



Changes in size distributions of commercially exploited sharks over 25 years in northern Australia using a Bayesian approach

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ARTICLE INFO

Article history:

Received 14 October 2011

Received in revised form 10 March 2012

Accepted 12 March 2012

Keywords:

Bayesian model averaging

Carcharhinus

Exploitation

Fisheries

Recovery

ABSTRACT

Long-term vital rate and life-history data essential for sustainable harvest management are rare in tropical fisheries. Two commercially important shark species, Australian blacktip (*Carcharhinus tilstoni*) and spot-tail (*C. sorrah*) sharks in northern Australia have changed in size and population status over the last 25 years. These populations were exploited heavily from the early 1970s to the mid-1980s by foreign fishers, and since then have been harvested by a relatively small domestic fishery. We examined the differences in fork length of these species caught in 1983–1985 and 2002–2006 using Bayesian forms of generalised linear and mixed-effects models. We found clear regional differences and changes in size over time. For blacktips, sharks from the Gulf of Carpentaria have become smaller, and those from the western Northern Territory, larger over time. For spot-tail sharks, average size increased from the 1980s in the Gulf of Carpentaria, but not in the western Northern Territory. On average, sharks from the Gulf of Carpentaria were larger than those on the west coast of the Northern Territory, and females were larger than males. We suggest that changes over time and between regions in the size of spot-tail sharks are most likely due to over-exploitation in the past and subsequent recovery of populations. We discuss the uncertainty in trends for blacktip sharks in relation to fishing effort, availability of resources and species identification errors.

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1. Introduction

The effects of over-fishing reach far beyond the relatively simple reduction of yields (FAO, 2006); over-exploitation of certain species within complex marine ecosystems can disrupt important biological processes, thereby exacerbating population declines of the target and collateral species (Dulvy et al., 2003; Jennings and Kaiser, 1998; Myers et al., 1995; Reynolds et al., 2005). Over-exploitation, leading to a reduction in population size from harvesting, is often only identified after it has already occurred by measuring declin-

ing catches and/or increasing effort (Hilborn and Walters, 2001). Further, the subtle biological implications of over-exploitation are also typically overlooked, with managers focusing more on the fishery than the status of the remaining fishes themselves. For example, high fishing effort can disproportionately remove particular size classes via gear selectivity (Walker et al., 1998), thus altering age structure, age at maturity, or growth patterns (Jennings and Kaiser, 1998). Indeed, such changes in size distributions are some of the most important determinants driving extinction risk of harvested species (Jennings et al., 1998, 1999; Reynolds et al., 2005). Changes in these attributes have been suggested as indicators of over-exploitation (Greenstreet and Rogers, 2006; Rochet et al., 2000).

Over-fishing has led to population declines and in some cases, the commercial collapse of many economically important fish species. In the last few decades there has been much controversy

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regarding the underlying causes of fishery collapses (Hutchings and Reynolds, 2004; Reynolds et al., 2005), but there is now a substantial body of evidence demonstrating that shark species are highly susceptible due to their slow replacement rates relative to teleost (bony) fishes (Dulvy et al., 2008; Field et al., 2009b). For most fisheries that catch sharks, not only are the causes uncertain, so too are the magnitudes of the population declines (Baum et al., 2005; Burgess et al., 2005; Robbins et al., 2006; Stevens et al., 2000a; Walker, 1998). The implications of removing these top-order predators and the potential effects on marine ecosystem function are poorly understood and as yet unresolved (Coll et al., 2006; Jackson et al., 2001; Myers et al., 2007; Stevens et al., 2000a; Walker, 1998; Ward and Myers, 2005; Worm et al., 2006). This uncertainty is particularly acute in tropical systems such as those in northern Australia.

As with many fisheries, the history of shark exploitation in northern Australia is complex. From the early 1970s until the mid-1980s, a Taiwanese pelagic gill-net fleet operated in the waters around northern Australia targeting shark, longtail tuna (*Thunnus tonggol*) and Spanish mackerels (*Scomberomorus* spp.) (Stevens and Davenport, 1991). The size and largely unmanaged nature of the gill-net fleet caused concern over potential over-exploitation of shark (and other aquatic animal) populations in the region (Stevens and Davenport, 1991). This motivated the Australian Fisheries Service at the time to reduce substantially the maximum allowable length of surface-set drift nets, causing the industry to abandon its endeavours largely for economic reasons (Stevens and Davenport, 1991).

The areas around northern Australia accessible to the Taiwanese fleets changed over time. During its initial years of operation, the area fished by the Taiwanese gill-net fleet was unclear, but the advent of mandatory reporting following the implementation of the Australian Fishing Zone (AFZ) in 1979, shows that foreign fishing (gill-net and long-line) in north Australian waters was mainly offshore from approximately 22 km off the coast from the North West Shelf to north of the Gulf of Carpentaria. Prior to 1979, there were no quotas for catches; the average total annual catch was 17,000 tonnes. Once restrictions came into force in 1979 with the implementation of the AFZ, an annual quota for the gill-net fleets was set to 7000 tonnes (Fig. 1). Taiwanese long-line catch data are poor, but between February 1990 and September 1991, 1700 tonnes of shark were landed by eight Taiwanese long-liners. Before 1980, reporting of catch and effort was limited (Walter, 1981). However afterwards, basic catch composition, catch and effort data were collected by both Taiwanese and independent logbook programmes. These records indicated that total catch composition by weight was approximately 80% shark species, with blacktip (primarily *Carcharinus tilstoni*, with an unknown proportion of *C. limbatus*) and spot-tail (*C. sorrah*) sharks accounting for 60% of the total catch (Stevens and Davenport, 1991). During the early 1980s, the fishing effort almost doubled, while catch per unit effort (CPUE) decreased from 16 to 7 kg/km/h (Stevens and Davenport, 1991). Further restrictions were imposed in 1986, leading to the fishery's abandonment. However, Taiwanese long-lining and gill-netting continued outside the Australian Fishing Zone until 1991, albeit at reduced rates.

In the early 1980s, a small (order of magnitude smaller than the Taiwanese take) domestic Australian shark fishery was developed within inshore waters (Fig. 1). The fishery was concentrated around the Northern Territory, harvesting between 100 and 485 tonnes annually from 1984 to 1988 (Stevens and Davenport, 1991), but subsequently extended to Western Australia and Queensland. Shark resources in the Australian Fishing Zone were only moderately exploited until 1979 when Taiwanese long-lining vessels started fishing, taking around 3500 tonnes in the first year (Fig. 1; Stevens and Davenport, 1991). This sudden increase in the

northern shark fishery generated considerable research directed toward improving management capacity (Davenport and Stevens, 1988; Lyle, 1984, 1987; Lyle and Griffin, 1987; Lyle et al., 1984; Lyle and Timms, 1984; Stevens and Church, 1984; Stevens and Wiley, 1986). Despite the demonstration that a domestic pelagic fishery could be economically viable and sustainable (Lyle and Timms, 1984), data from the Taiwanese gill-net fleet suggested some signs of over-exploitation (Stevens and Davenport, 1991). Some signs included a decrease in the proportion of mature *C. tilstoni* caught from 1981 to 1986, although no such trend was observed for *C. sorrah* (Stevens and Davenport, 1991). Furthermore, the median size of the sharks caught decreased for both *C. tilstoni* and female *C. sorrah*.

Currently, a small tropical shark fishery, the Offshore Net and Line (NTONL) fishery, operates in the Northern Territory (DEH, 2005). In this fishery, which targets various sharks and grey mackerel (*Scomberomorus semifasciatus*), catches have increased slowly from 1984 to the present, so that there are now 17 licences held by 7–9 vessels that currently catch approximately 1089 tonnes of fish annually (NTDPFIM, 2005). The fishery's primary target species is grey mackerel, followed by blacktip and spot-tail sharks, and a variety of secondary shark species including tiger (*Galeocerdo cuvier*), pignoreye (*C. amboinensis*) and spinner sharks (*C. brevipinna*). An increase in catch per unit effort and in the proportional catch of non-primary target shark species from 2000 to 2003 prompted questions regarding the industry's future sustainability (NTDPFIM, 2005). In response, management changes were put in place to reduce fishing effort and halt the industry's growth. Currently, grey mackerel dominates in terms of single-species catch (NTDPFIM, 2005). Research projects to address concerns about sustainability were implemented in 2004. These included fisheries observation (Field et al., 2008; NTDPFIM, 2005), risk assessments to determine the sustainability of shark and rays around northern Australia (Salini, 2007), and tagging studies. The influence of illegal fishing in the region is unclear; however, most is thought to occur farther offshore from the coastal fisheries, and it is unlikely to have affected shark populations greatly in the Gulf of Carpentaria (Field et al., 2009a).

Since the studies of the 1980s, there have been no subsequent analyses of catch composition and size data of these shark populations to assess the status of the fishery. Specifically, we aimed to (1) compare catch compositions between the 1980s and recently (2002–2007), and (2) determine if there have been any changes in overall length of sharks from an over-exploited population during Taiwanese fishing operations, compared to the relatively small fishery of the present. We used a Bayesian model-averaging approach to account for the effects of sex, season and water depth. Recent molecular evidence suggests that shark populations of western Northern Territory and the Gulf of Carpentaria are genetically distinct (Ovenden, 2007), so we also examined the data for differences between geographic regions.

2. Methods

2.1. Shark catches

From 1983 to 1985, approximately 10,500 sharks were tagged and released from locations all around northern Australia (Stevens et al., 2000b). Species and sex of each shark were recorded and fork length measured (± 5 mm). More recently (October 2002 to May 2007), we collected species composition and length data as part of a number of observer and tagging studies, including the NTONL fishery observer and tagging programme and the FRDC project (Salini, 2007) to determine the sustainability of sharks and rays commercially caught in northern Australia. In both latter studies, fisheries observers recorded the catch composition and size of individual

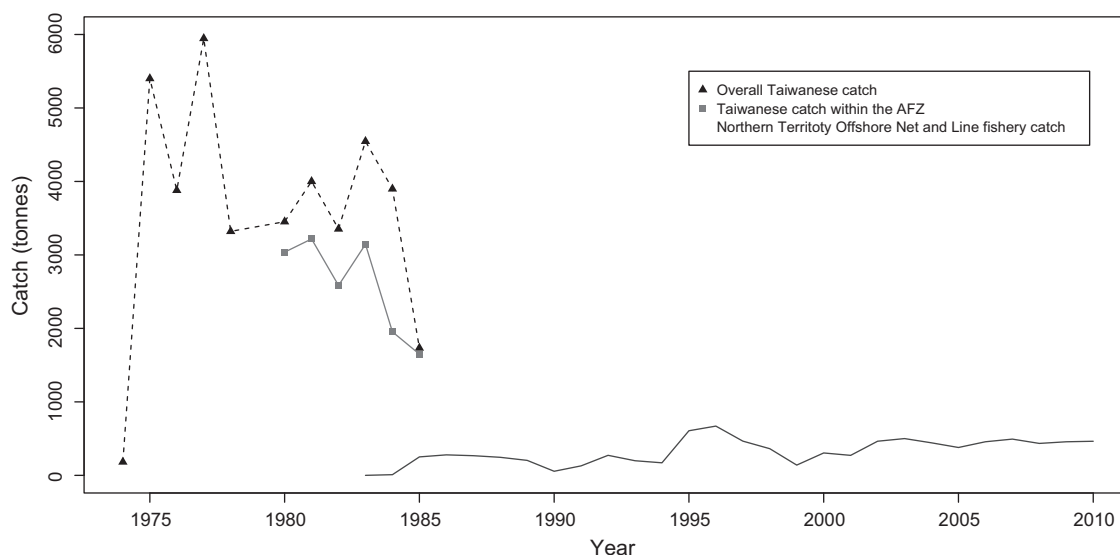


Fig. 1. Catches of blacktip and spot-tail sharks by the Taiwanese fleet from 1974 to 1978 (\blacktriangle) based on catch records described in Stevens and Davenport (1991), and by the recent Northern Territory Offshore Net and Line fishery from 1983 to 2010 (\bullet). Also shown are catches of sharks within the Australian Fisheries Zone by the Taiwanese fleet from 1979 to 1985 (\blacksquare) based on fishery observations (Stevens and Davenport, 1991).

sharks caught on commercial fishing vessels around the Northern Territory. Fork and total lengths were measured (± 5 mm).

To compare datasets collected in the 1980s (CSIRO) to recent ones (=FRDC & NT), we limited our analyses to those sharks caught within comparable areas during the two periods (Fig. 2) and using the same fishing gear. Due to regional genetic differences within the two shark species' (blacktip and spot-tail sharks) populations in the Gulf of Joseph Bonapart and the Gulf of Carpentaria (Ovenden, 2007), we examined whether size distributions also differed between regions. The size of net mesh and gear type can influence the size of sharks caught, so we limited our analyses to sharks caught using same gear sizes (i.e., 6-in. [~ 165 mm] mesh commercial gillnet). We identified twenty-four different shark species; however, we only compared common species (those that accounted for $>5\%$ of the total catch – only blacktip and spot-tail sharks) for all analyses.

2.2. Analysis

To test whether there was a difference in the catch composition of blacktip and spot-tail sharks between the two time periods, we tested whether the proportions of the total catch for these two species changed, using a 2×2 G-test of independence (contingency analysis) in the R Package (R Development Core Team, 2011).

Even in large fisheries datasets, unequal sample sizes and can lead to heterogeneity issues. We therefore used a hierarchical statistical design to optimise our analyses. To negate sample size differences and incorporate model uncertainty, especially when trying to examine the distribution-free effects of region, time of capture and sex on shark size (fork length), we developed a Bayesian model-averaging approach (Hoeting et al., 1999) using generalised linear mixed-effects models. Bayesian models do not force any prior model assumptions regarding error distributions, with posterior distributions for parameters not pre-specified. Shark size can vary between sexes and has been found to increase with distance from shore and water depth (Heupel et al., 2004; Stevens et al., 2000b). Because water depth is also a proxy for distance from shore, we incorporated depth as a fixed effect and considered all interactions with *time* (the sampling periods), *sex* and *region*. We divided the dataset by season, coded as a random factor, to account for shark growth over the sample periods. Here, 'season' refers to

the wet (October to March) and dry seasons (April to September). Data were not available for *C. tilstoni* across all months during the sampling, so we were obliged to regress to generalised linear models for that species. However, it was essential to account for the non-independence of sharks within *season* for *C. sorrah* to partial the variances appropriately.

Each model in the set represented specific hypotheses about the drivers of variation in shark size. We used similar Bayesian (uninformed, flat, i.e., $-\infty$ to ∞ , and uniform) priors for each parameter with error distributions not specified. We then ranked those models using Bayesian model-averaging weights (BMA_w), which is analogous to other Bayesian or deviance information criteria (Wintle et al., 2003), and used these posterior weights to estimate model-averaged parameter estimates. This approach gives a coherent and conceptually simple way to take account of model uncertainty, or uncertainty about statistical structure when making inferences (Hoeting et al., 1999), and it provides better average predictive performance than any single model that could be selected.

For both species, we started by constructing a total of 18 generalised linear models derived from the saturated form:

$$\mu_i = \beta_0 + \beta_1 time_i + \beta_2 sex_i + \beta_3 region_i + \beta_4 time_i sex_i + \beta_5 time_i region_i + \beta_6 sex_i region_i$$

where μ_i = fork length (cm) for i to n sharks in the sample, β_i = parameter coefficients. Models (M) are constructed as M_1, M_2, \dots, M_{18} with parameter sets = $\theta^1, \theta^2, \dots, \theta^{18}$ (each θ^k is a vector). We set parameter priors as $p(\theta^1|M_1), p(\theta^2|M_2), \dots, p(\theta^{18}|M_{18})$, and model priors as models $p(M_1), p(M_2), \dots, p(M_{18})$, with precision parameters given a gamma distribution. Likelihoods of data x are then

$$p(x|\theta^1, M_1), p(x|\theta^2, M_2), \dots, p(x|\theta^{18}, M_{18}),$$

with joint posterior probability

$$p(\theta^k, M_k|x) \propto p(x|\theta^k, M_k) p(\theta^k, M_k) p(M_k).$$

After the initial modelling phase, we determined whether the unexplained residual spatial and temporal variation observed could be explained, in part, by the addition of depth. For spot-tail sharks for which we had enough data, we used the most parsimonious generalised linear model (highest model weight) to construct

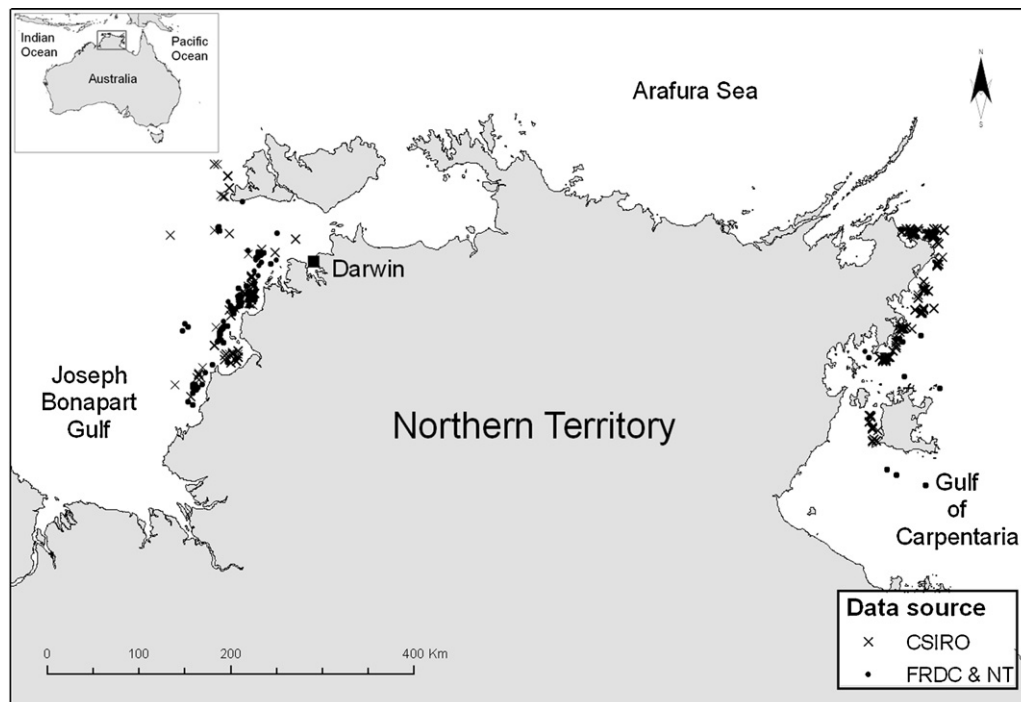


Fig. 2. Areas of overlapping data from the Australian Government's Commonwealth Scientific and Industrial Research Organisation's (CSIRO) tagging study in the 1980s and the recent Northern Territory Offshore Net and Line fishery observer programme, 2004 Fisheries Research and Development Corporation Phase 2 project and current ongoing tagging study (FRDC & NT). Insert box shows the location of the study area.

generalised linear mixed-effects models including depth with their interactions in the fixed effects, while including season as a random effect. For blacktip sharks, the uncertainty of model support for a single model or suite of models supporting similar terms and the reduced sample size across factor levels prevented the inclusion of depth and season into the model structure. This uncertainty might be due to the misidentification of *C. tilstoni* with its larger close relative *C. limbatus*, the larger pan-tropical blacktip shark (Ovenden, 2007). The inadvertent inclusion of an unknown number of *C. limbatus* specimens with *C. tilstoni* in catch data could bias the size measurements, although the magnitude of this potential bias is unknown. For spot-tail sharks, we therefore constructed a total of 26 models derived from the saturated form with similar parameters to the previous 18 generalised linear model set:

$$\begin{aligned} \mu_{it} = & \beta_0 + \beta_1 \text{time}_{it} + \beta_2 \text{sex}_{it} + \beta_3 \text{region}_{it} + \beta_4 \times \text{time}_{it} \text{sex}_{it} \\ & + \beta_5 \text{time}_{it} \text{region}_{it} + \beta_6 \text{sex}_{it} \text{region}_{it} + \beta_7 \text{depth}_{it} \\ & + \beta_8 \text{depth}_{it} \text{time}_{it} + \beta_9 \text{depth}_{it} \text{sex}_{it} + \beta_{10} \text{depth}_{it} \text{region}_{it} \\ & + (1 | \text{season}_t) \end{aligned}$$

where μ_{it} = fork length (cm), β = parameter coefficients, and $1 | \text{season}_t$ is a random effect.

We did all analyses in WinBUGS (Lunn et al., 2000) using Markov Chain Monte Carlo (MCMC) simulation and the Gibbs variable selection sampler (Dellaportas et al., 2002; Dellaportas and Karlis, 2001). Our WinBUGS codes are included as online supplementary materials. Each model averaging run used five chains, with the initial 5000 iterations discarded for burn-in, followed by 50,000 iterations to reach convergence that was checked with a further 5000 iterations. We only considered model terms found in models with greater than 95% of the total Bayesian model-averaging weight to calculate model-averaged posterior shark size estimates. We present parameter coefficients and estimates for the terms in the suite of supported models to indicate the average shark size and magnitude (mean \pm SD) and direction of influence for each term.

3. Results

3.1. Overall catch composition

A total of 4119 sharks were caught and measured (Table 1) from 25 species in the two sampling periods in the west coast of the Northern Territory and the western Gulf of Carpentaria combined ($n_{1980s} = 1654$; $n_{current} = 2465$). Two species dominated the catch: Australian blacktip and spot-tail sharks and accounted for $\sim 75\%$ of the total number of sharks caught (Fig. 3). However, there was a decrease in the proportions of these two species from the 1980s to the 2000s. There was evidence for a change in the proportion of species caught (G -test of independence Type I error $P = 0.0034$): the proportion of blacktips declined from 56 to 42%, and from 29 to 27% for spot-tails (Table 1).

3.2. Shark lengths

Overall, it appeared that the blacktip and spot-tail sharks (Table 1 and Fig. 4) caught in the 1980s were similar in size to those caught more recently. However, when analysed to account for sex and region, there were clear differences between regions and between sexes in fork length for both species (Tables 2 and 3 and Fig. 5). Generally, sharks were larger in the western Gulf of Carpentaria than on the west coast of the Northern Territory, and females were larger than males. It is also noteworthy that in both periods, few male individuals caught of either species were over 1100 (blacktips) and 825 mm (spot-tails) – the species-specific lengths of maturity reported by Stevens and Wiley (1986). There are a number of interacting effects for each species' model set that we describe below.

For blacktip sharks, the six models with the greatest support included *region*, *time* and *sex* terms, and an interaction between region and time. These three variables accounted for $>96\%$ of the total model weight (Table 2; parameter coefficients and

Table 1
The mean fork length for all species and measured by the CSIRO tagging study by the 1980s and during the Fisheries Research and Development Corporation observer program (Project No. 2002/064) and Northern Territory shark tagging study since 2002, in overlapping regions using 6-in. (165 mm) mesh pelagic gill nets.

Common name	Scientific name	<i>n</i>		Mean fork length (mm ± SD)		Minimum fork length (mm)		Maximum fork length (mm)	
		CSIRO	FRDC & NT	CSIRO	FRDC & NT	CSIRO	FRDC & NT	CSIRO	FRDC & NT
Australian blacktip shark	<i>Carcharhinus tilstoni</i>	922	1027	863 ± 178	782 ± 176	493	440	1322	1510
Blacktip reef shark	<i>Carcharhinus melanopterus</i>	–	3	–	820 ± 80	–	740	–	900
Bull shark	<i>Carcharhinus leucas</i>	–	6	–	742 ± 92	–	650	–	890
Common blacktip shark	<i>Carcharhinus limbatus</i>	–	1	–	1630	–	1630	–	1630
Creek whaler	<i>Carcharhinus fitzroyensis</i>	9	76	805 ± 102	737 ± 87	615	585	958	990
Fossil shark	<i>Hemipristis elongatus</i>	2	20	1006 ± 23	978 ± 110	990	790	1022	1160
Graceful shark	<i>Carcharhinus amblyrhynchoides</i>	18	1	927 ± 98	910	722	910	1129	910
Great hammerhead	<i>Sphyrna mokarran</i>	8	17	1362 ± 174	1115 ± 413	1135	740	1620	2010
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	1	12	631	923 ± 161	631	610	631	1220
Hardnose shark	<i>Carcharhinus macloti</i>	104	19	657 ± 37	631 ± 36	486	540	727	690
Lemon shark	<i>Negaprion acutidens</i>	–	1	–	1790	–	1790	–	1790
Milk shark	<i>Rhizoprionodon acutus</i>	57	70	649 ± 41	654 ± 66	416	400	705	740
Narrow sawfish	<i>Anoxypristis cuspidata</i>	1	78	1620	1743 ± 447	1620	930	1620	2810
Pigeon shark	<i>Carcharhinus amboinensis</i>	3	98	1115 ± 431	769 ± 188	778	500	1600	1290
Scalloped hammerhead	<i>Sphyrna lewini</i>	13	117	1114 ± 274	931 ± 276	674	500	1433	1910
Sharpnose shark	<i>Rhizoprionodon taylori</i>	2	1	527 ± 168	760	408	760	645	760
Spinner shark	<i>Carcharhinus brevipinna</i>	4	117	766 ± 165	734 ± 83	616	560	946	960
Spot-tail shark	<i>Carcharhinus sorrah</i>	483	670	743 ± 91	752 ± 97	505	460	1003	1070
Tiger shark	<i>Galeocerdo cuvier</i>	–	2	–	1315 ± 332	–	1080	–	1550
Weasel shark	<i>Hemigaleus microstoma</i>	–	1	–	650	–	650	–	650
Whitecheek shark	<i>Carcharhinus dussumieri</i>	20	8	628 ± 31	676 ± 109	555	585	680	930
Whitespotted guitarfish	<i>Rhynchobatus australiae</i>	–	3	–	907 ± 342	–	680	–	1300
Whitetip Reef shark	<i>Triaenodon obesus</i>	–	1	–	1000	–	1000	–	1000
Winghead shark	<i>Eusphyra blochii</i>	7	116	902 ± 83	868 ± 195	805	490	1065	1260

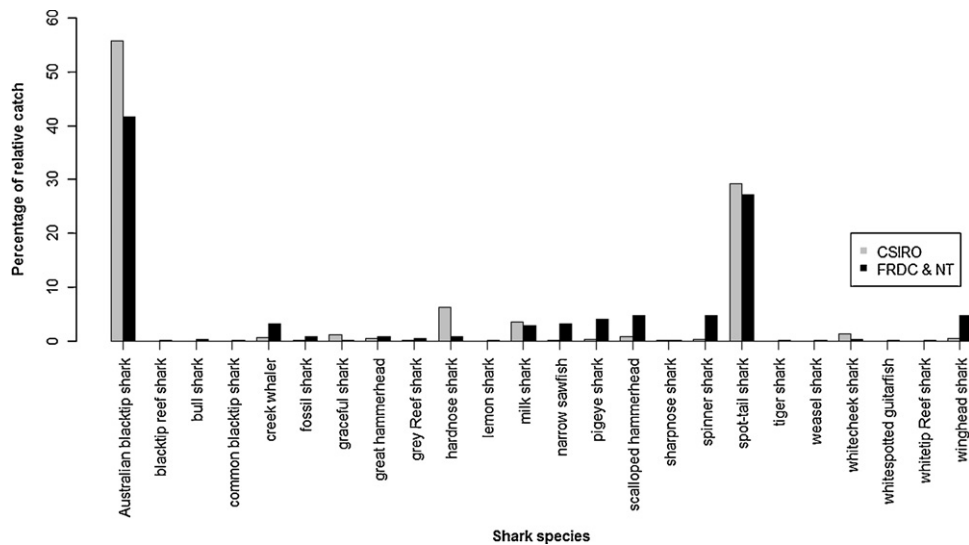


Fig. 3. Catch composition: (%) of sharks caught in the 1980s (CSIRO) and recently (FRDC & NT) in the two overlapping regions using 165-mm mesh.

estimates for the supported models are presented in Table 4). On average, sharks were larger in the western Gulf of Carpentaria (supported in all six models), but the region × time interaction (from two models with combined model weights ~34%) showed that Gulf sharks have become smaller and western Northern Territory sharks, larger. Also, from three of the models with lesser support (combined weights of 27%), females were larger than males.

In the initial Bayesian model averaging (18 models) for spot-tail sharks, the model with the greatest support (86%) contained time, sex, region and the time × region interaction. The second- and third-ranked model added sex × region and time × sex interactions, but only contributed ~20% of the model weight. To reduce further uncertainty in the Bayesian model averaging (using 26 models including depth and season effects and their potential interactions to the most parsimonious model) we again found region, sex and time differences (Table 3) accounting for the influence of depth and season. The three top-ranked models accounted for ~94% of

the total model weight (parameter coefficients in Table 4). This indicated that overall, individuals tended to be larger in the Gulf, females were larger than males, and those caught recently were larger than in the 1980s. Interactions demonstrated that females in the Gulf were relatively larger than in the past (but not in the western Northern Territory), and that there was a trend of increasing size for females in the different regions. Males remained similarly sized over time in the western Northern Territory, but became larger in the Gulf of Carpentaria.

Table 2

Strength of support for the effects of time (t), sex (s) and region (r) and their interactions (denoted by ‘×’) to explain variation in fork length of blacktip sharks (C. tilstoni) caught in Northern Territory waters by Bayesian model averaging of generalised linear models. Shown are the Bayesian model-averaging weight (BMA_w) and standard deviation of BMA_w for each model (SD). The model weights indicate the strength of evidence for any individual model relative to the entire model set and provide evidence for which terms are most influential.

Model	BMA _w	SD
~r	0.323	0.468
~t+r+t×r	0.273	0.446
~s+r	0.170	0.376
~t+r	0.091	0.288
~t+s+r+t×r	0.077	0.267
~t+s+r	0.041	0.198
~s+r+s×r	0.011	0.102
~t+s+r+t×r+s×r	0.005	0.068
~t+s+r+t×s+t×r	0.004	0.065
~t+s+r+s×r	0.003	0.050
~t+s+r+t×s	0.002	0.046
~t+s+r+t×s+t×r+s×r	0.000	0.021
~t+s+r+t×s+s×r	0.000	0.014
~intercept	0.000	0.000
~t	0.000	0.000
~s	0.000	0.000
~t+s	0.000	0.000
~t+s+t×s	0.000	0.000

Table 3

Strength of support for the effects of time (t), sex (s) and region (r), and including depth (d), and season (sn) to explain variation in fork length of spot-tail sharks (C. sorrah) caught in Northern Territory waters. Interactions are denoted by ‘×’. Season is a random effect in the generalised linear mixed-effect model structure (1|sn) Shown are the Bayesian model-averaging weight (BMA_w) and standard deviation of BMA_w for each model (SD). The model weights indicate the strength of evidence for any individual model relative to the entire model set and provide evidence for which terms are most influential.

Model	BMA _w	SD
~t+s+r+t×r+d+d×t+(1 sn)	0.624	0.485
~t+s+r+t×r	0.207	0.405
~t+s+r+t×r+d+(1 sn)	0.115	0.320
~t+s+r+t×r+d+d×r+(1 sn)	0.016	0.126
~t+s+r+t×r+s×r	0.016	0.125
~t+s+r+t×s+t×r	0.013	0.112
~t+s+r+t×r+d+d×t+d×r+(1 sn)	0.004	0.060
~t+s+r	0.002	0.048
~t+s+r+t×r+d+d×t+d×s+(1 sn)	0.001	0.035
~t+s+r+s×r	0.001	0.026
~t+s+r+t×s+t×r+s×r	0.001	0.025
~t+s+r+t×r+d+d×s+(1 sn)	0.001	0.023
~t+s+r+t×s	<0.001	0.011
~t+s+r+t×r+d+d×t+d×s+d×r+(1 sn)	<0.001	0.008
~t+s+r+t×s+s×r	<0.001	0.008
~intercept	<0.001	<0.001
~t	<0.001	<0.001
~s	<0.001	<0.001
~r	<0.001	<0.001
~t+s	<0.001	<0.001
~t+r	<0.001	<0.001
~s+r	<0.001	<0.001
~t+s+t×s	<0.001	<0.001
~t+r+t×r	<0.001	<0.001
~s+r+s×r	<0.001	<0.001
~t+s+r+t×r+d+d×s+d×r+(1 sn)	<0.001	<0.001

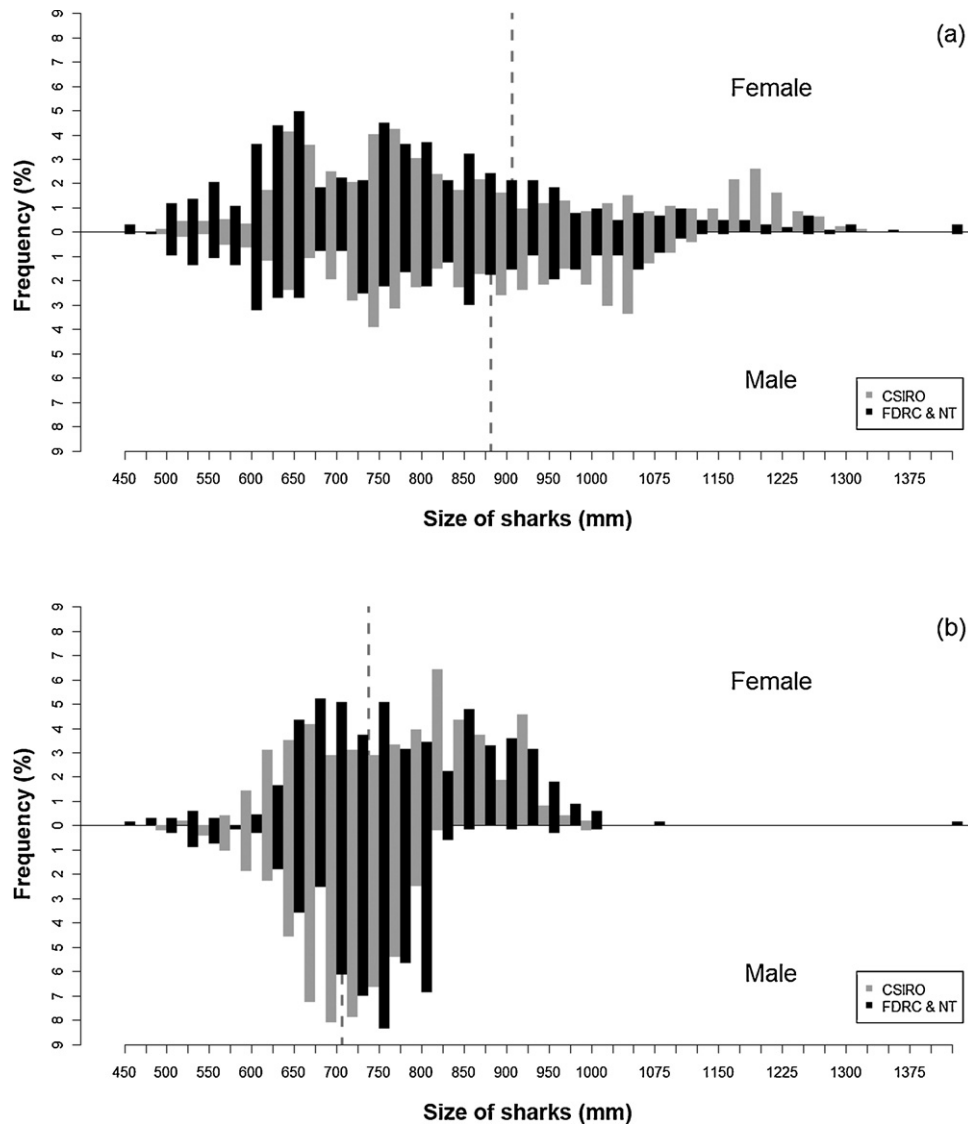


Fig. 4. Fork length size frequency distributions for male and female: (a) Australian blacktip (*C. tilstoni*) and (b) spot-tail (*C. sorrah*) sharks caught in the two overlapping regions using 165-mm mesh. Dashed lines indicate the size of maturity reported by Stevens and Wiley (1986) for males and females of each species.

4. Discussion

Temporal changes in the size of individuals and catch composition provide indices of fisheries over-exploitation and/or recovery (Jennings et al., 1999; Jennings and Kaiser, 1998; Rochet et al., 2000), and changes in catch composition give an indication of community change and ecosystem status (Greenstreet and Rogers, 2006; Jennings and Kaiser, 1998; Shepherd and Myers, 2005). Therefore, monitoring size changes over time can assist in identifying the forces driving observed population trends (Rochet et al., 2000). We observed both an increase in the diversity of shark species caught and greater numbers of larger shark species caught recently, which coincides with a change in fishing pressure (Fig. 1). We also observed changes in size of the fishery's focal shark species, but these differences were not uniform across the species' range, e.g., blacktip sharks in the Gulf of Carpentaria and might be confounded by issues of species misidentification.

Changes in growth rates in response to exploitation have been observed in relatively few shark species compared to teleosts (Walker, 1998; Walker et al., 1998; Daan et al., 2005; Bradshaw et al., 2008; Fenberg & Roy, 2008). Our results show some clear changes in the size of individuals of both the sharks (*C. tilstoni*

and *C. sorrah*) targeted by the north Australian fisheries, regionally and over time. Spot-tail sharks have increased in size throughout their distribution in this study and over time, with the exception of males in the western Northern Territory, although there is some variation in trends of blacktip sharks. We observed a general trend of larger fish being caught in the Gulf of Carpentaria, and of individuals becoming larger on average over time after the cessation of intense exploitation. We hypothesise that the primary reason for the changes in size we observed was the large reduction in exploitation rates after the departure of Taiwanese fishers (Fig. 1), although the spatio-temporal complexities we observed complicate simple conclusions about temporal patterns. This highlights the necessity of incorporating potential explanatory factors in a multi-model inferential framework like the one adopted here to account for model and parameter estimate uncertainty (Burnham and Anderson, 2002).

For both commercially important species, the size of individuals varied mainly between regions. After controlling for gear differences, both *C. tilstoni* and *C. sorrah* were larger in the Gulf of Carpentaria than in the western Northern Territory, although the difference between regions was not as pronounced for the

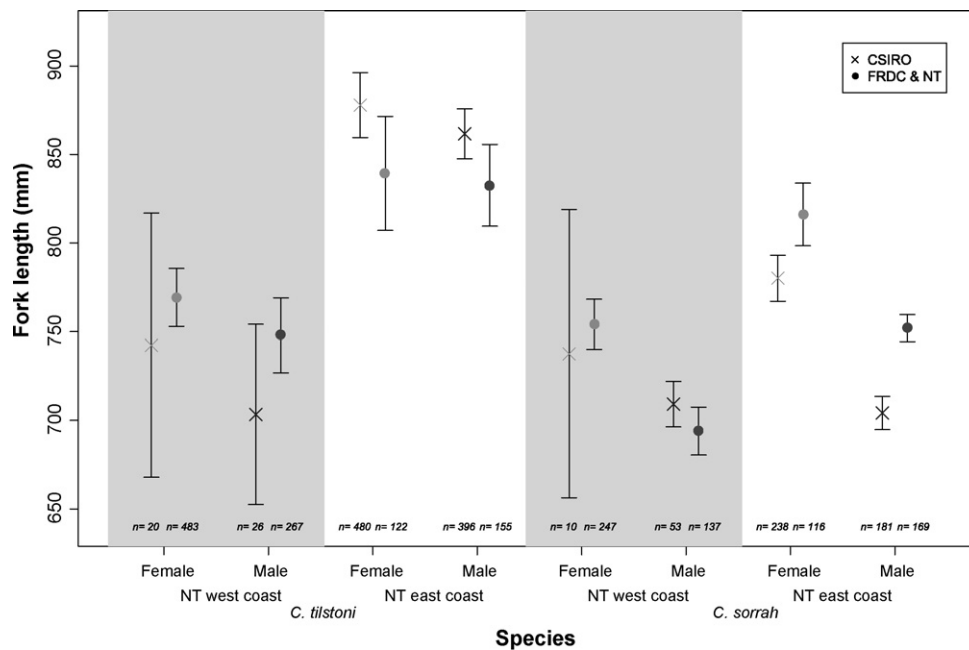


Fig. 5. Spatial differences in mean fork length (mm; error bars indicate ± 2 SE) for male and female Australian blacktip (grey background) and spot-tail sharks caught in the two overlapping regions using 165-mm mesh in the 1980s (CSIRO) and recently (FRDC & NT). Note: Error bars are only indicative of relative uncertainty and do not necessarily reflect the partial residual variances estimated in the Bayesian models.

latter species. This regional difference potentially results for two main, inter-linked reasons: the phenotypic plasticity influenced by the distribution of past fishing effort and food availability, and possible genetic differences. From an exploratory study in the mid-1980s, both blacktip and spot-tail sharks caught in the Gulf of Carpentaria were larger than those caught in Fog and Anson Bays on the west coast of the Northern Territory (Lyle and Timms, 1984), although those authors did not speculate on the reasons for the observed differences. Taiwanese fishing reports indicated that there was extensive fishing across Arnhem Land and western Northern Territory, but comparatively little activity in the Gulf of Carpentaria. Thus, it is entirely plausible that there were localised depletions in the former region causing reductions in mean body size (Stevens and Davenport, 1991; Walker and Hislop, 1998). Similar downward shifts in body size due to over-exploitation have been observed for gummy sharks in southern Australia (Walker et al., 1998).

Table 4

Model-averaged (from entire model set) parameter estimates for black tip and spot-tail sharks. Only terms included in the models that had over 95% of the model weight support from the Bayesian model averaging are shown. For coefficient interpretation, directions indicate the coding: sex (1 = male; 0 = female), time (1 = 1980 s; 0 = 2000 s) and region (1 = Gulf of Carpentaria; 0 = NT west coast).

Species	Parameter symbol	Parameter name	Parameter estimate (mean \pm SD)
Blacktip sharks	β_0	intercept	853.2 \pm 15.8
	β_1	time	15.1 \pm 709.1
	β_2	sex	-5.0 \pm 829.3
	β_3	region	-91.0 \pm 16.7
	β_5	time \times region	-27.3 \pm 802.3
Spot-tail sharks	β_0	intercept	759.8 \pm 39.6
	β_1	time	13.7 \pm 43.6
	β_2	sex	-64.7 \pm 5.5
	β_3	region	-47.6 \pm 13.9
	β_5	time \times region	39.6 \pm 57.6
	β_7	depth	0.6 \pm 487.0
	β_8	depth \times time	-1.5 \pm 611.3
	β_{10}	depth \times region	1.4 \pm 991.2

An alternative driver of the observed changes in size of blacktip sharks could arise from temporal and spatial dynamic patterns of shark distribution, or by misidentification of *C. tilstoni* and *C. limbatus*. Recent genetic analysis has revealed that what once might have been considered *C. tilstoni* catches off the Northern Territory coast are now more likely to be a 'complex' of blacktip species (including both *C. tilstoni* and *C. limbatus*, with some evidence of hybridisation; Ovenden et al., 2010). The magnitude of this potential source of bias is unclear, but it is worthy of consideration. If the catch is still primarily *C. tilstoni* and the observed changes are real, then increase or decreases in size might be due to phenotypic plasticity associated with density-dependent responses of these exploited populations (Sosebee, 2005), or as selection resulting from different fishing histories.

Another driver, and potentially confounding influence, might be the genetic separation of the two populations (Ovenden, 2007) for each of the target species. These genetic differences could have influenced growth and size of maturity due to random genetic drift or selection resulting from different fishing histories. Such genetic differences suggest some regional isolation of populations, which is congruent with the observation that the average long-term movement of these species is only around 50 km (Stevens et al., 2000b). Furthermore, Stevens and Wiley (1986) found no evidence for regional differences in the size of maturity in the past. Therefore, as with our changes in size of these species, we expect to see regional differences in the size of maturity that might partially explain the status of these populations.

Other hypotheses to explain overall regional size differences include the possibility that Fog and Anson Bays in western Northern Territory might be used as nursery areas for blacktip sharks (Lyle and Timms, 1984), or that there is an overall difference in the average productivity between regions. Fewer larger males of both species were caught in this region, supporting the hypothesis that the area is a nursery. Thus, ontogenetic changes in migratory behaviour of adult sharks moving out of the region, rather than differences in vulnerability to the fishing gear, is a more plausible explanation. Also, sharks have become larger in Fog and Anson Bays, with the exception of male spot-tail sharks. If spot-tail growth rates

have increased with reduced fishing, then larger individuals might be expected to disperse from the nursery areas sooner as is the case in other carcharhinid species (Heupel et al., 2004), thus increasing the probability of catching smaller individuals in this area. This could easily be tested by comparing juvenile growth rates between regions.

The western Gulf of Carpentaria is a highly productive region in which the lucrative northern prawn fishery operates (Stobutzki and Mcloughlin, 2007). The increased size for spot-tails and decrease for blacktip sharks in the Gulf of Carpentaria might result from phenotypic differences in response to amount of available food resources. However, no differences in diet have been found between the two regions (Spracklen, 2003; Stevens and Wiley, 1986), although this does not rule out differences in food availability. An additional source of uncertainty is the misidentification of *C. limbatus*, the larger pan-tropical blacktip shark (Ovenden, 2007), with its smaller local close relative, *C. tilstoni*. This larger species is similar in appearance to *C. tilstoni* and matures later (Last and Stevens, 1994). The inadvertent inclusion of an unknown number of *C. limbatus* specimens with *C. tilstoni* in catch data could bias the size measurements (e.g., a higher proportion of *C. limbatus* in the Gulf of Carpentaria would bias size estimates upwards).

For fisheries monitoring programmes it is often difficult to measure the abundance of target species due to the spatial and temporal dynamics of target populations and fishing effort. In these cases where monitoring is difficult, alternative measures of the fisheries effects such as fish length (Walker and Hislop, 1998), can provide useful insights relative to historical baselines, as these rates will have implications for population growth rates and subsequent consequences for community structure and function. From our results, we contend that the general increase in individual size is a positive sign of recovery. Fishing pressure has been greatly reduced since the 1970s by at least an order of magnitude (Fig. 1), so it is plausible that there has been some maintenance or recovery of the commercially targeted shark species under current management. This conclusion does not, however, have any bearing on assessments pertaining to the sustainability of current catch rates.

5. Conclusions

The plausible recovery we report via size changes are contrary to current global trends in many elasmobranch populations, especially in South-East Asian fisheries (Field et al., 2009b; Sodhi et al., 2007). This indication and the relatively pristine marine environment (Halpern et al., 2008) around northern Australia might provide something of a conservation haven for shark diversity in the region, although little is known about other target and by-catch species caught within the fishery. Spatial differences in size trends still need further investigation to understand potential drivers of population change, and conclusions regarding 'sustainability' will require more and better data on the age, size and maturity and diet of sharks caught each year.

Acknowledgements

We thank all the fishers and research staff involved in the CSIRO Northern Pelagics tagging study, Fisheries Research Development Corporation project 2002/064, and the Northern Territory Shark Tagging study for their assistance during tagging and data collection, in particular C. Tarca. The Northern Territory Tagging Study is funded by an Australian Research Council Linkage Grant (LP0667702) to CJAB and MGM, and permitted by the Charles Darwin University Animal Ethics Committee.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.fishres.2012.03.005.

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