CSIRO PUBLISHING

Marine and Freshwater Research, 2013, **64**, 20–30
http://dx.doi.org/10.1071/MF11234

Population metrics and movement of two sympatric carcharhinids: a comparison of the vulnerability of pelagic sharks of the southern Australian gulfs and shelves

P. J. Rogers[A,B,E], *C. Huveneers*[A,B], *S. D. Goldsworthy*[A], *W. W. L. Cheung*[C], *G. K. Jones*[A], *J. G. Mitchell*[B] *and L. Seuront*[B,D]

[A]SARDI Aquatic Sciences, Henley Beach, SA 5022, Australia.
[B]School of Biological Sciences, Flinders University, GPO Box 2100, Australia.
[C]Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
[D]Centre National de la Recherche Scientifique, Laboratoire d'Océanologie et de Géosciences, UMR 8187 LOG, Université des Sciences et Technologies de Lille, Station Marine, Wimereux, France
[E]Corresponding author. Email: paul.rogers@sa.gov.au

Abstract. The dusky shark *Carcharhinus obscurus* and the bronze whaler *Carcharhinus brachyurus* are large-bodied, marine predators that inhabit coastal and shelf waters of southern Australia. *C. obscurus* is considered to be among the most vulnerable pelagic sharks to overexploitation. This study focussed on population metrics and movement patterns of these sympatric species. Litters from two pregnant *C. brachyurus* were examined; these comprised 20 and 24 embryos, respectively. Tagging data indicated that 75% of whaler sharks tagged in this region by recreational fishers were juveniles, and 58% of recaptures occurred within 50 km of the tagging locations. Fishery catch samples comprised 99% juvenile *C. brachyurus* and *C. obscurus*. Our findings suggested that semi-protected gulf waters represented ecologically significant habitats of juveniles. A fuzzy-logic model showed that in terms of relative vulnerability to fishing, *C. brachyurus* ranked in the mid to lower end of the spectrum, when compared with six sympatric pelagic shark species, including the white shark, *Carcharodon carcharias*. Our findings emphasised a need for improvement to management measures for these carcharhinids, which are likely to play a significant role in the functioning of the temperate gulf and shelf ecosystems.

Additional keywords: ecologically significant habitats, ecosystems, fidelity, tagging.

Received 21 October 2011, accepted 18 October 2012, published online 6 February 2013

Introduction

Almost half of the global diversity of Chonrichthyans inhabit the continental shelves (Compagno 1990), and this is where many populations are targeted or taken as by-catch by fisheries. The collection of traits that together form the life-history strategies of some exploited species render them vulnerable to overfishing (Walker 1998), which is predicted to have flow-on ecosystem impacts (Stevens *et al.* 2000). Despite this, shark fisheries throughout the world are often managed using the same strategies as those used for more productive teleost fisheries.

Carcharhinids often use coastal habitats for parturition, foraging and as nurseries (Knip *et al.* 2010). Nurseries are where sharks: (i) are more commonly encountered compared with other areas; (ii) demonstrate a tendency to remain, or return, over extended periods; and (iii) use an area or site repeatedly over multiple years (Heupel *et al.* 2007). Conventional tag–recapture studies have provided valuable information on the movements and patterns of fidelity within nursery areas (Merson and Pratt 2001).

Previous studies of bronze whaler (copper shark) (*Carcharhinus brachyurus*) population demographics off South Africa (Smale 1991; Walter and Ebert 1991; Cliff and Dudley 1992; Dudley and Simpfendorfer 2006) and Argentina (Lucifora *et al.* 2005, 2009) indicated that this species grows slowly and is late to mature. No published demographic or movement data are available for *C. brachyurus* populations in Australia or New Zealand. Populations in these regions are genetically segregated from each other and those in Africa, making regional-scale assessments important as the data become available (Benavides *et al.* 2011). Past studies of the dusky shark (*Carcharhinus obscurus*) have used tag–recapture data to determine the growth rates of neonates and juveniles (Simpfendorfer 2000), and demographic data to assess the impacts of fishing mortality (McAuley *et al.* 2007; Kinney and Simpfendorfer 2009). *C. obscurus* were recently listed as globally 'vulnerable' by the International Union for Conservation of Nature (IUCN; IUCN Red List of Threatened Species) due to declining catch rates in several regions. In the north-west and western central

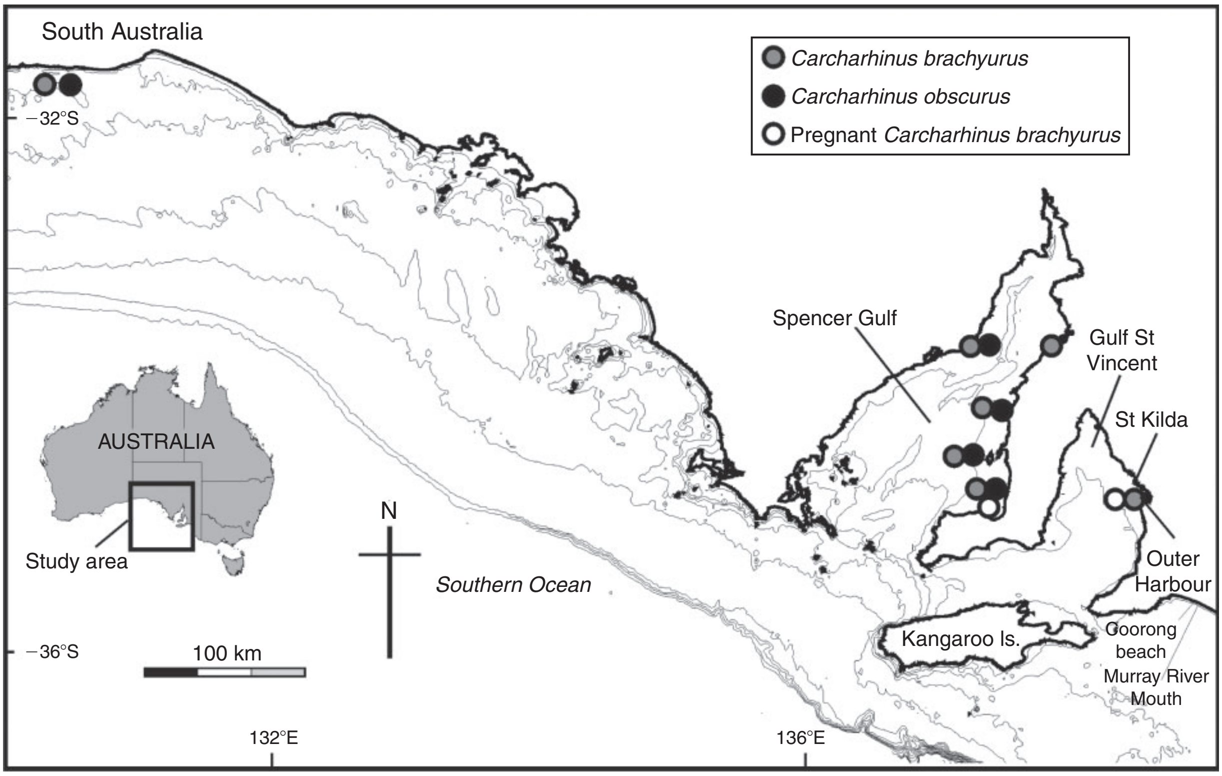

Fig. 1. Map showing the regions where bronze whalers (grey symbols) and dusky sharks (black symbols) were collected from commercial gill-net or long-line catches. White symbols indicate locations where pregnant bronze whalers were captured on long lines.

Atlantic, where this species has been commercially fished for several decades, it is currently listed as 'endangered'. Recent assessments showed substantial declines in Australian waters, yet the species was assessed as 'near threatened'. There is currently minimal published information with which to assess the status of *C. brachyurus* populations in Australian waters, and the species is listed globally as 'near threatened'.

The pelagic shark assemblage that inhabits the gulfs and shelves off southern Australia includes *C. brachyurus*, *C. obscurus*, blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), common thresher (*Alopias vulpinus*), white shark (*Carcharodon carcharias*), smooth hammerhead (*Sphyrna zygaena*) and porbeagle (*Lamna nasus*) (Last and Stevens 2009). South Australia (Fig. 1) represents the centre of the Australian distribution of *C. brachyurus*, and part of the southern range of *C. obscurus* (Cappo 1992; Last and Stevens 2009). The objective of the present study was to use the fuzzy-logic-based approach of Cheung *et al.* (2005, 2007) to test the hypothesis that *C. brachyurus* would have a similar intrinsic vulnerability to *C. obscurus*, and is more vulnerable than other pelagic sharks found in the gulf and shelf ecosystems off southern Australia. To test our hypothesis, we integrated new data on the population demographics and movement patterns of *C. brachyurus* and *C. obscurus* with published information for the other pelagic shark species that inhabit this ecologically important region.

Materials and methods

Study region

Gulf St Vincent and Spencer Gulf in South Australia (Fig. 1) are the only south-facing gulf systems in the southern hemisphere. The region has a temperate climate and the shelf ecosystem in the adjacent Great Australian Bight (GAB) is oceanographically unique, as it has northern boundary currents at the shelf-slope (Middleton and Bye 2007). Maximum water depths in the southern gulfs are ~50 m, and in shelf waters the depths predominantly range between 30 and 100 m. At the continental shelf slope the depths shelve rapidly from 160–200 to >1000 m.

Fishery information

Total annual landings of *C. brachyurus* (including misidentified *C. obscurus*) in the State-managed Marine Scalefish Fishery (MSF) were estimated from logbooks provided by commercial fishers to Primary Industries and Resources South Australia Fisheries. Gear types used in the MSF included surface and bottom-set long lines (undifferentiated in logbook data), hand lines and large mesh gill-net sizes (>15 cm). Maximum net lengths are 600 m in the State-managed gill-net fishery. Long lines consisted of floating rope main lines (7-mm diam.) with 1.7-mm stainless steel leaders with up to 400, 12–14/0 J-style hooks attached to the main line at even intervals by way of a stainless steel long-line clip. Main lines on long-lines were up to seven nautical miles long. Each terminal end was anchored and marked with large floats. Small floats were used to suspend the main line off the benthos between the hooks.

Estimates of total annual landings of *C. brachyurus* (now known to also include *C. obscurus*) in the Commonwealth-managed gill-net sector of the Gill-net Hook and Trap Fishery were provided by the Australian Fishery Management Authority and CSIRO, Hobart. This fishery operates in shelf waters of South Australia outside the two gulfs, including the area south and east of Kangaroo Island (Fig. 1). Large mesh monofilament gill-nets are used by the Commonwealth-managed gill-net fishery. The target species is the gummy shark (*Mustelus antarcticus*). Nets were ~4200-m long with a 1.5-m drop, and mesh sizes were 15.25–16.50 cm. The head line of the net generally consisted of floating rope and the foot line comprised sinking rope of a smaller diameter than that of the head-line.

Recreational fishery catch data were obtained from the National Recreational and Indigenous Fishery Survey for 2000–01 (Henry and Lyle 2003; Jones and Doonan 2005) and the South Australian Recreational Fishing survey in 2007–08 (Jones 2009). Recreational fishers suspended bait under balloons from boats and metropolitan jetties in Gulf St Vincent using heavy tackle (30–80-lb line) and leaders of 1.5–1.7-mm nylon-coated wire attached to 12/0 or 14/0 J-style hooks.

Sampling

C. brachyurus and *C. obscurus* were sampled from catches taken in the commercial and recreational fisheries in the spring–summer periods (October–March) in 2007, 2008, 2009 and 2010. Data were examined for 206 *C. brachyurus*, including 169 collected in Spencer Gulf in 2009 and 2010, 36 collected by observers in the GAB in 2007, and a single large mature female taken by a game fisher in Gulf St Vincent in 2009. Samples were collected during 37 separate commercial fishing days and comprised *C. brachyurus* (78%) and *C. obscurus* (22%). Sampling was based on access to commercial vessels and landed catches. Biological samples and associated metrics were collected from recreational-line, commercial gill-net and long-line catches.

Biological data

Body length, including total length (TL), fork length, pre-caudal length and trunk lengths (TK-L), were measured over the curve of the body on the dorsal side. All lengths were natural TL, unless otherwise indicated. For TK-L, the measurements were made between the head cut that coincided with the approximate position of the second or third post-cranial vertebrae and the pre-caudal pit. The approximate locations of the head cuts were consistent between the two commercial vessels on which TK-L were measured.

Two dissections of pregnant females (hereafter referred to as S1 and S2) were conducted; one in the laboratory and another onboard a commercial vessel. Linear regressions of the length metrics were fitted for both species. Percentage frequency histograms of TL were shown in 10-cm intervals. Body mass could not be measured onboard fishing vessels, and was estimated using available mass–length relations for *C. brachyurus* (Cliff and Dudley 1992) and *C. obscurus* (Dudley *et al.* 2005). Means ± 1 s.e. for metrics are provided in parentheses.

Sharks sampled on commercial long-line vessels in Spencer Gulf were assessed for sexual maturity. Sharks collected by observers on gill-net vessels in the GAB were only measured and sexed (due to time constraints). Males were assessed for sexual maturity by assessing the state and rigidity of claspers. Females were assessed for the presence of mating scars, developing follicles in ova and developing embryos. Size metrics and sexes of developing embryos and weight–yolk mass ratios were assessed for litters from two pregnant sharks.

Conventional tag–recapture information

Sharks identified as *C. brachyurus* were caught, tagged and released ($n = 1806$) by game fishers in South Australian waters between 1977 and 2008. Due to the likelihood that some *C. obscurus* were misidentified as *C. brachyurus*, we hereafter refer to this dataset as 'whaler spp.'. New South Wales Fisheries' conventional plastic tags with plastic or stainless-steel heads were inserted in the dorsal musculature of each shark using a tag pole. Each tag had an individual identification number, and return mailing details. Length (TL) was estimated for each shark and the capture–release date and location were written on tag cards and returned to the New South Wales Fisheries Game Fish Tagging Program, Cronulla Fisheries. Fishers returned the recapture information to Cronulla Fisheries.

To reduce the likelihood of other carcharhinids being included through misidentification, tag–recapture data recorded for 'whaler sharks' tagged between southern Western Australia and Tasmania were selected, as this precluded the known distributions of species with similar physical characteristics to *C. brachyurus* and *C. obscurus.*

MapInfo (Ver. 8) software was used to estimate minimum distance travelled along point to point vectors or around the coastline (where required) between the tag and recapture locations. The number of days at liberty following tagging was estimated by subtracting the tag and release date from the captured date. Size distributions of sharks based on estimated lengths-at-release were reported as a percentage-based length–frequency histogram.

Estimation and comparison of intrinsic vulnerabilities

The fuzzy-logic expert system model of Cheung *et al.* (2005, 2007) was used to assess the relative intrinsic vulnerabilities of *C. brachyurus* and *C. obscurus* to extinction, and to compare them to the vulnerabilities of five other pelagic shark species that inhabit southern gulf and shelf waters. In summary, this model used sets of logical rules to calculate vulnerability based on six life-history parameter estimates and baseline information on the strength of spatial behaviour, and geographic range. The fuzzy-logic indices have been shown to be significantly and positively related to rates of population decline, with species with higher intrinsic vulnerability generally declining at a faster rate given certain levels of fishing mortality (Cheung *et al.* 2005; Cheung and Pitcher 2008).

Input data included those collected during this study, and published life-history parameter estimates, including maximum length (fork-length was used in all cases), age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality rate and fecundity (median number of pups per female per year). Parameter rates were adjusted to reflect annual time scales. Based on the parameter estimates, the model classified each species into categories of life history and ecological characteristics with 'associated degrees of membership' using the fuzzy membership functions in Cheung *et al.* (2005, 2007). These then trigger the 'firing' of rules, developed from available published literature (refer to Cheung *et al.* 2005). Also, an intrinsic vulnerability index score (VI) was calculated, which scales from 1 to 100, with 100 being more vulnerable to fishing. The sensitivity of the model is described in detail by Cheung *et al.* (2005).

Results

Size distributions and estimated body mass

A total of 59 *C. obscurus* were collected from catches, including 10 from the GAB and 49 from Spencer Gulf. Of these, 58 were measured. In Spencer Gulf, males and females were 112–240 cm ($n = 25$) and 96–260 cm ($n = 22$), respectively (Fig. 2*a*). Ten *C. obscurus* from the GAB ranged from 107 to 256 cm and comprised six males, three females and one unsexed individual. In the GAB, males and females were 108–256 cm ($n = 6$) and 107–143 cm ($n = 3$), respectively. Body masses of *C. obscurus* estimated from a mass–length regression equation were between 6.7 and 107.3 kg for the sexes combined (35.9 ± 3.26, $n = 46$).

C. brachyurus sampled from catches in Spencer Gulf ranged in size between 71 and 305 cm TL (117 ± 2.2 cm, Fig. 2*b*). Two females were sexually mature, one of which was pregnant. Ninety-nine percent of *C. brachyurus* sampled from catches ranged between 71 and 177 cm TL (115 ± 1.5 cm), indicating a large gap in the size distribution between juveniles and the two mature females (Fig. 2*b*, *c*). Of the *C. brachyurus* that were sexed and measured ($n = 204$), males and females were 71–188 cm TL ($n = 96$) and 74–305 cm TL ($n = 108$), respectively. *C. brachyurus* sampled in the GAB ($n = 36$) ranged in size between 90 and 188 cm. Based on the size relationships of Lucifora *et al.* (2005), all specimens were probably immature. Two small juveniles of 71 and 74 cm with umbilical scars were observed in Spencer Gulf in mid-October 2009 and early February 2010, respectively. Body masses of *C. brachyurus* estimated from the mass–length regression equation of Cliff and Dudley (1992) ranged between 1.73 and 45.71 kg for males (9.35 ± 0.95 kg) and between 1.96 and 179.60 kg for females (14.93 ± 1.46 kg). Body length regression relationships are provided in the Supplementary Material.

Reproductive characteristics

Two pregnant female *C. brachyurus* (S1 and S2) and one mature female with vitellogenic follicles were examined. S1 was caught in northern Gulf St Vincent in January 2009, and S2 was taken in southern Spencer Gulf in February 2010 (Fig. 1). A total of 44 embryos were examined from two litters, including 24 late-term embryos in S1 (288 cm TL) and 20 late-term embryos in S2 (302 cm TL). The size range of embryos from S1 was 53–60.3 cm (58 ± 0.42 cm).

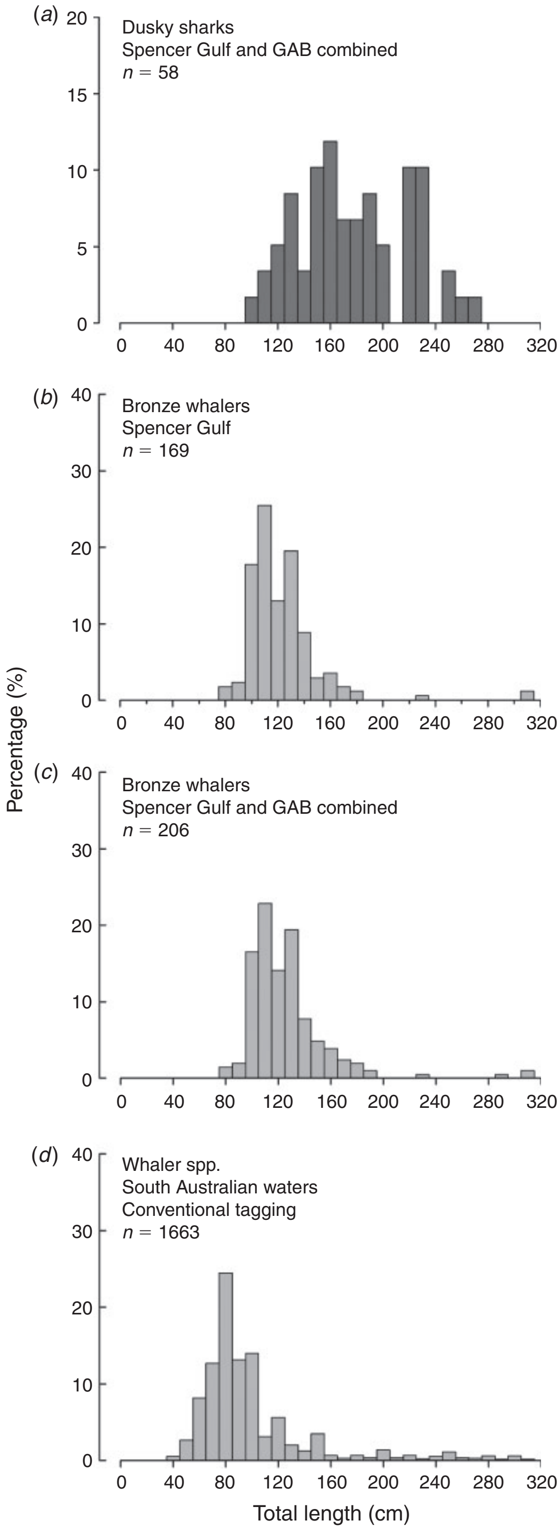

Fig. 2. Length–frequency distributions of (*a*) dusky sharks sampled in Spencer Gulf during this study and in the Great Australian Bight by observers, (*b*) bronze whalers sampled in Spencer Gulf during this study, bronze whalers sampled in Spencer Gulf and the Great Australian Bight, and (*d*) whaler spp. conventionally tagged by game fishers between November 1977 and April 2008. Bins are the upper end of 10-cm ranges.

Within the two uteri, embryos were separated by thick capillary tissue, and individually encapsulated within separate transparent sacs that contained 110–250 mL of clear uterine fluid. Embryo weights from S1 ranged between 889 and 1213 g (1214 ± 17.62 g). Embryo weight–yolk mass ratios for S1 ranged between 5.1 and 8.5% (6.9 ± 2.3%). The size range of embryos from S2 was 61–66 cm (64 ± 0.31 cm). Embryo weights and yolk mass could not be measured for S2 as the shark was dissected onboard a commercial vessel. The sex ratios of the litters were (0.50 : 0.50) 10 males : 10 females in S1, and (0.67 : 0.33) 16 males : 8 females) in S2. S1 and S2 both had light yellow-yolked follicles in the uteri that were 50–100 mm in diameter. In the uteri of S1, some mustard-coloured follicles were present.

A third mature female (305 cm TL) was sampled during February 2010 on the same day and at the same location as S2 (see Supplementary Material). Its uteri contained 34 vitellogenic follicles ranging in diameter from 5 to 21 mm (11.00 ± 0.78 mm). The uteri weighed 540 g. Another pregnant shark was captured in late September 2009 by commercial fishers and the litter size was reported to be 20 embryos.

Male to female sex ratios of *C. brachyurus* collected from gill-net catches in the GAB were 0.47 : 0.53 ($n = 36$). The sex ratio of males to females for samples collected from commercial long-line catches in Spencer Gulf was identical ($n = 165$) to those sampled in the GAB. Male to female sex ratios of *C. obscurus* collected from long-line catches in Spencer Gulf were 0.54 : 0.46 ($n = 48$).

Table 1. Release and recapture information for whaler sharks tagged off southern Australia between 1977 and 2008

DAL, days at liberty between tagging and recapture; Est. TL, estimated total length (cm); MDT, minimum distance travelled (km)

Release				Recapture				
Date	Locality	State	Est. TL	Date	Locality	State	DAL	MDT
18/04/1981	Perth	WA	105	3/03/1982	City Beach Perth	WA	319	0
2/12/1984	Outer Harbor	SA	66	12/12/1984	Outer Harbor	SA	10	0
26/01/1991	Port Adelaide	SA	113	12/12/1991	Outer Harbor	SA	320	0
3/04/1994	Black Pt	SA	100	28/12/1994	Black Pt	SA	269	0
5/02/1995	Nth Neptune Is.	SA	200	27/01/1998	N Neptune Is.	SA	1087	0
23/01/2000	Port Gawler	SA		15/02/2000	Port Gawler	SA	23	0
28/01/2001	Sealers Cove	Vic.		3/03/2001	Wilsons Prom.	Vic.	34	0
17/11/2006	St Kilda	SA	270	1/11/2008	St Kilda	SA	715	0
19/11/2007	St Kilda	SA	260	4/11/2008	St Kilda	SA	351	0
15/02/1987	C. Elizabeth	SA	100	9/03/1988	Port Hughes	SA	388	4
26/01/1995	Black Pt	SA	90	21/02/1995	Pine Pt	SA	26	6
5/03/1994	Sealers Cove	Vic.	80	5/11/1994	Rabbit Island	Vic.	245	12
10/10/1998	Outer Harbor	SA	60	26/02/2000	Port Gawler	SA	504	13
4/01/2008	Murray Mouth	SA	75	15/01/2008	S of Murray Mouth	SA	11	13
4/11/1990	Outer Harbor	SA	45	30/11/1990	Holdfast Bay	SA	26	25
18/03/1994	Ardrossan	SA	90	16/10/1994	Dublin	SA	212	25
1/02/1998	Sibsey Is.	SA	120	13/03/1998	Port Lincoln	SA	40	28
22/11/1996	Tickera	SA	60	4/12/1996	Port Broughton	SA	12	30
16/11/2000	Sealers Cove	Vic.	200	11/01/2001	Port Albert Entrance	Vic.	56	32
3/04/1994	Black Pt	SA	100	5/03/1995	Giles Pt	SA	336	41
27/03/1993	Sealers Cove	Vic.	61	29/11/1993	Toora	Vic.	247	41
25/04/1998	Pt. Perpendicular	SA	74	4/03/1999	Foul Bay	SA	313	45
26/11/1994	Pt Gawler	SA	70	14/12/1994	Ardrossan	SA	18	50
2/01/1988	Outer Harbor	SA	90	30/10/1990	Port Parham	SA	1032	64
26/11/2000	Rabbit Island	Vic.	120	3/01/2001	Woodside Bch	Vic.	38	65
29/01/1990	Sealers Cove	Vic.	76	21/03/1990	Seaspray	Vic.	51	105
23/03/1998	Stokes Bay	SA	70	6/04/2001	Cape Hart	SA	1110	109
15/03/1986	Carnac Is.	WA	100	30/03/1986	Bunbury	WA	15	133
28/12/1994	Black Pt	SA		22/07/1995	Cape Hart	SA	206	148
22/02/1989	Convention Bch	SA	100	14/05/1989	Spilsby Is.	SA	81	194
2/03/1995	English Is.	SA		4/01/1996	Yarraville Light	SA	308	199
11/02/1987	Convention Bch	SA	110	1/06/1989	Peake Bay	SA	841	203
18/02/1995	Sealers Cove	Vic.	100	14/04/1996	Pt Phillip Bay	Vic.	421	231
18/02/1995	Sealers Cove	Vic.	80	24/04/1995	C. Conran	Vic.	65	240
28/01/1991	Convention Bch	SA	90	2/02/1991	Outer Harbor	SA	5	249
14/12/1991	C. Spencer	SA	91	4/08/1994	Pearson Is.	SA	964	373
16/01/1990	Port River	SA	90	8/12/2000	Woodside Bch	Vic.	3979	1088
20/11/1982	Port Gawler	SA		18/01/1988	Isaacs Pt	Tas.	1885	1343
29/12/1986	Torrens Is.	SA	80	6/08/1989	Esperance	WA	951	1587
2/12/1990	Semaphore	SA	150	25/09/1993	Naturaliste Reef	WA	1028	2315

Tag–recapture data

Of the whaler spp. tagged in South Australia, 40 (2%) were recaptured in South Australia, Western Australia, Victoria and Tasmania for which useable data were recorded. Due to the coastal nature of most of the fishing, most of the latitude–longitude data were unreliable, as many positions were on land. Hence, only the tag–release and recapture location names were used (Table 1). The majority of whaler spp. tagged and released were juveniles estimated to be <120 cm (75%), and the remainder ranged up to ~310 cm TL (Fig. 2*d*). Most were tagged and released between November and March (Fig. 3). Of the 40 recaptures, 60% occurred during spring and summer, 30% occurred in autumn, and 10% occurred during winter. Fig. 4 shows the locations of tag and recapture events. Times elapsed between tag and recapture ranged between 5 days and 10.9 years. Minimum distances travelled were estimated at between 0 and 2315 km. Four sharks made broad-scale movements to Western Australia, Victoria and eastern Tasmania (Fig. 4). Table 2 provides a summary of further information on time scales of recaptures.

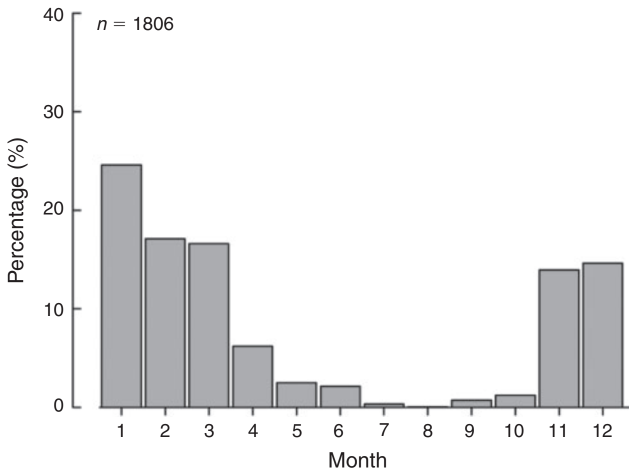

Fig. 3. Seasonal pattern of whaler species tagged and released using conventional game fish tags between 1977 and 2008.

Fishery information

Total annual landings of whaler spp. in the State-managed MSF increased from 23 t in 1984 to ~60 t in 1988 (see Supplementary Material). Total annual landings then ranged between 60 and 100 t between 1988 and 2008. Landings in the Commonwealth-managed fishery in South Australian waters fluctuated between 0 and 21 t per year. All estimated catch weights were based on

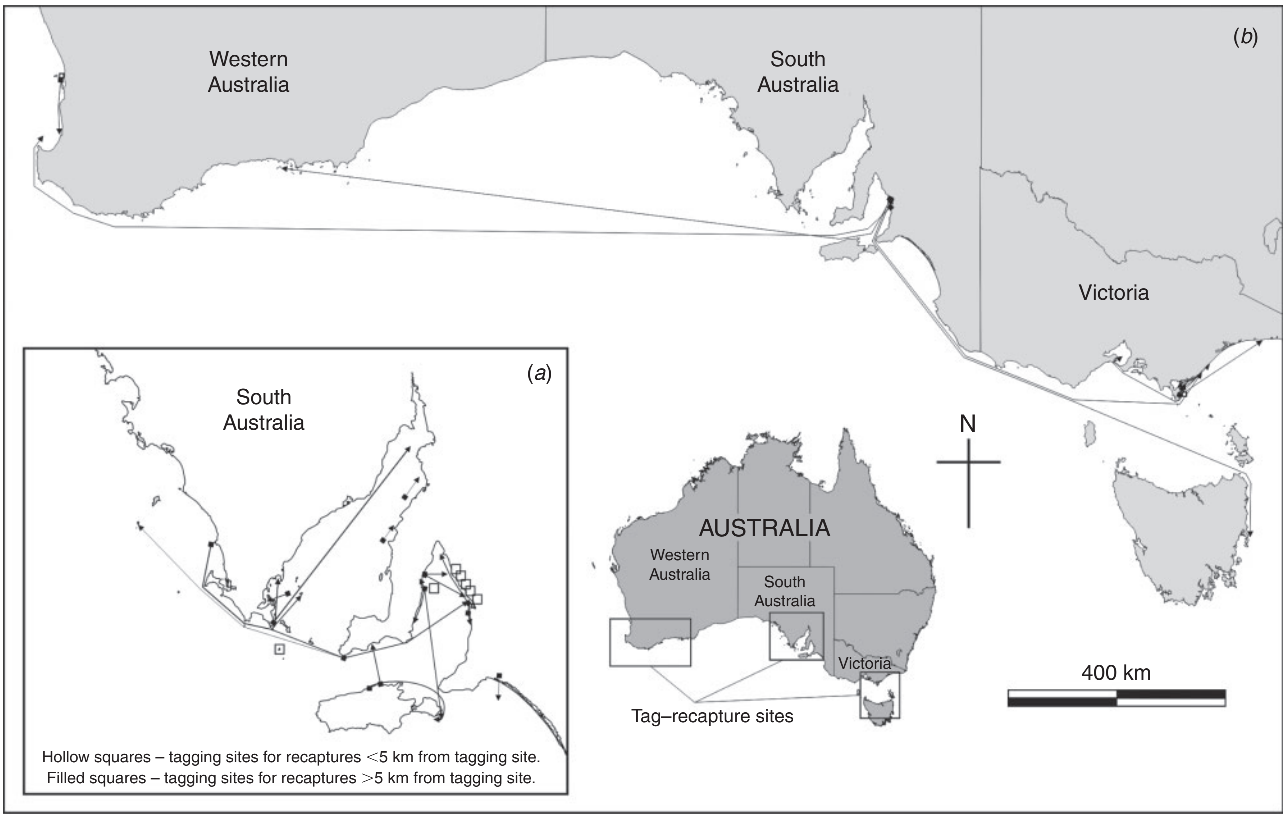

Fig. 4. Maps showing sites where whaler species were tagged, released and recaptured between 1977 and 2008. (*a*) Short-distance movements of 0–373 km within South Australian gulfs and the Great Australian Bight. (*b*) Long-distance movements from South Australia to Western Australia, Victoria and Tasmania, and short-distance movements within Western Australia and Victoria. Filled arrow heads represent the recapture locations for sharks recaptured >5 km from the tagging location.

trunks only. Cumulative landing of whaler spp. between 1984 and 2008 in the State-managed MSF was 1677 t (67 ± 4 t per year). In the Commonwealth fishery, between 1997 and 2008, the cumulative landing was 151 t. The total cumulative commercial landing for the State and Commonwealth fisheries combined over this period was 1828 t.

Data from the South Australian Recreational Fishing survey in 2000–01 showed 3447 individual whaler sharks were landed, of which 2889 (84%) were retained. In 2007–08, total landings declined substantially to 2195 individuals, of which 1413 (64%) were retained. A regional breakdown is provided in the Supplementary Material. Based on length–whole weight (L-W) relationships, mean weight by sex, and sex ratios for *C. brachyurus* in Spencer Gulf, we estimated that the retained recreational landings were 36 t in 2000–01 and 21 t in 2007–08.

Estimation and comparison of vulnerabilities

The best and most geographically relevant estimates of life-history parameters were compiled for *C. brachyurus*, *C. obscurus*, *P. glauca*, *I. oxyrinchus*, *C. carcharias*, *L. nasus* and *A. vulpinus* (Table 3) to calculate their intrinsic vulnerability index scores using the fuzzy-logic model (following Cheung *et al.* 2005). Analysis of the intrinsic vulnerability index scores of *C. obscurus* (VI = 81) and *C. brachyurus* (VI = 78) indicated that both carcharhinids were vulnerable to overfishing. *C. obscurus* were lower in terms of their vulnerability than *C. cacharias* (VI = 86) (Table 4), and higher than *I. oxyrinchus* and *L. nasus*, which both had VI of 80 (Table 4). *C. brachyurus* (VI = 78) scored in the middle of the vulnerability spectrum when compared with the other pelagic shark species we examined (Table 4). Model outputs showed that *C. brachyurus* had a higher score than two highly migratory species, *P. glauca* and *A. vulpinus*, which each had VI equal to 76.

Discussion

Misidentification of dusky sharks

Medium to large juvenile *C. obscurus* constituted approximately one-fifth of the samples we collected from catches in the commercial fishery for *C. brachyurus* off South Australia during this study. Previous studies have shown that the *C. obscurus*

Table 2. Summary of game fish tagging statistics for recaptured whaler sharks (*n* = 40) between 1977 and 2008

Statistic	*n*	%
Tagged in South Australia recaptured and in interstate waters	4	10
Recaptured ≤5 km from tagging locality	10	25
Recaptured ≤50 km from tagging locality	23	58
Recaptured >50 km from tagging locality	17	43
Recaptured in same year as tagged	17	43
Recaptured 1 year/season after tagging	13	33
Recaptured 2 years/seasons after tagging	6	15
Recaptured ≥3 years/seasons after tagging	4	10

Table 4. Comparisons of estimates of the vulnerability index scores (VI) of seven species of coastal and oceanic pelagic shark found in southern Australian shelf and gulf waters

The global the International Union for Conservation of Nature (IUCN) Red List status for each species is shown as are the ecological risk assessment (ERA) values provided by Simpfendorfer *et al.* (2008) for the highly migratory species. V = vulnerable, NT = near threatened

Common name	IUCN Red List status	VI	ERA
C. carcharias	V	86	–
C. obscurus	V	81	–
I. oxyrinchus	V	80	0.80
L. nasus	NT	80	0.48
C. brachyurus	NT	78	–
A. vulpinus	V	76	0.38
P. glauca	NT	76	0.29

Table 3. Life-history input parameter estimates of vulnerability for seven species of coastal and oceanic pelagic sharks

Parameters included maximum length (Lmax), age at sexual maturity (Tmat), length at sexual maturity (Lmat), von Bertallanfy growth constant (*K*), fecundity (annual female pup production, F), natural mortality rate (M) and maximum age (Tmax). Total lengths were converted to fork length using L-L equations in Fishbase (www.fishbase.org, verified 2 Feb 2012). K, F and M have the unit $year^{-1}$. Estimates of female pup production for *C. brachyurus* collected during this study were included in the median of the range based on published data

Scientific name	Lmax	Tmat	Lmat	*K*	F	M	Tmax	Parameter estimate sources (L to R)
C. brachyurus	266	20	177	0.0385	4	0.113	30	A, B, B, B, C, D, B
C. obscurus	297	29.6	254	0.037	2	0.113	55	E, F, F, F, F, D, F
P. glauca	318	7	180	0.126	15	0.223	20	E, G, H, I, J, D, J
I. oxyrinchus	364	19	281	0.013	2	0.160	28	K, K, K[m], L, M, D, L
A. vulpinus	274	5	160	0.129	0.5	0.234	22	N, O, O, O, P, D, O
C. carcharias	599	15	443	0.071	1	0.077	45	Q, R, R[m], R, R[m], S, R
L. nasus	183	13	172	0.066	3.75	0.150	26	T, U, H, U, T, U[m], U

[m]The estimate was the median of the published range.

Sources: [A]Randall *et al.* 1990; [B]Walter and Ebert 1991; [C]current study; [D]Smith *et al.* 1998; [E]Compagno 1984; [F]McAuley *et al.* 2007; [G]Stevens 1975; [H]Francis and Duffy 2005; [I]Manning and Francis 2005; [J]Nakano and Stevens 2008; [K]Stevens 2008; [L]Bishop *et al.* 2006; [M]Mollet *et al.* 2000; [N]Fishbase (www.fishbase.org, verified 2 Feb 2012); [O]Smith *et al.* 2008; [P]Mancini and Amorim 2006; [Q]Mollet *et al.* 1996; [R]Bruce 2008; [S]Mollet and Cailliet 2002; [T]Francis and Stevens 2000; [U]Francis *et al.* 2008.

population in neighbouring Western Australian waters was susceptible to the exploitation of these large juveniles (McAuley *et al.* 2005, 2007). Further studies are required to determine the degree of variation in the composition of the fishery catch in this southern portion of the range of *C. obscurus*, the extent to which this may be explained by seasonal variation in movement, and the degree of genetic connectivity within the broader South-West Marine Bioregion.

Sampling challenges

Sampling bias due to the differing size selectivities of commercial fishing gear types can be a challenging issue when undertaking fishery-dependent research. During this study, size selectivity was not considered to be a significant issue for 83% of samples collected from commercial long lines. However, the samples collected from commercial gill-net catches in the GAB were more likely to have been subject to size selectivity (the largest *C. obscurus* taken in gill nets was 256 cm TL). Despite this, the gill-net sampling occurred during an observer program and provided a rare opportunity to determine the pelagic shark species composition in an extremely isolated region of the fishery that is adjacent to a multiple-use marine protected area.

Characteristics of embryos and litters

Embryos examined from three pregnant *C. brachyurus* taken off Argentina had mean sizes of 57, 59 and 63 cm (Chiaramonte 1996; Lucifora *et al.* 2005). By comparison, examination of 46 litters of *C. brachyurus* collected off Africa showed the mean embryo size 54 cm (Cliff and Dudley 1992). The mean sizes of the two pregnant *C. brachyurus* (S1 and S2) we examined were similar at 58 and 64 cm, and the larger pup sizes occurred in the larger female, which is consistent with observations for *C. obscurus* (Hussey *et al.* 2010). The embryo sizes in the two litters we examined were similar to the observed size at birth (Smale 1991; Cliff and Dudley 1992), suggesting both sharks may have been near suitable pupping habitats. Previous estimates of litter size of *C. brachyurus* range between 8 and 20 embryos (Compagno 1984; Cliff and Dudley 1992), and 16 embryos were described from two litters off Argentina (Lucifora *et al.* 2005). Despite our small sample size, our litter size and embryo lengths for S1 were among the highest recorded for *C. brachyurus*. This was also interesting in the context of the genetic population structure, which shows that the Indian Ocean represents a geographical barrier to gene flow between Australian and South African populations (Benavides *et al.* 2011). While the existence of this genetic break represented a potential weakness in our study as some of the life-history data used in the vulnerability model were sourced from previous studies of distant southern hemisphere populations, we are confident the model provides a defensible starting point for future regional assessments. Future studies of the population demographics and reproductive biology of *C. brachyurus* within the Australian region will provide the information required to refine the model.

Tag–recapture information

There was a distinct seasonal trend in the conventional game-fish tag–release data, suggesting that this fishery targets *C. brachyurus* and *C. obscurus* that make predictable movements in the gulfs. A concerning finding during our study was that 43% of the recaptures occurred within the same year the sharks were tagged, indicating that fishing mortality in some areas may be particularly high. Tag–recapture data also suggested that site fidelity occurred, with several recaptures at and near the original tagging locations. A long-term acoustic tagging study of *C. brachyurus* and *C. obscurus* is underway within the northern gulfs of South Australia. This will help to resolve questions regarding the degree of philopatry and seasonal movement of these species over 10-year timeframes, as well as the manner in which juveniles and adults interact and differ in their site fidelity in coastal regions.

Evidence of ecologically significant habitats

Our study provided the first evidence that the southern Australian gulfs represent ecologically significant habitats for *C. brachyurus* and *C. obscurus.* Specifically, this included the presence of neonates with umbilical scars, pregnant females and the occurrence of fidelity and/or return movements by juveniles. Furthermore, a significant percentage (99%) of *C. brachyurus* and all *C. obscurus* collected from commercial catches were juveniles. Our findings also went part way to satisfying two of the three criteria that Heupel *et al.* (2007) used to define nurseries, e.g. sharks demonstrated a tendency to remain in or return to the region for extended periods, and used the same habitats over multiple years. However, given our low sample sizes for mature sharks, we suggest that further information is required on the spatial and temporal dynamics of these populations before these habitats can definitively be classified as nursery areas. The previously mentioned acoustic tagging study will provide further insights into the extent of residency of juveniles, which will be used to assess the importance of this region to these coastal predators.

Estimation and comparison of vulnerability

We rejected our hypothesis that *C. brachyurus* had a similar intrinsic vulnerability to *C. obscurus*, and was more vulnerable than other pelagic sharks that inhabit the southern Australian gulfs and shelves. The intrinsic vulnerability index estimates we calculated for *C. obscurus* and *C. brachyurus* were similar to those calculated previously for a broad group of Requiem sharks (carcharhinidae) (Cheung *et al.* 2007). By comparison, the VI were lower than for some slow-growing, deepwater sharks for which there is conservation and management concern, such as the gulper shark *Centrophorus granulosus* (VI = 90) (Cheung *et al.* 2007). Our results were also in agreement with earlier vulnerability estimates for *C. obscurus* and *C. brachyurus* that were based on previously available life-history parameter estimates (Cheung *et al.* 2007). Although our results suggested that *C. brachyurus* may be less vulnerable than *C. obscurus*, it is important to consider that both species had higher VI than some overfished teleosts, such as Orange roughy *Hoplostethus atlanticus* (VI = 64) (Hilborn *et al.* 2006; Cheung *et al.* 2007).

Interestingly, the VI we calculated for *C. brachyurus* using the most geographically relevant life-history parameter estimates available was also slightly higher than that for *A. vulpinus*, which is listed by the IUCN Red List as globally 'vulnerable'. In contrast, *C. brachyurus* is currently listed globally as 'near threatened', and as 'least concern' in Australia and New Zealand (Cavanagh *et al.* 2003). While the vulnerability of *C. obscurus* to overfishing has been described previously (Smith *et al.* 1998; Romine *et al.* 2009), our findings suggest that consideration should be given to improving management measures for both species. By comparison, *C. carcharias* is listed as 'vulnerable' by the IUCN, and protected by government legislation in Australian and New Zealand waters; *I. oxyrinchus* and *L. nasus* are listed as 'vulnerable' by the IUCN (Dulvy *et al.* 2008) and live by-caught sharks are protected from commercial fishing in Australian Commonwealth waters (Table 4); and *A. vulpinus* is protected in Australian Commonwealth waters between Cape Yorke and the Victorian–South Australian border under an agreement developed by the Indian Ocean Tropical Commission.

Our VI scores for the highly migratory pelagic shark species followed a similar pattern to ecological risk assessment (ERA) values calculated for key species taken in Atlantic long-line fisheries (Simpfendorfer *et al.* 2008). Table 4 shows a comparison of our VI scores and values used during the ERA. Notably, the largest incongruity between our VI scores and the ERA occurred for *L. nasus* and *I. oxyrinchus* populations. This may partially be explained by the different life-history metrics in the northern and southern hemispheres in the case of *L. nasus* (Simpfendorfer *et al.* 2008; Last and Stevens 2009), thus demonstrating the importance of regional-scale re-assessments for some species as improved life-history data becomes available in the future.

Conclusions

This study adopted the modelling framework developed by Cheung *et al.* (2005) for assessing the intrinsic vulnerabilities of marine species with different life-history strategies. We provided an example of a cost-efficient meta-analytical approach that could be readily adopted in other data-poor regions where listed and/or vulnerable species are being exploited for recreational and commercial purposes. This study was significant as it built on the findings of Cheung *et al.* (2007) and provided further evidence that *C. brachyurus* were ranked within the bounds of six other sympatric pelagic sharks, in terms of their intrinsic vulnerability to fishing. It also provided evidence that *C. obscurus* is vulnerable to additional mortality, in the targeted *C. brachyurus* fishery off southern Australia. This may be significant as a recent study demonstrated migratory connectivity in *C. obscurus* between South Australian and Western Australian waters (Rogers *et al.* 2013). Our findings provided government agencies with information required to reconsider the manner in which management strategies for these species are currently structured. Future consideration should be given to identifying and protecting the key juvenile and breeding life-history stages of both species, and implementing precautionary limitations on exploitation in ecologically significant habitats. Potential ecosystem impacts of removing large parts of the biomass of these coastal shark pelagic populations are uncertain, and therefore we suggest more precaution is urgently required.

Acknowledgements

This project was funded by Wildlife Conservation Fund. SARDI Aquatic Sciences and Flinders University provided logistical support. We thank fishers in the Marine Scalefish and the Gill-net Hook and Trap Fisheries for providing valuable logistical assistance. We acknowledge the contributions of the game fishers that tagged and recaptured sharks, and provided the data used in this study. Adam Welfare from the New South Wales Game Fish tagging Program (New South Wales Department of Primary Industries) provided access to the tag–recapture data. Derek Hamer and Alex Ivey helped collect biological data during a fishery observer program. Procedures were undertaken within Primary Industries and Resources of South Australia/SARDI Aquatic Sciences guidelines for animal ethics, and Flinders University's Animal Welfare Committee approval (project number 309). Fieldwork was undertaken under South Australian State government ministerial exemptions (Section 115, 9902094 and Section 59, 9902064). We thank two anonymous reviewers for constructive comments that helped to improve the manuscript. This is contribution #5 of the Southern Shark Ecology Group.

References

Benavides, M. T., Feldheim, K. A., Duffy, C. A., Wintner, S., Braccini, J. M., Boomer, J., Huveneers, C., Rogers, P., Mangel, J. C., Alfaro-Shigueto, J., Cartamil, D. P., and Chapman, D. D. (2011). Phylogeography of the copper shark (*Carcharhinus brachyurus*) in the southern hemisphere: implications for the conservation of a coastal apex predator. *Marine and Freshwater Research* **62**(7), 861–869. doi:10.1071/MF10236

Bishop, S. D. H., Francis, M. P., Duffy, C., and Montgomery, J. C. (2006). Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research* **57**, 143–154. doi:10.1071/MF05077

Bruce, B. D. (2008). The biology and ecology of the white shark, *Carcharodon carcharias*. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 69–76. (Blackwell Publishing: Oxford.)

Cappo, M. (1992). Bronze whaler sharks in South Australia. *SA Fisheries* **15–17**, 10–12.

Cavanagh, R. D., Kyne, P. M., Fowler, S. L., Musick, J. A., and Bennett, M. B. (2003). The Conservation Status of Australian Chondrichthyans: Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop. The University of Queensland, School of Biomedical Sciences, Brisbane, Australia.

Cheung, W. W. L., and Pitcher, T. J. (2008). Evaluating the status of exploited taxa in the northern South China Sea using intrinsic vulnerability and spatially explicit catch-per-unit-effort data. *Fisheries Research* **92**, 28–40. doi:10.1016/J.FISHRES.2007.12.018

Cheung, W. W. L., Pitcher, T. J., and Pauly, D. (2005). A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* **124**, 97–111. doi:10.1016/J.BIOCON.2005.01.017

Cheung, W. W. L., Pitcher, T. J., and Pauly, D. (2007). Intrinsic vulnerability in the global fish catch. *Marine Ecology Progress Series* **333**, 1–12. doi:10.3354/MEPS333001

Chiaramonte, G. E. (1996). Placentación en la "bacota", *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae): tipificación, descripción macroscópica y otros aspectos reproductivos. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Extra (Nueva Serie)* **130–145**, 1–7.

Cliff, G., and Dudley, S. F. J. (1992). Sharks caught in the protective gillnets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Gunther). *South African Journal of Marine Science* **12**, 663–674. doi:10.2989/02577619209504731

Compagno, L. J. V. (1984). FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Carcharhiniformes. FAO Fisheries Synopsis (125) Vol. 4(2). pp. 251–655.

Compagno, L. J. V. (1990). Alternative life-history styles of cartilaginous fishes in time and space. *Environmental Biology of Fishes* **28**, 33–75. doi:10.1007/BF00751027

Dudley, S. F. J., and Simpfendorfer, C. A. (2006). Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978–2003. *Marine and Freshwater Research* **57**, 225–240. doi:10.1071/MF05156

Dudley, S. F. J., Cliff, G., Zungu, M. P., and Smale, M. J. (2005). Sharks caught in the protective gill nets of KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818). *African Journal of Marine Science* **27**(1), 107–127. doi:10.2989/18142320509504072

Dulvy, N. K., Baum, J. K., Clarke, S. C., Compagno, L. J. V., Cortés, E., Domingo, A., Fordham, S., Fowler, S. L., Francis, M. P., Gibson, C., Martínez, J., Musick, J. A., Soldo, A., Stevens, J. D., and Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine & Freshwater Ecosystems* **18**, 459–482. doi:10.1002/AQC.975

Francis, M. P., and Duffy, C. (2005). Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fish Bulletin* **103**, 489–500.

Francis, M. P., and Stevens, J. D. (2000). Reproduction, embryonic development and growth of the porbeagle shark, *Lamna nasus*, in the Southwest Pacific Ocean. *Fish Bulletin* **98**, 41–63.

Francis, M. P., Natanson, L. J., and Campana, S. E. (2008). The biology and ecology of the Porbeagle shark, *Lamna nasus*. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 105–113. (Blackwell Publishing: Oxford.)

Henry, G. W., and Lyle, J. M. (2003). The National Recreational and Indigenous Fishing Survey. Report to the Fisheries Research and Development Corporation, 99/158, Canberra.

Heupel, M. R., Carlson, J. K., and Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definitions, characterization and assumptions. *Marine Ecology Progress Series* **337**, 287–297. doi:10.3354/MEPS337287

Hilborn, R., Analla, J., and Holland, D. S. (2006). The cost of overfishing and management strategies for new fisheries on slow growing fish: Orange roughy *Hoplostethus atlanticus* in New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2149–2153. doi:10.1139/F06-115

Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., and McNeil, M. A. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology* **79**, 184–193. doi:10.1111/J.1365-2656.2009.01623.X

Jones, K. (2009). South Australian Recreational Fishing Survey. PIRSA Fisheries Report, South Australian Fisheries Management Series Paper, No. 54. Adelaide.

Jones, K., and Doonan, A. M. (2005). 2000–01 National Recreational and Indigenous Fishing Survey: South Australian Regional Information, PIRSA Fisheries Report. Adelaide.

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

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. (2009). 'Sharks and Rays of Australia.' 2nd edn. (CSIRO Publishing: Melbourne)

Lucifora, L. O., Menni, R. C., and Escalante, A. H. (2005). Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from north Patagonia, Argentina. *ICES Journal of Marine Science* **62**, 107–115. doi:10.1016/J.ICESJMS.2004.09.003

Lucifora, L. O., Garcia, V. B., Menni, R. C., Escalante, A. H., and Hozbor, N. M. (2009). Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* **24**, 109–118. doi:10.1007/S11284-008-0487-Z

Mancini, P. L., and Amorim, A. F. (2006). Embryos of common thresher shark *Alopias vulpinus* in southern Brazil, South Atlantic Ocean. *Journal of Fish Biology* **69**, 318–321. doi:10.1111/J.1095-8649.2006.01107.X

Manning, M. J., and Francis, M. P. (2005). Age and growth of blue shark (*Prionace glauca*) from the New Zealand Exclusive Economic Zone. New Zealand Fisheries Assessment Report 2005/26. Ministry of Fisheries, Wellington, New Zealand.

McAuley, R., Lenanton, R., Chidlow, J., Allison, R., and Heist, E. (2005). Biology and stock assessment of the thick skin (sandbar) shark, *Carcharhinus plumbeus*, in Western Australia and further refinement of the dusky shark, *Carcharhinus obscurus*, stock assessment, Final FRDC Report – Project 2000/134, Fisheries Research Report No. 151. Department of Fisheries, Western Australia.

McAuley, R. B., Simpfendorfer, C. A., and Hall, N. G. (2007). A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. *ICES Journal of Marine Science* **64**, 1710–1722. doi:10.1093/ICESJMS/FSM146

Merson, R. R., and Pratt, H. L., Jr (2001). Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. *Environmental Biology of Fishes* **61**, 13–24. doi:10.1023/A:1011017109776

Middleton, J. F., and Bye, J. A. T. (2007). A review of the shelf-slope circulation along Australia's southern shelves: Cape Leeuwin to Portland. *Progress in Oceanography* **75**, 1–41. doi:10.1016/J.POCEAN.2007.07.001

Mollet, H. F. D., and Cailliet, G. M. (2002). Comparative population demography of elasmobranchs using life history tables. Leslie matrices and stage-based matrix models. *Marine and Freshwater Research* **53**, 503–516. doi:10.1071/MF01083

Mollet, H. F. D., Cailliet, G. M., Klimley, A. P., Ebert, D. A., Testi, A. D., and Compagno, L. J. V. (1996). A review of length validation methods and protocols to measure large white sharks. In 'Great White Sharks: The biology of *Carcharodon caracharias*'. (Eds P. Klimley and D. G. Ainley.) pp. 91–108. (Academic Press: San Diego, CA.)

Mollet, H. F., Cliff, G., Pratt, H. L., and Stevens, J. D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fish Bulletin* **98**, 299–318.

Nakano, H., and Stevens, J. D. (2008). The biology and ecology of the blue shark. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 140–148. (Blackwell Publishing: Oxford.)

Randall, J. E., Allen, G. R., and Steene, R. C. (1990). 'Fishes of the Great Barrier Reef and Coral Sea.' (University of Hawaii Press: Honolulu.)

Rogers, P. J., Huveneers, C., Goldsworthy, S. D., Mitchell, J. G., and Seuront, L. (2013). Broad-scale movements and pelagic habitat of the dusky shark *Carcharhinus obscurus* off southern Australia determined using pop-up satellite tags. *Fisheries Oceanography* **22**, 102–112. doi:10.1111/FOG.12009

Romine, J. G., Musick, J. A., and Burgess, G. H. (2009). Demographic analyses of the dusky shark, *Carcharhinus obscurus*, in the Northwest Atlantic incorporating hooking mortality estimates and revised reproductive parameters. *Environmental Biology of Fishes* **84**, 277–289. doi:10.1007/S10641-008-9435-6

Simpfendorfer, C. A. (2000). Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag-recapture data. *Fish Bulletin* **98**, 811–822.

Simpfendorfer, C., Cortés, E., Heupel, M. R., Brooks, E., Babcock, E. A., Baum, J. K., McAuley, R., Dudley, S. F. J., Stevens, J. D., Fordham, S., and Soldo, A. (2008). An integrated approach to determining the risk of over-exploitation for data-poor pelagic Atlantic sharks. An Expert Working Group Report. Lenfest Ocean Program, Washington.

Smale, M. J. (1991). Occurrence and feeding of three shark species, *Charcharhinus brachyurus, C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape Coast of South Africa. *South African Journal of Marine Science* **11**, 31–42. doi:10.2989/025776191784287808

Smith, S. E., Au, W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**, 663–678. doi:10.1071/MF97135

Smith, S. E., Rasmussen, R. C., Ramon, D. A., and Calliet, G. M. (2008). The biology and ecology of thresher sharks. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 60–68. (Blackwell Publishing: Oxford.)

Stevens, J. D. (1975). Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *Journal of the Marine Biological Association of the United Kingdom* **55**, 657–665. doi:10.1017/S0025315400017318

Stevens, J. D. (2008). The biology and ecology of the shortfin mako shark, *Isurus oxyrinchus*. In 'Sharks of the Open Ocean'. (Eds M. D. Camhi, E. K. Pikitch and E. A. Babcock.) pp. 87–94. (Blackwell Publishing: Oxford.)

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**, 476–494. doi:10.1006/JMSC.2000.0724

Walker, T. I. (1998). Can shark resources be managed sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* **49**, 553–572.

Walter, J. P., and Ebert, D. A. (1991). Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from Southern Africa, with a review of some life history parameters. *South African Journal of Marine Science* **10**, 37–44. doi:10.2989/02577619109504617