

Evaluating catch and mitigating risk in a multispecies, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area

Alastair V. Harry^{A,E}, Andrew J. Tobin^A, Colin A. Simpfendorfer^A,
David, J. Welch^{A,B}, Amos Mapleston^A, Jimmy White^A,
Ashley J. Williams^{A,C} and Jason Stapley^D

^AFishing & Fisheries Research Centre, School of Earth & Environmental Sciences,
James Cook University, Townsville, Qld 4811, Australia.

^BDepartment of Employment, Economic Development and Innovation, PO Box 1085,
Oonoonba, Qld 4811, Australia.

^COceanic Fisheries Program, Secretariat of the Pacific Community, BP D5, 98848,
Noumea, New Caledonia.

^DDepartment of Employment, Economic Development and Innovation,
Northern Fisheries Centre, Cairns, Qld 4870, Australia.

^ECorresponding author. Email: alastair.harry@gmail.com

Abstract. Small-scale and artisanal fisheries for sharks exist in most inshore, tropical regions of the world. Although often important in terms of food security, their low value and inherent complexity provides an imposing hurdle to sustainable management. An observer survey of a small-scale commercial gill-net fishery operating within the Great Barrier Reef World Heritage area revealed at least 38 species of elasmobranch were present in the catch. Of the total elasmobranch catch, 95% was 25 species of Carcharhiniformes from the families Carcharhinidae, Hemigaleidae and Sphyrnidae. Individual species were captured in a variety of ways by the fishery, often with strongly biased sex ratios and in a variety of life stages (e.g. neonates, juveniles, adult). Despite this, the main carcharhiniform taxa captured could be qualitatively categorised into four groups based on similar catch characteristics, body size and similarities in life history: small coastal (<1000 mm); medium coastal (1000–2000 mm); large coastal/semi-pelagic (>2000 mm); and hammerheads. Such groupings can potentially be useful for simplifying management of complex multispecies fisheries. The idiosyncrasies of elasmobranch populations and how fisheries interact with them provide a challenge for management but, if properly understood, potentially offer underutilised options for designing management strategies.

Additional keywords: Carcharhiniformes, coastal shark fishery, elasmobranch.

Introduction

Ongoing worldwide fisheries exploitation continues to fuel a growing debate on the future of wild-caught fisheries (Jackson 2008; Worm *et al.* 2009). Higher trophic-level predators such as elasmobranchs (sharks and rays) have fared particularly poorly, with some collapses, often rapid, of populations where they are targeted or taken as by-catch (Ripley 1946; Olsen 1959; Graham *et al.* 2001; Devine *et al.* 2006). Recently, international concern over the ongoing exploitation of sharks has led to the development of the International Plan of Action for Sharks (FAO 2000). The vulnerability of sharks and rays to overfishing stems largely from their life-history characteristics, including late maturation, low fecundity, low natural mortality and long life-spans (Cortes 2000). These characteristics mean there is a close relationship between stock size and recruitment, and consequently long

recovery times after overexploitation has occurred (Holden 1974).

Other factors, such as naturally low abundance as well as complex migration patterns and spatial usage (e.g. sex segregation, site fidelity; Heupel and Simpfendorfer 2005; Sims 2005), can further increase the vulnerability of some elasmobranchs to overfishing. This is relevant to carcharhiniform sharks, particularly of the families Carcharhinidae and Sphyrnidae, which occur abundantly throughout inshore continental shelf regions of the tropics and subtropics worldwide (Musick *et al.* 2004).

Species of these families vary greatly both in their life histories and their utilisation of inshore habitats (Knip *et al.* 2010). For example, many small to medium-sized carcharhinids (e.g. *Rhizopriondon taylori*, *Carcharhinus sorrah*) remain within inshore areas throughout the duration of their lives. These

species are often fast growing and relatively short lived (Davenport and Stevens 1988; Simpfendorfer 1993). Other carcharhiniform sharks utilise inshore habitats only during discrete stages of their lives. These species are generally larger in size and have moderate to slow growth rates. *Negaprion brevirostris* and *C. leucas* are examples of species that use inshore areas as neonate and juvenile nurseries (Springer 1950; Castro 1993). Conversely, neonates of other species (e.g. *Galeocerdo cuvier*, *Sphyrna mokarran*) are absent from close inshore waters whereas adults are present (Hueter and Tyminski 2007). The wide variety of life-history characteristics and space utilisation means inshore shark populations are likely to be affected in a range of different ways and to varying extents by anthropogenic influences such as fishing.

Artisanal and commercial fisheries for carcharhiniform sharks exist in most equatorial and tropical regions and are particularly common throughout Asia, especially in the Indo-Pacific region and the Indian subcontinent (Kasim 1991; Hanfee 1999; Henderson *et al.* 2007; White 2007), as well as parts of Africa, the Caribbean, and throughout central America (Motta *et al.* 2005), notably Mexico (Castillo-Géniz *et al.* 1998). Despite the important contribution these fisheries make to regional economies and food security, management of such fisheries is often neglected (Fowler *et al.* 2005). Many countries lack the resources to adequately monitor their fisheries (White and Kyne 2010), and even in more affluent states, the inherent low value of inshore shark fisheries often means research and management are given low priority. Where monitoring is conducted, catch composition is rarely established because of the difficulties in identifying many species so, at best, sharks are identified to family or order (Shotton 1999). The paucity of data on most inshore tropical shark fisheries along with wide variation among life histories and complex spatial ecology provides an imposing hurdle to sustainable harvest of carcharhiniform sharks in these fisheries and raises concerns given the vulnerability of elasmobranchs to overfishing.

In tropical northern Australia, carcharhiniform sharks make up large components of several small-scale, inshore fisheries targeting a range of teleost and shark species (Stevens 1999; Salini *et al.* 2007). The low value of tropical shark (AU\$2–3 kg⁻¹ processed weight) means that despite Australia's status as a developed nation, many of these fisheries are similar to those in developing nations: fishing effort is highly fragmented along those coastline; fishing vessels are usually small in size (<7 m); and nets are frequently hauled by hand. Aside from the period between 1974 and 1986 when Taiwanese gill-net vessels targeted sharks off northern Australia, the total harvest of elasmobranchs in Australia's tropical fisheries has been between 2000 and 3000 t year⁻¹ (Bensley *et al.* 2010). While some components of northern Australian shark fisheries have been reasonably well monitored and formal risk assessments or stock assessments have been used to inform management, other areas, including the east coast of Queensland, have received little attention (Anon 1990; Stobutzki *et al.* 2002; Salini *et al.* 2007). This is somewhat surprising given that on the east coast of Queensland, these fisheries occur within the Great Barrier Reef World Heritage Area (GBRWHA), one of the world's largest networks of marine protected areas (GBRMPA 2009).

Changes to legislative requirements concerning sustainability in Australian fisheries (*Environmental Protection and Biodiversity*

Conservation Act 1999, Cth), combined with a 200% increase in shark landings on Queensland's east coast between 1993 and 2004 (Bensley *et al.* 2010) and concern from managers about shark exploitation within the GBRWHA (GBRMPA 2009) recently created a need to describe the shark component of the inshore net fishery. Consequently, between 2006 and 2009 an onboard-vessel observer study recorded the catch composition and harvest practices of the fishery. The aims of this study were to quantify the composition, to species level, of carcharhiniform sharks caught by net fisheries in the GBRWHA and to examine the characteristics of the catch to qualitatively establish patterns of catch susceptibility. To this end, we compared catch rates between three nominal zones (rivers, intertidal and inshore coastal), examined the sex ratio of the catch and compared male and female length-frequency distributions. We discuss emergent patterns in the catch in relation to life-history characteristics and consider the threats to carcharhiniform sharks in the GBRWHA. Given these new data, we also suggest fisheries management strategies aimed at mitigating the risk of overfishing, and we consider the implications for management in data-poor, inshore fisheries for carcharhiniform sharks throughout tropical regions of the world.

Methods

Fishery observer program

Between June 2006 and July 2009, fishery observers monitored vessels operating in the commercial gill-net sector of the Queensland East Coast Inshore Finfish Fishery (ECIFF) within the boundaries of the GBRWHA (between Cape York (10.5°S) and Bundaberg (24.5°S); Fig. 1). Owing to the vast area of the fishery, data were collected simultaneously by two groups, James Cook University Fishing & Fisheries Research Centre and Fisheries Queensland. Data were subsequently combined to provide the most robust dataset. Fisher participation in the observer survey was voluntary. Prior to commencing a trip, the observer interviewed the fisher to determine the length, depth and mesh size of net to be used, so fishing effort could be calculated. Fishing start time for an individual net shot was recorded as the time when the net was completely in the water, and finish time was when hauling of the net began. Location of nets was recorded using a hand-held GPS and depth was measured using an onboard depth-sounder. Catch composition of elasmobranchs was recorded to species level using a species identification key derived from Last and Stevens (1994). Owing to the small-scale nature of the fishery, a single observer assessed each individual trip. When conditions permitted, the stretch-total length, fork length and pre-caudal length (sharks) or disk width (rays) of a subsample of the catch was recorded in mm (Compagno 1984) and weight measured in kg. When possible, sex and maturity stage of sharks processed at sea was also recorded using a standard staging system (Walker 2005a).

Fishery zones

Data were grouped into three broad zones (river, intertidal and inshore coastal) that corresponded to discrete subcomponents of the ECIFF, each with different resident species, targeting and harvest practices and management strategies (Table 1). In river zones, barramundi (*Lates calcarifer*) was targeted using set

nets with stretched mesh sizes of 165–216 mm. Nets were usually set overnight and fishing occurred between February and October. Within intertidal zones (defined as waters <2 m depth), several teleost species (mostly *Eleutheronema tetradactylum*, *Polydactylus macrochir* and species of the family Mugilidae) were targeted using set nets with stretched mesh

sizes of 114–216 mm. Fishing in intertidal zones occurred throughout all periods of the day and throughout the year. Within inshore coastal zones (defined as coastal waters of between 2 and 25 m depth), *Scomberomorus semifasciatus* was targeted during winter and spring, while a generalist shark fishery targeting mainly *Carcharhinus tilstoni* and *C. sorrah* operated throughout the year. Some fishers were licensed to use up to 1200 m of 165 mm stretched mesh net, although most were licensed to use 600 m.

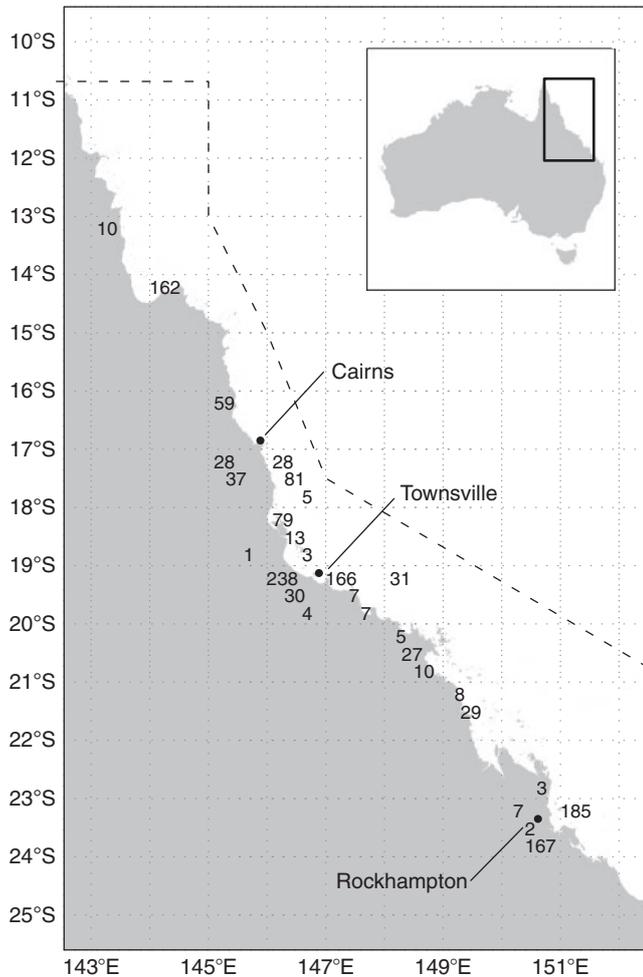


Fig. 1. Study area showing observed fishing effort (km-net-hours) by one degree squares of latitude and longitude. Within each square, observed effort is shown for the three zones: inshore coastal (upper left), intertidal (centre), and river (bottom right). The dashed black line indicates the outer boundary of the Great Barrier Reef World Heritage Area.

Data analysis

Some of the earlier Fisheries Queensland observer trips were primarily focussed on recording teleost catch, so identification of Carcharhinidae and Sphyrnidae species was limited to family level (e.g. ‘whaler shark’). With the exception of overall catch composition (Table 3), these trips were excluded from further analyses, which focussed only on carcharhiniform sharks. Mean length at capture was calculated and, although not all animals were measured, the recorded lengths were assumed to represent a random subsample of the total catch. Mean weight at capture was calculated using length–weight regressions derived from the present study or, if unavailable, from previous studies in northern Australia (Stevens and Lyle 1989; Stevens and McLoughlin 1991). Catch was standardised to number per unit effort (individuals km-net-hour⁻¹) and weight per unit effort (kilograms km-net-hour⁻¹). To further examine characteristics of the overall catch (data pooled between zones), two-sample Kolmogorov–Smirnov (KS) tests were used to test whether length-frequency distributions of males and females of individual species were significantly different. The sex ratio (females/males) of the catch was also calculated and, where there were at least five individuals from each sex, Chi-square tests were used to determine any significant differences in sex ratio. All of the Carcharhiniformes species caught in the present study had a reproductive mode of placental viviparity (except for the tiger shark, *Galeocerdo cuvier*), so the percentage of neonates in the catch could be inferred from the presence of an open or unhealed umbilical scar, thus indicating recent birth. The catch characteristics above were used to qualitatively establish the susceptibility of different species to the fishery. Capture susceptibility was defined as the culmination of factors that result in an individual of a species being killed by the fishery (e.g. availability, encounterability, selectivity). We considered susceptibility in the general sense of the term and no attempt was made to quantify it (e.g. Stobutzki *et al.* 2002). Emergent patterns in the catch were further discussed in relation to the

Table 1. Nominal fishery zones in the East Coast Inshore Finfish Fishery

	River	Intertidal	Inshore coastal
Depth (m)	Any depth	0–2	2–25
Number of nets permitted	3	3	1
Total net length permitted (m)	150–360	600	600 (some to 1200)
Net mesh size (mm)	165–216	114–216	165
Principal target species	<i>Lates calcarifer</i>	<i>Eleutheronema tetradactylum</i> <i>Polydactylus macrochir</i> Mugilidae spp.	<i>Scomberomorus semifasciatus</i> Shark

life-history characteristics of captured species, such as length at 50% maturity, growth characteristics and habitat preferences. Life-history data were obtained from the published literature or, if available, from unpublished data obtained during the present study.

Results

Fishery observer survey

Between June 2006 and July 2009, observers were deployed on 149, often multiday, fishing trips within the GBRWHA. Observations were on 1188 separate net shots during 297 days onboard vessels, giving a total of 1452 km-net-hours (Table 2).

Spatial distribution of fishing effort

Although 60% of trips occurred in intertidal zones, the greatest amount of fishing effort was observed in inshore coastal zones (Table 2). This reflected the generally shorter duration of trips occurring in intertidal and river zones ($\bar{x} = 1.3$ days, and $\bar{x} = 2.4$ days respectively), compared with those in inshore coastal zones ($\bar{x} = 3.5$ days), and also the generally shorter net lengths used in intertidal and river zones. The longest trip observed in all zones was 7 days, while the shortest was <1 day (i.e. a single-day trip). Total effort observed was 202 km-net-hours in river zones, 237 km-net-hours in intertidal zones and 1013 km-net-hours in inshore coastal zones (Table 2). All observed fishing effort was between 13°S and 24°S (Fig. 1).

Catch composition

In total, 18 625 fish were recorded by observers including 6828 elasmobranchs that constituted 37% of the catch by number. Overall, 38 species of elasmobranchs from 11 families and 4 orders were identified (Table 3), of which Carcharhiniformes was both the most diverse order (25 species) and the largest component of the catch by number (94.5%). Rajiformes was the next most diverse order (>10 species) but only contributed 3.9% of the elasmobranch catch by number. The remaining 1.6% came from two species of Pristiformes, three species of Orectolobiformes and a small number of unidentified sharks. After the removal of trips that contained fish identified only to family level, species-level catch composition was determined for 126 trips with a total effort of 905 km-net-hours. Among the Carcharhiniformes (Table 4), the morphologically identical blacktip sharks *C. tilstoni* and *C. limbatus* were the most numerous (28%, Table 4). These species could not be separately

identified in the field and were therefore grouped together. The spot-tail shark (*C. sorrah*) and scalloped hammerhead (*S. lewini*) were also relatively large contributors to the catch number (17 and 11%, Table 4). By weight, the target species of the fishery, *C. tilstoni/C. limbatus* and *C. sorrah*, also dominated the catch, contributing ~51% of the catch (Table 4). Despite being only 2.4% of the catch by number, the great hammerhead shark (*Sphyrna mokarran*) was the third largest component of the total weight (9.64%), owing to its large mean size at capture (Table 4). Conversely, catch by weight of some smaller species (e.g. *R. acutus*, *R. taylori*) as a proportion of total catch was lower than their respective proportion of catch by number.

Diversity of carcharhiniform sharks captured increased with distance from the coast, with 7 species recorded in rivers, 17 species in intertidal zones, and 25 species recorded in inshore zones (Table 3). Number and weight per unit effort of Carcharhiniformes also increased with distance from the coast (Table 4). Compared with river zones, the catch of Carcharhiniformes was ~5 times greater in intertidal zones, and 9 times greater in inshore coastal zones. *C. tilstoni/C. limbatus* were by far the most captured species in both the intertidal and inshore coastal zones, and also accounted for the greatest weight. *C. sorrah* accounted for a large component of the catch in inshore coastal zones, but was rarely caught in intertidal zones. Although few were caught, the large size of *S. mokarran* meant that it accounted for a relatively large component of weight in both intertidal and inshore coastal zones. The bull shark (*C. leucas*) was the only species regularly captured in river zones.

Catch characteristics

Mean lengths of species within the overall catch (all zones pooled) ranged from 637 mm for *R. taylori* males to 1544 mm for *S. mokarran* females (Table 5, Fig. 2). Sex-specific differences in the length-frequency distributions were found for 6 of the 14 species where there were sufficient data to carry out the KS test (Table 5). A significant difference in the sex ratio of the catch was also found for 6 of the 14 species tested (Table 5). No clear trends in sex ratio were evident, with females greatly outnumbering males in some species such as *S. mokarran* and *R. taylori*, and males greatly outnumbering females in other species such as *S. lewini* and *R. acutus*. There was also considerable interspecific variation in the different life stages present within the catch (Table 5). Percentages of neonates recorded in the catch ranged from 0% for many species up to 62.1% for *C. leucas*. The percentages of mature animals in the catch was

Table 2. Total fishing effort observed from 2006–2009 in the East Coast Inshore Finfish Fishery in the Great Barrier Reef World Heritage Area
The observer coverage was the most comprehensive fisheries observer program ever applied to the East Coast Inshore Finfish Fishery, and included considerable coverage of fishing in river and intertidal zones, the most data-poor sectors of the fishery

	River			Total	Intertidal			Total	Inshore coastal				Total	Grand total
	2007	2008	2009		2007	2008	2009		2006	2007	2008	2009		
Trips	4	11	6	21	20	32	39	91	3	12	17	5	37	149
Duration (days)	4	32	14	50	26	45	45	116	11	49	51	20	131	297
Net shots	26	179	187	392	133	161	197	491	18	110	131	46	305	1188
Km-net-hours	11	70	121	202	103	73	61	237	120	397	306	190	1013	1452

Table 3. Catch composition of elasmobranchs caught by the East Coast Inshore Finfish Fishery in the Great Barrier Reef World Heritage Area
Data, grouped by order and sorted by numerical abundance, are from all 149 trips observed across the three nominal zones (river, intertidal, and inshore coastal).
The dominance of carcharhiniform sharks in the elasmobranch component of the catch is typical of many tropical, inshore fisheries

Order	Family	Species	River	Intertidal	Inshore coastal	Component of catch (%)
Carcharhiniformes						94.5
	Carcharhinidae	<i>Carcharhinus altimus</i>			7	0.1
		<i>Carcharhinus amblyrhynchos</i>			7	0.1
		<i>Carcharhinus amblyrhynchoides</i>			23	0.3
		<i>Carcharhinus amboinensis</i>		38	53	1.3
		<i>Carcharhinus brevipinna</i>	1		227	3.3
		<i>Carcharhinus cautus</i>			3	<0.1
		<i>Carcharhinus dussumieri</i>		11	247	3.8
		<i>Carcharhinus fitzroyensis</i>		41	164	3.0
		<i>Carcharhinus leucas</i>	83	10	3	1.4
		<i>Carcharhinus macroti</i>			275	4.0
		<i>Carcharhinus melanopterus</i>	1	46	27	1.1
		<i>Carcharhinus sorrah</i>		12	995	14.7
		<i>Carcharhinus</i> spp.			843	12.3
		<i>Carcharhinus tilstoni/C. limbatus</i>		164	1154	19.3
		<i>Galeocerdo cuvier</i>		1	19	0.3
		<i>Loxodon macrorhinus</i>		1	331	4.9
		<i>Negaprion acutidens</i>	11	7	3	0.3
		<i>Rhizoprionodon acutus</i>	1	82	457	7.9
		<i>Rhizoprionodon taylori</i>		45	260	4.5
		<i>Triaenodon obesus</i>			2	<0.1
	Hemigalidae	<i>Hemipristis elongata</i>		4	17	0.3
		<i>Hemigaleus australiensis</i>		3	7	0.1
	Sphyrnidae	<i>Eusphyrna blochii</i>		6	18	0.4
		<i>Sphyrna lewini</i>	1	128	475	8.8
		<i>Sphyrna mokarran</i>	1	15	86	1.5
		<i>Sphyrna</i> spp.			34	0.5
Rajiformes						3.9
	Dasyatidae	<i>Dasyatis fluviatorum</i>		4		0.1
		<i>Himantura astra</i>		1		<0.1
		Unidentified ray	9	17	7	0.5
	Mobulidae	<i>Manta</i> spp.			3	<0.1
		<i>Mobula</i> spp.			3	<0.1
	Myliobatidae	<i>Aetobatus narinari</i>		8	13	0.3
		<i>Aetomylaeus nichofii</i>			2	<0.1
		<i>Aetomylaeus vespertilio</i>			1	<0.1
		<i>Rhinoptera</i> spp.		93	6	1.4
		Unidentified eagle ray			3	<0.1
	Rhinobatidae	<i>Glaucostegus typus</i>	4	20	3	0.4
	Rhynchobatidae	<i>Rhynchobatus</i> spp.	1	14	53	1.0
Pristiformes						1.2
	Pristidae	<i>Anoxypristis cuspidata</i>		40	35	1.1
		<i>Pristis zijsron</i>	1	4	2	0.1
Orectolobiformes						0.3
	Stegastomatidae	<i>Stegostoma fasciatum</i>			11	0.2
	Hemiscylliidae	<i>Chiloscyllium punctatum</i>		3	5	0.1
	Brachaeluridae	<i>Brachaelurus colcloughi</i>			1	<0.1
Unknown			11			0.2
Total			114	829	5885	6828

inversely related to maximum size for many species, as small species (<1000 mm) were typically caught as adults, and moderate to large species (>1000 mm) were caught as juveniles. Exceptions to this trend included the snaggletooth shark (*Hemipristis elongata*) and the winghead shark (*Eusphyrna blochii*), which were both moderate sized species (up to 2000 mm)

mainly caught as adults. Large sex-specific differences were also found in the percentage of the catch that was mature for some species, including *R. acutus* and *S. lewini*, where adult males were present in the catch, but adult females were either rare or absent. For the blacktip complex of *C. tilstoni/C. limbatus*, the percentage of mature animals should be

Table 4. Catch per unit effort and catch composition of carcharhiniform sharks caught by the East Coast Inshore Finfish Fishery within the boundaries of the Great Barrier Reef World Heritage Area

Species are sorted by the proportion of the total observed catch across all habitats by weight. Data are from a subsample of 126 observer trips, where all individuals were identified to species level. Blank records indicate no recorded occurrence in catch

Species	Catch				Catch per unit effort					
	Mean size (mm)	Mean weight (kg)	Number (%)	Weight (%)	River (individuals.km-net-hour ⁻¹)	Intertidal	Inshore coastal	River	Intertidal (kg km-net-hour ⁻¹)	Inshore coastal
<i>Carcharhinus tilstoni/C. limbatus</i>	910	4.1	28.2	30.6		0.8	1.3		3.3	5.4
<i>Carcharhinus sorrah</i>	963	4.7	16.6	20.5		0.1	0.9		0.3	4.3
<i>Sphyrna mokarran</i>	1563	15.5	2.4	9.7	<0.1	0.1	0.1	0.1	1.2	1.6
<i>Sphyrna lewini</i>	809	2.3	11.4	6.8		0.5	0.5		1.0	1.1
<i>Carcharhinus brevipinna</i>	943	3.7	6.7	6.5			0.4			1.4
<i>Carcharhinus amboinensis</i>	955	5.9	2.4	3.9		0.2	0.1		1.1	0.4
<i>Rhizoprionodon acutus</i>	746	1.8	7.8	3.8		0.3	0.3		0.6	0.6
<i>Carcharhinus leucas</i>	879	4.2	2.7	3.7	0.4	<0.1		1.7	0.1	
<i>Carcharhinus dussumieri</i>	829	3.0	4.8	2.9		0.1	0.3		0.2	0.8
<i>Carcharhinus macroti</i>	836	2.6	3.7	2.5			0.2			0.5
<i>Rhizoprionodon taylori</i>	623	1.1	6.9	1.9		0.2	0.3		0.2	0.3
<i>Carcharhinus melanopterus</i>	753	2.5	2.4	1.6	<0.1	0.2	<0.1	<0.1	0.6	0.1
<i>Carcharhinus fitzroyensis</i>	881	4.0	1.4	1.5		0.2			0.8	
<i>Hemipristis elongata</i>	1318	9.7	0.5	1.2		<0.1	<0.1		0.2	0.2
<i>Galeocerdo cuvier</i>	1283	8.8	0.4	1.0		<0.1	<0.1		<0.1	0.2
<i>Eusphyrna blochii</i>	1363	8.3	0.4	0.9		<0.1	<0.1		0.3	0.1
<i>Negaprion acutidens</i>	891	3.1	0.7	0.6	0.1	<0.1		0.2	0.1	
<i>Hemigaleus australiensis</i>	940	3.1	0.3	0.3		<0.1	<0.1		<0.1	<0.1
<i>Carcharhinus caudatus</i>	955	5.7	0.1	0.2			<0.1			<0.1
<i>Carcharhinus altimus</i>	839	2.3	0.2	0.1			<0.1			<0.1
<i>Loxodon macrorhinus</i>	872	2.3	<0.1	<0.1		<0.1			<0.1	
Total					0.5	2.8	4.5	2.0	10.1	17.1

considered an approximation, as it was based on length at maturity of *C. tilstoni* and likely included some *C. limbatus* specimens. Off eastern Australia, *C. limbatus* is known to mature at sizes >2000 mm (Macbeth *et al.* 2009), which is larger than any individuals measured during the observer survey. Therefore, although an accurate estimate of the percentage of mature *C. tilstoni* specimens was not possible, we have a high level of confidence that no *C. limbatus* adults were caught.

Discussion

Capture susceptibility and threats to carcharhiniform sharks in the GBRWHA

The present survey of the mesh-net commercial fishery operating within the GBRWHA revealed the complex nature of tropical shark fisheries. At least 38 species of elasmobranchs were recorded in the catch, with catch rates varying between habitats, life stages (neonate, juvenile, adult) and by sex. Despite this complexity, some broad trends in capture susceptibility were seen among the carcharhiniforms (Table 6). For example, small species <1000 mm in total length (e.g. *R. acutus*, *R. taylori*) were, by virtue of their small size relative to the net mesh size, almost exclusively susceptible to capture as adults in the fishery. Moderate sized species 1000–2000 mm total length (e.g. *C. tilstoni*, *C. sorrah*) were susceptible to some extent at all sizes, with neonates large enough and young adults small enough to be caught by the nets. In contrast, large species

>2000 mm total length (e.g. *C. amboinensis*, *C. brevipinna*) were subject to a gauntlet effect by the fishery (Simpfendorfer 1999; Prince 2005). Large species were frequently captured as neonates and juveniles and rarely caught as adults, possibly due to adults migrating away from fished habitats or growing too large to be meshed or entangled by the nets. Hammerhead sharks typified another group of species susceptible in similar ways. Despite growing to a large size, they were susceptible to capture at all sizes due to their head morphology.

The results of this study confirm that Carcharhiniformes dominate the catch of the ECIF and it is elasmobranchs of this order that are probably most at risk from the fishery. Many of the species caught by the ECIF were also identified by risk assessments as among the least likely to be sustainable across other northern Australia fisheries (Stobutzki *et al.* 2002; Salini *et al.* 2007) and are also probably affected to some extent by recreational fishing within the GBRWHA (Lynch *et al.* 2010). Stocks of some species are known to be shared with other nearby jurisdictions, so unsustainable fishing practices in these areas would also potentially affect GBRWHA populations (Ovenden *et al.* 2009), as would illegal fishing encroaching on northern Australian waters (Field *et al.* 2009). In contrast to the threats posed by fishing, an integrated risk assessment for climate change of the GBRWHA suggested that most of the carcharhiniforms caught in the ECIF were unlikely to have a high vulnerability to climate change owing to their high adaptive capacities (Chin *et al.* 2010).

Table 5. Tabulation of sex-specific length at capture details, sex ratio and the percentage of catch mature or neonate for carcharhinid sharks caught in the Great Barrier Reef World Heritage Area

The results of Kolmogorov–Smirnov (KS) tests comparing length-frequency distributions of males and females and chi-square tests on the sex ratio of the catch are also given. Where only a single length measurement was available it was given as maximum size at capture and other fields were left blank. Bold text indicates statistical significance ($P < 0.05$)

Species	Length (mm)		Area		KS-Test		Sex ratio (F/M)	χ^2 test	Mature animals (%)			Neonates (%)
	Min.	Max.	Male	Female	P	Male			Female	Combined		
<i>Carcharhinus tilstoni</i> /C. <i>limbatus</i>	580	1600	877	1930	904	0.26	0.98	0.80	3.3	5.8	9.1	5.2
<i>Carcharhinus sorrah</i>	580	1130	939	1301	966	0.01	0.76	0.03	36.1	24.8	60.9	0.0
<i>Sphyrna mokarran</i>	916	2830	1542	4280	1544	0.95	2.21	<0.01	4.9	6.6	11.5	0.0
<i>Sphyrna lewini</i>	465	1930	893	1236	662	<0.01	0.53	<0.01	8.5	0.0	8.5	8.9
<i>Carcharhinus brevipinna</i>	771	2480	1016	2830	1019	0.38	0.90	0.58	0.8	0.8	1.7	0.0
<i>Carcharhinus dussumieri</i>	670	892	824	915	853	<0.01	0.74	0.19	54.9	42.7	97.6	0.0
<i>Carcharhinus amboinensis</i>	663	2400	994	1380	915	0.34	0.82	0.45	1.6	0.0	1.6	17.6
<i>Rhizoprionodon acutus</i>	385	931	779	940	713	<0.01	0.31	<0.01	56.2	11.2	67.4	0.6
<i>Carcharhinus leucas</i>	715	1850	852	1750	830	0.47	1.69	0.01	0.0	0.0	0.0	62.1
<i>Carcharhinus macloti</i>	706	980	794	910	850	<0.01	1.26	0.24	43.3	55.8	99.0	0.0
<i>Rhizoprionodon taylori</i>	456	730	637	796	686	<0.01	1.98	<0.01	22.8	60.8	83.5	0.0
<i>Carcharhinus melanopterus</i>	543	1390	750	1600	723	0.67	1.58	0.08	4.8	3.2	8.1	4.8
<i>Carcharhinus fitzroyensis</i>	505	1070	765	1304	849	0.36	1.20	0.46	15.2	19.7	34.8	5.5
<i>Hemipristis elongata</i>	788	1690	1288	2003	1431	0.13	0.45	0.13	43.8	25.0	68.8	0.0
<i>Galeocerdo cuvier</i>	1060	1123	1088	1090	1019		1.00		0.0	0.0	0.0	
<i>Eusphya blochii</i>	633	1720	1106	1700	1520		0.57		40.0	30.0	70.0	0.0
<i>Negaprion acutidens</i>	755	1000	867	1790	901		1.43		0.0	0.0	0.0	15.0
<i>Hemigaleus australiensis</i>	870	1060	966	1060			0.10		90.9	9.1	100.0	0.0
<i>Carcharhinus cautus</i>	1025			885			1.00		50.0	0.0	50.0	0.0
<i>Carcharhinus alimus</i>	795	928	849	925	834		2.00		0.0	0.0	0.0	0.0
<i>Loxodon macrorhinus</i>		990					0.00		100.0	0.0	100.0	0.0

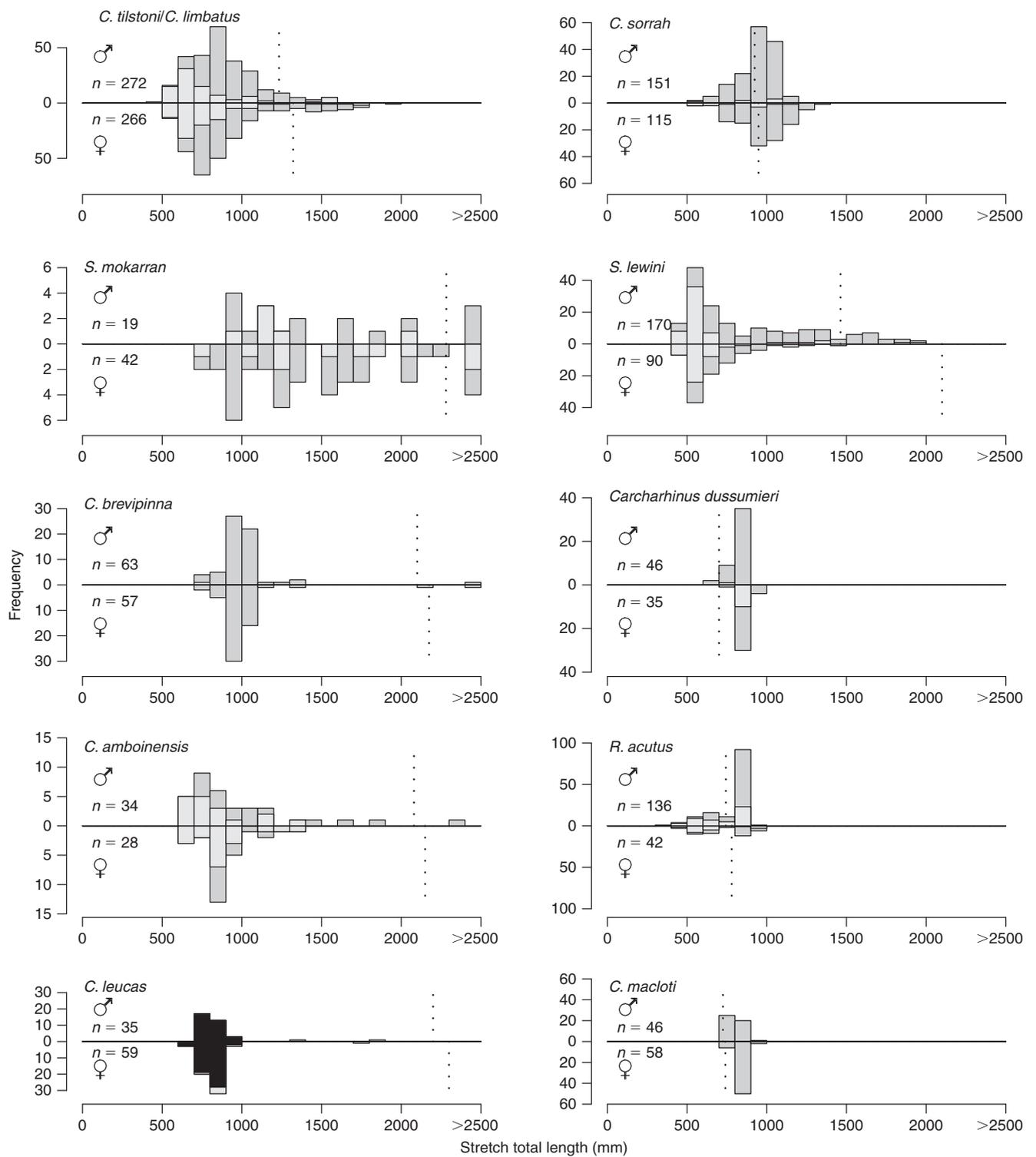


Fig. 2. Length-frequency distributions of the top 10 carcharhiniform sharks by weight (Table 4). Bar colour denotes the capture zone: solid black, river; dark grey, inshore coastal; and light grey, intertidal. Length at 50% maturity is denoted by the dashed black line.

Of the non-carcharhiniform elasmobranchs, most were caught in relatively low numbers, with the exception of cownose rays (*Rhinoptera* spp.), narrow sawfish (*Anoxypristis cuspidata*) and wedgefish (*Rhynchobatus* spp.), all of which were at least

1% of the overall catch by number. The record of seven green sawfish (*Pristis zijsron*) in the catch indicates this species is still present on the east coast of Queensland at least as far south as the Whitsundays (20°S), even though it is now considered to be

extinct in New South Wales waters (*Fisheries Management Act 1994*, NSW, No. 38). Recent protection of sawfish in Australian waters, as well as catch restrictions imposed on wedgefish in the ECIFF, are likely to mitigate the threats posed to at least two of the families listed above.

Risk mitigation strategies in multispecies, tropical shark fisheries

The diversity of elasmobranchs within the tropical coastal regions of the world, combined with the complex spatial ecology and behaviour patterns they exhibit, clearly provides a major challenge for sustainable management of extractive fishing. It has long been recognised that the idiosyncrasies of shark populations and fisheries require alternative approaches to management compared with teleost resources (Holden 1974). More recently it has also been shown that the features of elasmobranchs that make them vulnerable (e.g. close stock-recruitment relationships) can also be advantageous when properly managed (Walker 1998). Indeed, the idiosyncrasies of shark populations may provide many under-utilised opportunities for designing management strategies and, if properly understood, may help reconcile some of the impediments to sustainable management.

Perhaps one of the simplest observations that can be taken from the present study is that despite the large number of species caught within the ECIFF, there were only a few patterns in the way they were susceptible (Table 6). In many instances, similarly susceptible species also shared similar life-history traits.

Table 6. Groupings of similarly susceptible shark species caught in the East Coast Inshore Finfish Fishery

	Susceptible life stages
Small (<1000 mm) coastal species	Adults only
<i>Carcharhinus dussumieri</i>	
<i>Carcharhinus macloti</i>	
<i>Hemigaleus australiensis</i>	
<i>Loxodon macrorhinus</i>	
<i>Rhizoprionodon acutus</i>	
<i>Rhizoprionodon taylori</i>	
Medium-sized (1000–2000 mm) coastal species	All sizes
<i>Carcharhinus cautus</i>	
<i>Carcharhinus fitzroyensis</i>	
<i>Carcharhinus melanopterus</i>	
<i>Carcharhinus sorrah</i>	
<i>Carcharhinus tilstoni</i>	
<i>Hemipristis elongata</i>	
Large (>2000 mm) coastal and semi-pelagic species	Neonates and juveniles
<i>Carcharhinus altimus</i>	
<i>Carcharhinus amboinensis</i>	
<i>Carcharhinus brevipinna</i>	
<i>Carcharhinus leucas</i>	
<i>Carcharhinus limbatus</i>	
<i>Galeocerdo cuvier</i>	
<i>Negaprion acutidens</i>	
Hammerheads	All sizes
<i>Eusphyra blochii</i>	
<i>Sphyrna lewini</i>	
<i>Sphyrna mokarran</i>	

For example, many small, coastal tropical carcharhiniform sharks (<1000 mm, e.g. *R. acutus*, *R. taylori*) are amongst the fastest growing and most productive elasmobranchs studied (Simpfendorfer 1993; Harry *et al.* 2010). Medium-sized (1000–2000 mm, e.g. *C. cautus*, *C. sorrah*, *C. tilstoni*) coastal tropical species are somewhat less productive, typically living 10–20 years and maturing relatively young (Davenport and Stevens 1988; White *et al.* 2002). In contrast, large tropical Carcharhiniformes (>2000 mm e.g. *C. leucas*, *N. brevirostris*) typically conform to the slow-growing, long-lived paradigm more frequently associated with elasmobranchs (Brown and Gruber 1988; Neer *et al.* 2005). These similarities also extend to habitat and spatial usage. Most species within the small and medium-sized groups are restricted to coastal waters, while most large species are semi-pelagic, migrating offshore at larger sizes.

These life-history patterns have been recognised and described by a variety of authors (Hoenig and Gruber 1990; Cortes 2000; Frisk *et al.* 2001). While actual groupings are arbitrary (e.g. small, medium, large), the underlying concept of a life-history continuum, ranging from ‘slow’ to ‘fast’ species (Cortes 2002), has important implications in terms of simplifying management of multispecies fisheries. Although species-specific management may be unfeasible, it may be possible to direct management strategies at species that are not only susceptible in the same way, but also have similar life-history traits (e.g. the management of ‘Small Coastal Shark’ and ‘Large Coastal Shark’ complexes in the United States). In the case of the ECIFF, management of the fishery could potentially be simplified by directing management strategies at the four nominal groups identified in Table 6.

Examples of specific management strategies that could be used to mitigate the risk of overfishing to tropical carcharhiniform sharks may involve the use of gear restrictions and spatial and temporal closures. Modifying the gear selectivity in a fishery to take advantage of particular life-history traits may be one of the most effective measures for mitigating risk. This is especially relevant in gill-net fisheries for sharks where size-selectivity dynamics are well understood compared with other gear types, such as trawl and line (Kirkwood and Walker 1986). In the present study, the exclusive use of small-mesh gill-nets (typically <165 mm) by the ECIFF meant that sharks >1500 mm were rarely captured (with the exception of hammerheads). This in itself may be a good strategy for multispecies tropical shark fisheries, as only neonates and juveniles of the largest (and often least productive) species are captured by the fishery, while adults are subject to a ‘gauntlet’ effect and effectively excluded. The concept of the gauntlet fishery has been proposed as an effective method of harvesting long-lived species, providing that fishing mortality on adults remains extremely low (Simpfendorfer 1999; Prince 2005). Although such a harvest strategy is unlikely to provide the maximum sustainable yield (Gallucci *et al.* 2006), it may be preferable, depending on the goals of the fishery. In an artisanal fishery, for example, the harvest of large sharks is unlikely to contribute to food security given that the flesh from these animals often contains high levels of mercury and may not be suitable for human consumption (Lyle 1984; Clarkson 1997). In the case of the ECIFF, the use of a gauntlet-style harvest strategy potentially provides a lower-risk method of harvesting the large coastal/

semi-pelagic species, but at the same time allows for concurrent harvest of the more productive small and medium coastal sharks and teleosts.

Spatial and temporal closures may also be used to mitigate the risk to sharks in multispecies fisheries and may be the only way to protect some species that are particularly susceptible to certain gear types (e.g. hammerheads in the present study). Closures of inshore nursery areas have historically been used as a way of protecting sharks and have been considered a critical tool in managing shark populations (Olsen 1959; McCandless *et al.* 2007), although their usefulness has also been contested (Kinney and Simpfendorfer 2009). Demonstrating the effectiveness of spatial closures for protecting wide-ranging, migratory species (e.g. the large coastal/semi-pelagics and hammerheads) is challenging, although evidence suggests that these species may receive some benefits from spatial closures (Claudet *et al.* 2010). Many of the patterns observed in this study (e.g. segregation by size, sex and habitat) may also present further opportunities for spatial or temporal closures. Capitalising on the seasonal nature of reproduction displayed by many elasmobranchs could be one way to achieve this. Most carcharhiniform sharks across northern Australia give birth during a relatively restricted time period over summer (Stevens and Wiley 1986; Stevens and McLoughlin 1991). This is also true within the GBRWHA, where neonates of several species such as *S. lewini*, *C. tilstoni*/*C. limbatus* and *C. fitzroyensis* were captured in intertidal zones at the beginning of summer, but apparently moved away from this zone soon afterwards. Temporal closures of nursery habitats during this brief period may therefore be effective in protecting both neonates and adult females of the medium coastal and large coastal/semi-pelagic groups, should they be vulnerable at this time.

Perhaps one of the most promising and as yet under-utilised risk mitigation strategies for sharks is sex-differential harvest. Strong segregation by size, sex and reproductive stage are well documented characteristics of most shark populations (Springer 1967; Sims 2005). Mucientes *et al.* (2009), for example, reported strong sex segregation at large scales in the Pacific Ocean for shortfin mako (*Isurus oxyrinchus*) and suggested that differential exploitation of males was possible. Camhi *et al.* (1998) also suggested selective take of males only as a potential management measure for sharks. In the present study, sex-differential harvest was seen to be already occurring for some species. Where this was occurring for males (e.g. *R. acutus* and *S. lewini*) it may allow higher catches of these species with minimal effect on population growth rates. Conversely for species such as *S. mokarran*, the high bias towards catching females must also be recognised by managers as it is likely to have a disproportionately negative effect on the population growth rate compared with equal harvest of both sexes. A sex differential harvest strategy would probably be most suited to the wide-ranging large coastal/semi-pelagic species and hammerheads, where sex segregation is likely to be occurring over large spatial scales. Such a management strategy could be formalised by restricting fishing to depths or regions where high numbers of males occur. Sex differential harvest is also appealing because, in fisheries where sharks are landed live (and assuming low post-release mortality), it can be incorporated without the need for any spatial closures, as sex can easily be

established in sharks via examination of the pelvic fins. Enforcement of this management technique can also be achieved by requiring fishers to land sharks with pelvic fins intact (Walker 2005b).

Conclusions

The present study was the most comprehensive observer survey ever applied to the Queensland ECIFF. The high elasmobranch species diversity, dominated by Carcharhiniformes, was characteristic of many inshore, tropical fisheries. The data-poor and highly complex nature of the ECIFF and similar fisheries means that quantitative, species-specific management is unlikely to be possible. However, close scrutiny of the catch characteristics show that there are many aspects of elasmobranch biology that are likely to be useful in designing management strategies that can mitigate the risk of overexploitation posed by such fisheries. These include the tendencies of elasmobranchs to show strong segregation by size and sex, along with the use of discrete areas during different life stages (e.g. nurseries) and the existence of many interspecific patterns in life-history traits. Uptake and implementation of practical management strategies using this information is currently limited by a poor knowledge of life history and spatial ecology of sharks. Even across northern Australia, where the tropical carcharhiniform shark assemblage and fisheries are arguably among the best-studied worldwide, age and growth information is currently available for only a limited number of species. The location and movement of adult stocks of many of the large, semi-pelagic species are also poorly documented. This highlights the ongoing requirement for the study of life history and spatial ecology in elasmobranchs.

Acknowledgements

This work was funded by the Australian Commonwealth Government Marine and Tropical Scientific Research Facility (MTSRF), Project 4.8.4. The first author was supported by an Australian Postgraduate Award and a MTSRF scholarship. The authors thank fishers of the East Coast Inshore Finfish Fishery including G. Radley, T. Wiseman, R. Marriage, S. Howe, B. Gilland, T. Draper and T. Falzon. Without support from industry this work would not have been possible. We also thank Fisheries Queensland, particularly Julia Davies, for the use of data from the Fisheries Observer Program. Samples for this project were collected under a Queensland Government general fisheries permit (Permit number 90911). We thank members of the Fishing and Fisheries Research Centre for their assistance in sample collection throughout the study. Finally we wish to thank Ken Graham, Charlie Huvneers, the guest editor and an anonymous reviewer for their constructive and thoughtful comments on the manuscript.

References

- Anon (1990). Northern pelagic fish stock research. Final report to FIRDC projects 83/49 & 86/87. CSIRO Australia, Canberra.
- Bensley, N., Woodhams, J., Patterson, H. M., Rodgers, M., McLoughlin, K., *et al.* (2010). 2009 Shark Assessment Report for the Australian National Plan of Action for the Conservation and Management of Sharks. Department of Agriculture, Fisheries and Forestry, Bureau of Rural Sciences, Canberra.
- Brown, C. A., and Gruber, S. H. (1988). Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia* 3, 747–753. doi:10.2307/1445397
- Camhi, M., Fowler, S. L., Musick, J. A., Brautigam, A., and Fordham, S. V. (1998). 'Sharks and their Relatives – Ecology and Conservation.' (World Conservation Union: Gland, Switzerland.)

- Castillo-Géniz, J. L., Marquez-Farias, J. F., de la Cruz, M. C. R., Cortes, E., and del Prado, A. C. (1998). The Mexican artisanal shark fishery in the Gulf of Mexico: towards a regulated fishery. *Marine and Freshwater Research* **49**, 611–620. doi:10.1071/MF97120
- Castro, J. I. (1993). The shark nursery of Bulls Bay, South-Carolina, with a review of the shark nurseries of the southeastern coast of the United-States. *Environmental Biology of Fishes* **38**, 37–48. doi:10.1007/BF00842902
- Chin, A., Kyne, P. M., Walker, T. I., and Mcauley, R. B. (2010). An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology* **16**, 1936–1953. doi:10.1111/J.1365-2486.2009.02128.X
- Clarkson, T. W. (1997). The toxicology of mercury. *Critical Reviews in Clinical Laboratory Sciences* **34**, 369–403. doi:10.3109/10408369708998098
- Claudet, J., Osenberg, C. W., Domenici, P., Badalamenti, F., Milazzo, M., *et al.* (2010). Marine reserves: fish life history and ecological traits matter. *Ecological Applications* **20**, 830–839. doi:10.1890/08-2131.1
- Compagno, L. J. V. (1984). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO species catalogue, Hexanchiformes to Lamniformes. FAO Fisheries Synopsis 125 Vol. 4, Part 1. Food and Agriculture Organization, Rome.
- Cortes, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**, 299–344.
- Cortes, E. (2002). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology* **16**, 1048–1062. doi:10.1046/J.1523-1739.2002.00423.X
- Davenport, S., and Stevens, J. D. (1988). Age and growth of two commercially important sharks (*Carcharhinus tilstoni* and *C. sorrah*) from northern Australia. *Australian Journal of Marine and Freshwater Research* **39**, 417–433. doi:10.1071/MF9880417
- Devine, J. A., Baker, K. D., and Haedrich, R. L. (2006). Fisheries: deep-sea fishes qualify as endangered. *Nature* **439**, 29. doi:10.1038/439029A
- FAO (2000). 'Fisheries Management. 1. Conservation and Management of Sharks.' (Food and Agriculture Organization: Rome.)
- Field, I. C., Meekan, M. G., Buckworth, R. C., and Bradshaw, C. J. A. (2009). Protein mining the world's oceans: Australasia as an example of illegal expansion-and-displacement fishing. *Fish and Fisheries* **10**, 323–328. doi:10.1111/J.1467-2979.2009.00325.X
- Fowler, S. L., Cavanagh, R. D., Camhi, M., Burgess, G. H., Cailliet, G. M., *et al.* (2005) 'Sharks, Rays and Chimaeras: The status of Chondrichthyan Fishes. Status survey.' (IUCN/SSC Shark Specialist Group: IUCN, Gland, Switzerland.)
- Frisk, M. G., Miller, T. J., and 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. doi:10.1139/CJFAS-58-5-969
- Gallucci, V. F., Taylor, I. G., and Erzini, K. (2006). Conservation and management of exploited shark populations based on reproductive value. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 931–942. doi:10.1139/F05-267
- GBRMPA (2009). Great Barrier Reef outlook report 2009. Great Barrier Reef Marine Park Authority, Townsville.
- Graham, K. J., Andrew, N. L., and Hodgson, K. E. (2001). Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research* **52**, 549–561. doi:10.1071/MF99174
- Hanfee, F. (1999). Management of shark fisheries in two Indian coastal states: Tamil Nadu and Kerala. In 'Case Studies of the Management of Elasmobranch Fisheries. FAO Fisheries Technical Paper. No 378, part 1'. (Ed. R. Shotton.) pp. 316–338. (Food and Agriculture Organization: Rome.)
- Harry, A. V., Simpfendorfer, C. A., and Tobin, A. J. (2010). Improving age, growth, and maturity estimates for aseasonally reproducing chondrichthyans. *Fisheries Research* **106**, 393–403. doi:10.1016/J.FISHRES.2010.09.010
- Henderson, A. C., McIlwain, J. L., Al-Oufi, H. S., and Al-Sheili, S. (2007). The Sultanate of Oman shark fishery: species composition, seasonality and diversity. *Fisheries Research* **86**, 159–168. doi:10.1016/J.FISHRES.2007.05.012
- Heupel, M. R., and Simpfendorfer, C. A. (2005). Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology* **147**, 1239–1249. doi:10.1007/S00227-005-0004-7
- Hoening, J. M., and Gruber, S. H. (1990). Life-history patterns in the elasmobranchs: implications for fisheries management. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. NOAA Technical Report NMFS. Vol. 90'. (Eds H. L. J. Pratt, S. H. Gruber and T. Taniuchi.) pp. 1–16. (US Department of Commerce: Washington, DC.)
- Holden, M. J. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In 'Sea Fisheries Research'. (Ed. F. R. Harden Jones.) pp. 117–137. (Halsted Press, J. Wiley & Sons: New York.)
- Hueter, R. E., and Tyminski, J. P. (2007). Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States. American Fisheries Society, Symposium 50'. (Eds C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 193–225. (American Fisheries Society: Bethesda, MD.)
- Jackson, J. B. C. (2008). Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11 458–11 465. doi:10.1073/PNAS.0802812105
- Kasim, H. M. (1991). Shark fishery of Veraval Coast with special reference to population dynamics of *Scoliodon laticaudus* (Muller and Henle) and *Rhizoprionodon acutus* (Ruppell). *Journal of the Marine Biological Association of India* **33**, 213–228.
- Kinney, M. J., and Simpfendorfer, C. A. (2009). Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters* **2**, 53–60. doi:10.1111/J.1755-263X.2008.00046.X
- Kirkwood, G. P., and Walker, T. I. (1986). Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Gunther, taken in southeastern Australian waters. *Australian Journal of Marine and Freshwater Research* **37**, 689–697. doi:10.1071/MF9860689
- Knip, D. M., Heupel, M. R., and Simpfendorfer, C. A. (2010). Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series* **402**, 1–11. doi:10.3354/MEPS08498
- Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne.)
- Lyle, J. M. (1984). Mercury concentrations in four carcharhinid and three hammerhead sharkes from coastal waters of the Northern Territory. *Marine and Freshwater Research* **35**, 441–451. doi:10.1071/MF9840441
- Lynch, A. J., Sutton, S. G., and Simpfendorfer, C. A. (2010). Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 312–318. doi:10.1002/AQC.1056
- Macbeth, W. G., Geraghty, P. T., Peddemors, V. M., and Gray, C. A. (2009). Observer-based study of targeted commercial fishing for large shark species in waters off northern New South Wales. Cronulla Fisheries Research Centre of Excellence, Industry & Investment NSW, Sydney.
- McCandless, C. T., Kohler, N. E., and Pratt, H. L., Jr (2007). Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society, Symposium 50. (Bethesda, MD)
- Motta, F. S., Gadig, O. B. F., Namora, R. C., and Braga, F. M. S. (2005). Size and sex compositions, length-weight relationship, and occurrence of the Brazilian sharpnose shark, *Rhizoprionodon lalandii*, caught by artisanal

- fishery from southeastern Brazil. *Fisheries Research* **74**, 116–126. doi:10.1016/J.FISHRES.2005.03.010
- Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., and Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters* **5**, 156–159. doi:10.1098/RSBL.2008.0761
- Musick, J. A., Harbin, M. M., and Compagno, L. J. V. (2004). Historical zoogeography of the Selachii. In 'Biology of Sharks and their Relatives'. (Eds C. J. Carrier, J. A. Musick and M. R. Heithaus.) pp. 33–78. (CRC Press: Boca Raton, FL.)
- Neer, J. A., Thompson, B. A., and Carlson, J. K. (2005). Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. *Journal of Fish Biology* **67**, 370–383. doi:10.1111/J.0022-1112.2005.00743.X
- Olsen, A. M. (1959). The status of the school shark fishery in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **10**, 150–176. doi:10.1071/MF9590150
- Ovenden, J. R., Kashiwagi, T., Broderick, D., Giles, J., and Salini, J. (2009). The extent of population genetic subdivision differs among four co-distributed shark species in the Indo-Australian archipelago. *BMC Evolutionary Biology* **9**, 40.
- Prince, J. D. (2005). Gauntlet fisheries for elasmobranchs – the secret of sustainable shark fisheries. *Journal of Northwest Atlantic Fishery Science* **35**, 407–416.
- Ripley, W. E. (1946). The soupfin shark and the fishery. *California Department of Fish and Game Fish Bulletin* **64**, 7–37.
- Salini, J., McAuley, R., Blaber, S., Buckworth, R., Chidlow, J., *et al.* (2007). Northern Australia sharks and rays: the sustainability of target and bycatch fisheries. Phase 2. CSIRO Marine and Atmospheric Research, Cleveland, Qld.
- Shotton, R. (1999). Species identification practices of countries reported landings of chondrichthyan fishes in the FAO nominal catches and landings data base. Food and Agriculture Organization, Rome.
- Simpfendorfer, C. A. (1993). Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. *Environmental Biology of Fishes* **36**, 233–241. doi:10.1007/BF00001718
- Simpfendorfer, C. A. (1999). Demographic analysis of the dusky shark fishery in southwestern Australia. *American Fisheries Society Symposium* **23**, 149–160.
- Sims, D. W. (2005). Differences in habitat selection and reproductive strategies of male and female sharks. In 'Sexual Segregation in Vertebrates'. (Eds K. E. Ruckstuhl and P. Neuhaus.) pp. 127–148. (Cambridge University Press: Cambridge.)
- Springer, S. (1950). Natural history of the lemon shark, *Negaprion brevirostris*. *The Texas Journal of Science* **3**, 349–357.
- Springer, S. (1967). Social organisation of shark populations. In 'Sharks, Skates and Rays'. (Eds P. W. Gilbert, R. F. Mathewson and D. P. Rall.) pp. 149–174. (Johns Hopkins Press: Baltimore, MD.)
- Stevens, J. D. (1999). Management of shark fisheries in Northern Australia. Food and Agriculture Organization, Rome.
- Stevens, J. D., and Lyle, J. M. (1989). Biology of three hammerhead sharks (*Eusphyrna blochii*, *Sphyrna mokarran* and *S. lewini*) from northern Australia. *Marine and Freshwater Research* **40**, 129–146. doi:10.1071/MF9890129
- Stevens, J. D., and McLoughlin, K. J. (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. *Australian Journal of Marine and Freshwater Research* **42**, 151–199. doi:10.1071/MF9910151
- Stevens, J. D., and Wiley, P. D. (1986). Biology of two commercially important carcharhinid sharks from northern Australia. *Marine and Freshwater Research* **37**, 671–688. doi:10.1071/MF9860671
- Stobutzki, I. C., Miller, M. J., Heales, D. S., and Brewer, D. T. (2002). Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery. *Fishery Bulletin* **100**, 800–821.
- 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. doi:10.1071/MF98017
- Walker, T. I. (2005a). Reproduction in fisheries science. In 'Reproductive Biology and Phylogeny of Chondrichthyans: Sharks, Batoids, and Chimaeras'. (Ed. W. C. Hamlett.) pp. 81–127. (Science Publishers Inc.: Enfield, NH.)
- Walker, T. I. (2005b). Management measures. In 'Management Techniques for Elasmobranch Fisheries. FAO Fisheries Technical Paper No. 474'. (Eds J. A. Musick and R. Bonfil.) pp. 251. (Food and Agriculture Organization: Rome.)
- White, W. T. (2007). Catch composition and reproductive biology of whaler sharks (Carcharhiniformes: Carcharhinidae) caught by fisheries in Indonesia. *Journal of Fish Biology* **71**, 1512–1540. doi:10.1111/J.1095-8649.2007.01623.X
- White, W. T., and Kyne, P. M. (2010). The status of chondrichthyan conservation in the Indo-Australasian region. *Journal of Fish Biology* **76**, 2090–2117. doi:10.1111/J.1095-8649.2010.02654.X
- White, W. T., Hall, N. G., and Potter, I. C. (2002). Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre- and postnatal life. *Marine Biology* **141**, 1153–1164. doi:10.1007/S00227-002-0914-6
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., *et al.* (2009). Rebuilding global fisheries. *Science* **325**, 578–585. doi:10.1126/SCIENCE.1173146

Manuscript received 18 June 2010, accepted 30 January 2011