect subtle changes in population trends (Gerrodette, 1987) leads us to conclude that the mechanisms driving the observed decline in whale sharks are particularly pronounced. The recent cessation of one of the last remaining commercial harvests of whale sharks in Taiwan will most likely increase the average survival probability of whale sharks in the region; however, it is unlikely that the benefits of this shift in policy will be manifested in whale shark abundance patterns for some time given the relatively slow vital rates of this large species (Bradshaw et al., 2007) and unquantified illegal and artisanal harvests elsewhere. We predict, therefore, that the downward trend in relative abundance and mean body size will continue for the foreseeable future.

Given the higher statistical likelihood that exploitation, rather than natural climate cycles, is the principal driver of the decline in abundance and body size of the world's largest fish, the precautionary principle argues for the adoption of more proactive and internationally directed conservation efforts (Bradshaw, 2007). Although whale sharks are entirely protected in Australian waters, the seasonal outward migration of the Ningaloo population outside of Australian jurisdiction demonstrates that the observed population trend cannot be reversed by protection in only isolated parts of the species' range. Conservation of whale sharks will require international collaboration to reduce overall fishing mortality, potentially at the scale of entire ocean basins, and more tagging studies to identify migration pathways will be a vital part of this effort. Continued monitoring of relative abundance patterns, body size distributions and demographic parameters via capture-mark-recapture studies at all major aggregation sites are also important components of an ocean-wide approach to manage this species.

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REFERENCES

- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299, 389–392.

- Baum, J.K., Kehler, D., Myers, R.A., 2005. Robust estimates of decline for pelagic shark populations in the northwest Atlantic and Gulf of Mexico. *Fisheries* 30, 27–30.
- Bradshaw, C.J.A., 2007. Swimming in the deep end of the gene pool – global population structure of an oceanic giant. *Molecular Ecology* 16, 5111–5113.
- Bradshaw, C.J.A., Mollet, H.F., Meekan, M.G., 2007. Inferring population trends for the world's largest fish from mark-recapture estimates of survival. *Journal of Animal Ecology* 76, 480–489.
- Brook, B.W., Bradshaw, C.J.A., 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87, 1445–1451.
- Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortés, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K., Simpfendorfer, C.A., 2005a. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries* 30, 19–26.
- Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortés, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K., Simpfendorfer, C.A., 2005b. Reply to “Robust estimates of decline for pelagic shark populations in the Northwest Atlantic and Gulf of Mexico”. *Fisheries* 30, 30–31.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York, USA. pp. 488.
- Burnham, K.P., Anderson, D.R., 2004. Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33, 261–304.
- Caputi, N., Fletcher, W.J., Pearce, A., Chubb, C.F., 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research* 47, 147–155.
- Castro, A.L.F., Stewart, B.S., Wilson, S.G., Hueter, R.E., Meekan, M.G., Motta, P.J., Bowen, B.W., Karl, S.A., 2007. Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). *Molecular Ecology* 16, 5183–5192.
- Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F., Clobert, J., 2008. Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology* 77, 135–144.
- Chen, V.Y., Phipps, M.J., 2002. Management and Trade of Whale Sharks in Taiwan. TRAFFIC East Asia-Taipei, Taipei, Taiwan.
- Chen, C.-T., Liu, K.-M., Joung, S.-J., 1997. Preliminary report on Taiwan's whale shark fishery. *TRAFFIC Bulletin* 17, 53–57.
- CITES, 2002. CITES Appendix II nomination of the Whale Shark, *Rhincodon typus*. Proposal 12.35. CITES Resolutions of the Conference of the Parties in effect after the 12th Meeting, Santiago, Chile.
- Conover, D.O., Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297, 94–96.
- Davis, D., Banks, S., Birtles, A., Valentine, P., Cuthill, M., 1997. Whale sharks in Ningaloo Marine Park – managing tourism in an Australian marine protected area. *Tourism Management* 18, 259–271.
- de Little, S.C., Bradshaw, C.J.A., McMahon, C.R., Hindell, M.A., 2007. Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. *BMC Ecology* 7, 3.
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish and Fisheries* 4, 25–64.
- Eckert, S.A., Dolar, L.L., Kooyman, G.L., Perrin, W., Rahman, R.A., 2002. Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology* 257, 111–115.
- Food and Agriculture Organisation of the United Nations, 2006. The State of the World Fisheries and Aquaculture 2006, FAO, Rome.
- Fowler, S.L., 2000. Whale Shark *Rhincodon typus*. Policy and research scoping study. Nature Conservation Bureau, Newbury, United Kingdom.
- Freckleton, R.P., Watkinson, A.R., Green, R.E., Sutherland, W.J., 2006. Census error and the detection of density dependence. *Journal of Animal Ecology* 75, 837–851.
- Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 969–981.
- Gerrodette, T., 1987. A power analysis for detecting trends. *Ecology* 68, 1364–1372.
- Graham, R.T., Roberts, C.M., 2007. Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. *Fisheries Research* 84, 71–80.
- Greenstreet, S.P.R., Rogers, S.I., 2006. Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. *ICES Journal of Marine Science* 63, 573–593.
- Heyman, W.D., Graham, R.T., Kjerfve, B., Johannes, R.E., 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* 215, 275–282.
- IUCN-SSC Shark Specialist Group, 2002. The Role of CITES in the Conservation and Management of Sharks, IUCN, Gland, Switzerland.
- Jennings, S., Kaiser, J., 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34, 201–352.
- Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B* 265, 333–339.
- Jennings, S., Greenstreet, S.P.R., Reynolds, J.D., 1999. Structural change in exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* 68, 617–627.
- Lenanton, R.C., Joll, L., Penn, J., Jones, K., 1991. The influence of the Leeuwin Current on coastal fisheries of Western Australia. *Journal of the Royal Society of Western Australia* 74, 101–114.
- Link, W.A., Barker, R.J., 2006. Model weights and the foundations of multimodel inference. *Ecology* 87, 2626–2635.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science* 63, 1373–1385.
- Meekan, M.G., Bradshaw, C.J.A., Press, M., McLean, C., Richards, A., Quasnicka, S., Taylor, J.G., 2006. Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series* 319, 275–285.
- Morrow, R., Birol, F., 1998. Variability in the southeast Indian Ocean from altimetry-forcing mechanisms for the Leeuwin Current. *Journal of Geophysical Research-Oceans* 103, 18529–18544.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., Rosenberg, A.A., 1995. Population dynamics of exploited fish stocks at low population levels. *Science* 269, 1106–1108.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846–1850.
- Norman, B.M., 1999. Aspects of the biology and ecotourism industry of the whale shark *Rhincodon typus* in north-western Australia. MPhil Thesis, Murdoch University, Perth, Australia.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. *Science* 279, 860–863.

- Pearce, A.F., Griffiths, R.W., 1991. The mesoscale structure of the Leeuwin Current: a comparison of laboratory models and satellite imagery. *Journal of Geophysical Research* 96, 16-739-716-757.
- Pearce, A.F., Phillips, B.F., 1988. ENSO events, the Leeuwin Current and larval recruitment of the western rock lobster. *Journal du Conseil International pour l'Exploration de la Mer* 45, 13-21.
- Pravin, P., 2000. Whale shark in the Indian coast – need for conservation. *Current Science* 79, 310-315.
- Ratner, S., Lande, R., 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. *Ecology* 82, 3093-3104.
- R Development Core Team, 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B* 272, 2337-2344.
- Ricker, W.E., 1981. Change in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1636-1956.
- Robbins, W.D., Hisano, M., Connolly, S.R., Choat, J.H., 2006. Ongoing collapse of coral-reef shark populations. *Current Biology* 16, 2314-2319.
- Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* 62, 384-396.
- Sibert, J., Hampton, J., Kleiber, P., Maunder, M., 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* 314, 1773-1776.
- Smith, S.E., Au, D.W., Show, C., 1998. Intrinsic rebound potential of 26 species of Pacific sharks. *Marine and Freshwater Research* 49, 663-678.
- Speed, C.W., Meekan, M.G., Rowat, D., Pierce, S., Marshall, A.D., Bradshaw, C.J.A., 2008. Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology* 72, 1488-1503.
- Stergiou, K., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. *Fisheries Research* 55, 1-9.
- Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476-494.
- Stokes, K., Law, R., 2000. Fishing as an evolutionary force. *Marine Ecology Progress Series* 208, 307-309.
- Strong, D.R., 1986. Density-vague population change. *Trends in Ecology and Evolution* 1, 39-42.
- Taylor, G., 1994. *Whale Sharks*. Angus and Robertson Publishers, Sydney, Australia.
- Taylor, J.G., 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* 47, 637-642.
- Tenhumberg, B., Tyre, A.J., Pople, A.R., Possingham, H.P., 2004. Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? *Ecology* 85, 2003-2017.
- Terborgh, J., Winter, B., 1980. Some causes of extinction. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Ecological-Evolutionary Perspective*. Sinauer, Sunderland, MA, pp. 119-134.
- Theberge, M.M., Dearden, P., 2006. Detecting a decline in whale shark *Rhincodon typus* sightings in the Andaman Sea, Thailand, using ecotourist operator-collected data. *Oryx* 40, 337-342.
- Turchin, P., 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ, USA.
- Walker, T.I., 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* 49, 553-572.
- Walters, C., 1995. Estimation of historical stock sizes and recruitment anomalies from relative abundance time-series. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 1523-1534.
- Walters, C.J., Martell, S.J.D., 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, NJ.
- Wilson, S.G., Taylor, J.G., Pearce, A.F., 2001. The seasonal aggregation of whale sharks at Ningaloo reef, western Australia: currents, migrations and the El Niño/Southern oscillation. *Environmental Biology of Fishes* 61, 1-11.
- Wilson, S.G., Polovina, J.J., Stewart, B.S., Meekan, M.G., 2006. Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology* 148, 1157-1166.
- Yang, G.-J., Bradshaw, C.J.A., Whelan, P.I., Brook, B.W., 2008. Importance of endogenous feedback controlling the long-term abundance of tropical mosquito species. *Population Ecology*. doi:10.1007/s10144-008-0082-8.