

1 **Broad-scale coastal movements of white sharks off Western Australia described by**
2 **passive acoustic telemetry data**

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13

14 **Abstract**

15 Movements of 89 acoustically-tagged sub-adult and adult white sharks (*Carcharodon*
16 *carcharias*) were monitored off the South and West coasts of Western Australia (WA)
17 between December 2008 and May 2016 by a network of up to 343 passive acoustic
18 receivers. A total of 290 inter-regional movements, totalling 185,092km were recorded for
19 73 of these sharks. Estimated rates of movement in excess of 3 km per hour (mean=1.7
20 kmh⁻¹; max=5.6 kmh⁻¹) were common, even over distances of thousands of kilometres.
21 Detections indicated that white sharks may be present off most of the South and lower
22 West coasts of WA coast throughout the year, although they are more likely to be
23 encountered during spring and early summer and are least likely to be present during late
24 summer and autumn. There was limited evidence of predictable return behaviour; seasonal
25 movement patterns or coordination of the direction and timing of individual sharks'
26 movements. Nevertheless, the data suggested that further analyses of movements in
27 relation to ecological factors might be useful predictors of shark activity at local scales. It
28 is hoped that these data may be useful for informing public safety initiatives aimed at
29 mitigating the risks associated with human encounters with white sharks off the WA coast.

30

31 **Introduction**

32

33 White sharks (*Carcharodon carcharias*) have a circum-global distribution in temperate to
34 tropical latitudes (Compagno, 2001; Last and Stevens, 2009), where they are most

35 commonly found in temperate continental shelf waters and around oceanic islands,
36 although in some regions they may spend considerable periods in the open ocean (Weng et
37 al., 2007; Bruce, 2008; Domier and Nasby-Lucas, 2008). The species is most frequently
38 encountered off South Africa (Cliff et al., 1996; Kock et al., 2013), southern Australia
39 (Bruce et al., 2006), New Zealand (Duffy et al., 2012), northern California (Boustany et
40 al., 2012), Mexico (Domier and Nasby-Lucas, 2012; Santana-Morales et al., 2012) and the
41 north eastern United States (Casey and Pratt, 1985; Skomal et al., 2012). In regions where
42 *C. carcharias* is relatively common, individuals are widely but not evenly distributed and
43 occur in low abundance, although in some areas they may be more locally-abundant
44 around pinniped colonies (Bruce 1992; Bruce and Bradford, 2015; Francis et al., 2015;
45 Klimley, 1985; Kock et al., 2013; Malcolm et al., 2001; Robbins and Booth, 2012; Skomal
46 et al., 2012). Satellite-tagged white sharks have repeatedly been shown to travel thousands
47 of kilometres through continental shelf and oceanic waters (Bruce et al., 2006; Weng et al.,
48 2007; Domier and Nasby-Lucas, 2008; Duffy et al., 2012) and trans-oceanic return
49 movements have been documented for the species between South Africa and North-West
50 Australia (Bonfil et al. 2005). A common feature of previous studies has been seasonal or,
51 in some cases, more frequent returns to tagging sites (Bonfil et al., 2005; Boustany et al.,
52 2002; Domier and Nasby-Lucas, 2008; Weng and Honebrink, 2013).

53

54 In Australia, white sharks most commonly occur across the southern half of the continent,
55 from central Queensland on the East coast to North-West Cape in Western Australia but
56 may occasionally occur further north on both coasts (Paterson, 1990; Bruce et al., 2006;
57 Last and Stevens 2009). Adult and sub-adult white sharks appear to occur particularly
58 frequently around some fur seal and sea lion colonies off the south coast of the continent,
59 including the Neptune Islands in South Australia (SA), areas of the Great Australian Bight
60 and the Recherche Archipelago in Western Australia (Malcolm et al., 2001). Based on
61 observations of temporal changes in the size and sex of sharks around the Neptune Islands
62 (Robbins, 2007; Robbins and Booth, 2012; Bruce and Bradford, 2015), acoustic telemetry
63 data (Bruce et al., 2005a; Bruce and Bradford, 2011; Rogers and Huvaneers, 2016) and
64 satellite tracking (Bruce et al., 2005b; Bruce and Stevens, 2006), it is apparent that
65 individual sharks do not, however, permanently reside at these locations and actually
66 spend the majority of their time away from them. Satellite-tracking has shown sharks from
67 the Neptune Islands undertake extensive coastal movements to North West Cape in WA
68 and return movements to Rockhampton in Queensland (Bruce et al., 2006). Long-distance

69 movements have also been documented between eastern Tasmania and the southern Great
70 Barrier Reef (Bruce and Bradford, 2012). However, no individuals have been observed to
71 travel up both west and east coasts of Australia and, genetic evidence suggests that sharks
72 off the eastern and western coasts effectively form two functionally-separate populations
73 in Australian waters (Blower et al., 2012).

74

75 Despite their perceived association with pinniped prey, white sharks are versatile predators
76 that feed on teleosts and other elasmobranchs throughout life (Bruce, 1992), adding larger
77 prey items to their diet as sub-adults (Malcolm et al., 2001). White sharks first commonly
78 appear at fur seal (*Arctocephalus pusillus doriferus* and *Arctocephalus forsteri*) and
79 Australian sea lion (*Neophoca cinerea*) colonies in Australia by about 3.0m Total Length
80 (TL), which probably indicates the size at which marine mammals are added to their diet.
81 The smallest examined white shark from Australian waters to contain pinniped remains in
82 its stomach was 2.7m TL (Malcolm et al., 2001). These observations are consistent with
83 vertebral isotope analyses which indicate a dietary shift to include marine mammals by
84 approximately 3.4 m (Estrada et al., 2006). Adult, sub-adult and juvenile white sharks are
85 also frequently observed scavenging on whale carcasses (Carey et al., 1985; Curtis et al.,
86 2006; Dicken, 2008) and may be particularly active around whale stranding sites (Bruce
87 and Stevens, 2004). The species has also been recorded to feed on sunfish, tuna, birds, sea
88 otters and turtles (Ames et al. 1996; Fergusson et al., 2000; Kim et al., 2013). Due to their
89 large size, generally coastal distribution, dietary versatility and variety of predatory
90 behaviours, white sharks can pose a threat to human safety and have been responsible for
91 numerous injurious and fatal encounters with people throughout their range but especially
92 in Australian waters (West, 1993; 2011).

93

94 Although human encounters with sharks, including white sharks, very rarely result in
95 injuries, shark bites can have traumatic consequences for those involved, their families,
96 friends and affected communities. Furthermore, shark bites often receive
97 disproportionately high levels of media attention and may have flow-on economic effects
98 for tourism and other marine-related industries (Francis, 2011; Neff, 2012; Neff and Yang,
99 2012). Bites from white sharks can be especially traumatic and in the 50 years between
100 1966 and 2015, inclusive, this species has reportedly been responsible for twice as many
101 fatalities in Australia (n=42) than all other shark species combined (n=21; ASAF, 2015).
102 In WA waters, a total of 95 injurious and 26 fatal shark attacks have been recorded

103 between March 1803 and December 2015, inclusive (ASAF, 2015). Although the annual
104 frequency of those incidents has been highly variable, there has been an increasing trend
105 since the 1970s (West, 2011; Anon., 2012). Notwithstanding under-estimation of historical
106 shark bite records due to a lack of organised data collection programs before the late
107 1980s, approximately half of all recorded shark attacks (n=65) and fatalities (n=12) in WA
108 have occurred during the two decades between 1 January 1996 and 31 December 2015.
109 The last ten fatalities, all of which involved white sharks, took place over an
110 approximately 6 year period between August 2010 and June 2016.

111

112 In response to the increasing frequency of white shark bites and encounters around the WA
113 coast, a number of initiatives to monitor potential shark hazards and study white sharks'
114 local ecology have been introduced. The research reported here was undertaken to describe
115 when, where and why this species occurs off the most populated parts of the WA coastline,
116 to help in understanding the complex and dynamic interactions between sharks' and
117 humans' abundance, distributions and behaviours that contribute to white shark bites.
118 Specifically, the objectives of the study were to investigate (i) patterns of white sharks'
119 occurrence and movements off WA's south-west and lower-west coasts; (ii) their large-
120 scale movements between South and Western Australia and (iii) whether individual sharks
121 repeatedly visit or are resident at particular locations off the WA coast. It is intended that
122 results from this study of the species' coastal movements might be useful for developing
123 effective, evidence-based strategies for mitigating the risks associated with human
124 encounters with this species in Western Australia and internationally where white shark
125 bites are an issue of concern.

126

127 **Materials and methods**

128

129 *Tagging*

130

131 A total of 234 *C. carcharias* were 'tagged' with Vemco V16-6H, V16-6L and V16-5L
132 acoustic transmitters with random transmission intervals of between 50 and 130 seconds
133 (V16-6H, V16-6L) or 70 to 150 seconds (V16-5L). Transmitters were fitted to sharks
134 between 20 December 2007 and 30 December 2015, off South Australia (n=177) and
135 Western Australia (n=57), during cage diving tourism operations at the Neptune Islands,
136 targeted research activities in both States and opportunistically in WA, usually when

137 sharks were encountered scavenging whale carcasses (Figure 1). Transmitters were
138 externally-fitted to all of the sharks tagged in SA and to 48 of the WA-tagged sharks, via
139 1.6mm diameter 316-grade stainless steel wire rope tethers attached to sharpened stainless
140 steel anchors. These external ‘tags’ were embedded in sharks’ dorsal musculature using
141 applicator needles mounted on fiberglass hand-spears as they swam past tagging vessels.
142 Between October 2012 and September 2015, 37 sharks were caught off the lower west and
143 South coasts of WA during targeted research fishing with individual baited setlines.
144 Captured sharks (which included 28 of the 48 fitted with external tags in WA) were
145 secured in an inverted position alongside tagging vessels and V16-5L and V16-6L
146 transmitters were surgically-implanted in their abdominal cavities according to standard
147 techniques (eg. Heupel and Hueter, 2001). Internally-tagged sharks were also tagged with
148 uniquely-numbered Jumbo Rototags (Dalton ID Systems Ltd., Henley on Thames,
149 Oxon. UK) in their first dorsal fins for future visual recognition before being revived and
150 released. Two of the dual-acoustically sharks tagged with both internal and external
151 transmitters, were recaptured and re-tagged with new internal and external transmitters
152 after 347 and 372 days at liberty. A third shark which had previously been fitted with an
153 external tag at the Neptune Islands, was also re-tagged with new internal and external
154 transmitters, when captured off Albany (35.03°S 117.90°E) after 510 days at liberty.
155 Sharks were sexed and either measured to the nearest centimetre Fork Length (FL) when
156 captured for internal tagging; or Total Length (TL) was visually-estimated to the nearest
157 10cm when free-swimming sharks were externally-tagged (Figure 2). As data were not
158 collected to convert estimated and measured lengths, these length units are reported
159 separately below.

160

161 *Monitoring*

162

163 Tagged sharks were monitored by 13 arrays of up to 334 passive (Vemco VR2W and
164 VR4G) acoustic receivers off the WA coast between North-West Cape and Cape Le Grand
165 and in Gulf St. Vincent and at the Neptune Islands in South Australia (Figure 3A).
166 Receiver arrays were deployed in seven (7) different regions: Ningaloo Reef (n=42)¹,
167 metropolitan Perth (n=134-143)², South-West WA (n=52), Chatham Island (n=44),

¹ Integrated Marine Observing System’s (IMOS) Animal Tracking Facility (<http://imos.org.au/animaltracking>)

² Including 53 Ocean Tracking Network receivers (<http://oceantrackingnetwork.org/>)

168 Albany-Bald Island (n=35 plus 6 temporary receivers at Two Peoples Bay), the Recherche
169 Archipelago (n=5-18; Figure 3B-3F, respectively) and South Australia (n=3)³. The
170 locations of arrays to the south of Ningaloo Reef were chosen for logistical reasons and to
171 reflect the presumed area of greatest overlap between shark and human population
172 abundance. Because receivers were operated by four different organisations for six
173 separate projects, the numbers, configurations and operational periods of each array varied
174 over the course of this study (Table 1). As the occurrence and movements of sharks
175 outside of WA are largely beyond the scope of these analyses, only sharks' first and last
176 detections by SA-located receivers (ie. start and end points of each inter-state movement)
177 are referred to below.

178

179 **Figure 3.**

180

181 **Table 1.**

182

183 Data were generally retrieved annually from VR2W receivers (bi-annually from IMOS
184 Animal Tracking receivers at Ningaloo in some years) and weekly (until 31 May 2016)
185 from satellite-linked VR4G receivers. All the detection data reported below were collected
186 prior to May 31 2016.

187

188 ***Movement estimation***

189

190 Distances of tagged sharks' movements between acoustic receiver arrays and/or release
191 and recapture⁴ locations ($\Delta\sigma$), were calculated as least-possible distance vectors between
192 successive points, according to the great-circle (or orthodromic) equation:

$$193 \quad \text{distance} = \arccos[\sin\phi_1 \cdot \sin\phi_2 + \cos\phi_1 \cdot \cos\phi_2 \cdot \cos(\lambda_1 - \lambda_2)].r$$

194 Where ϕ_1 , λ_1 and ϕ_2 , λ_2 are the latitude and longitude of receivers 1 and 2 and r is the
195 radius of the earth (in radians).

196

³ Operated by Commonwealth Scientific and Industrial Research Organisation (CSIRO) at the Neptune Islands (Bradford et al., 2013) and IMOS in Gulf St. Vincent (Huveneers et al., 2014)

⁴ Including the location at which a 3.86m FL male shark beached itself.

197 To avoid unrealistically estimating movements across land, vectors were forced around
198 arbitrary turning points where necessary. Turning point locations were the same for all
199 sharks and defined as the following points off:

200 Dirk Hartog Island (25.5⁰S 118.0⁰E); Cape Naturaliste (33.5⁰S 115.0⁰E); Cape
201 Leeuwin (34.4⁰S 114.9⁰E); Black Point (35.0⁰S 116.0⁰E); Albany (35.2⁰S
202 118.0⁰E) and Cape Arid (34.1⁰S 123.3⁰E)

203 As movement vectors assume constant straight-line travel between points, they represent
204 the minimum possible distances travelled and by derivation, associated Rates of
205 Movement (RoM) are minimum constant speeds over those distances.

206

207 **Results**

208

209 Including release and recapture events, 89 acoustically-tagged white sharks were detected
210 a total of 29,171 times between December 2008 and May 2016, within the area monitored
211 by combined WA receiver arrays (Figure 4). The largest number of sharks (n=52) and
212 majority of detections (n=21,199) were recorded in the Perth metropolitan region, where
213 the largest number of receivers were located over the longest period. The next-largest
214 number of sharks (n=43) was detected over approximately 4 years by the Bald Island
215 array, followed by the Chatham Island (n=31 sharks) and Cape Leeuwin (n=24 sharks)
216 arrays, from which 3 years of data were available. Due to receivers' variable periods of
217 operation, detection data were standardised by the number of days receivers were in
218 operation. Three receivers in a temporary 6-receiver array, deployed between 24 July and
219 17 November 2011 at the site of a whale carcass stranding in Two People's Bay (25km
220 East of Albany; Figure 4D), were the most active in the network, with detection rates of
221 383-732 detections per 100 days of operation (100d⁻¹). These rates were 3.6 - 6.8 times
222 higher than the next highest detection rate by a receiver at Salisbury Island, in the
223 Recherche Archipelago (Figure 4E, right panel) and more than 80 times the mean rate of
224 all other WA-located receivers (4.5 100d⁻¹, S.D.= 8.6).

225 **Figure 4.**

226

227 Excluding the temporary receivers in Two Peoples Bay, the Recherche Archipelago array
228 was the most active in the network, with a mean detection rate of 18.6 detections 100d⁻¹
229 (S.D.=23.4). The two VR4G receivers in King George Sound off Albany recorded the next

230 highest mean rate of 8.5 detections $100d^{-1}$, followed by the combined metropolitan arrays
231 (6.1 detections $100d^{-1}$, S.D.=10.5), the Geographe Bay/Cape Naturaliste VR4G array (4.2
232 detections $100d^{-1}$, S.D.=7.1), Bald Island (3.0 detections $100d^{-1}$, S.D.=2.4), Cape Leeuwin
233 (2.3 detections $100d^{-1}$, S.D.=2.2) and Chatham Island (1.7 detections $100d^{-1}$, S.D.=1.4)
234 arrays. Unsurprisingly for a species with a primarily temperate distribution, receivers in
235 tropical waters of the IMOS Ningaloo array recorded the lowest mean rate of 0.1
236 detections $100d^{-1}$. Caution should be used in interpreting detection rates at these regional
237 levels however, as data were strongly influenced by extended detection periods of small
238 numbers of sharks. For example, 146 of the 153 *C. carcharias* detections by the Albany
239 receivers were of a single 5.04m FL female shark that was detected on 15 days between 26
240 March and 30 April 2014. In the Recherche array, two sharks accounted for 81% of
241 detections and in the combined Perth arrays, 78% of detections were from just six sharks
242 (9% and 12% of sharks detected in those regions, respectively).

243

244 Detection data from the cross-shelf arrays off metropolitan Perth, Cape Leeuwin, Chatham
245 Island and Bald Island, were characterised by discrete offshore peaks in detection rates by
246 receivers located in 70m to 120m depths (Figure 4B-D). Similarly, higher numbers of
247 individual sharks were detected in offshore waters off the Perth Metropolitan coast, Cape
248 Leeuwin, Chatham Island and Bald Island (Figure 5). Conversely, although the Recherche
249 array spanned a smaller extent of the continental shelf, detection rates were higher inshore
250 of Mondrain Island than offshore. However, in the most-thoroughly monitored region off
251 metropolitan Perth, tagged sharks were most-frequently but unevenly detected by receivers
252 within seven kilometres of the mainland coast. In the southern metropolitan region, sharks
253 were detected in and across the mouth of Cockburn Sound (17.0 $100d^{-1}$, S.D.=18.9) at
254 nearly 10 times the rate of receivers along the northern metropolitan coast (1.9 $100d^{-1}$,
255 S.D.=2.4; Figure 4B). Although the configuration and numbers of receivers differed
256 between northern and southern metropolitan waters, comparison of detection rates by
257 receivers located similar distances from shore, showed similar levels of disparity in
258 detection rates between north and south. In addition, Cockburn Sound receivers detected
259 nearly twice as many different sharks (max.=12, mean=6.6, S.D.=3.8) than receivers off
260 the northern coast (max.=7, mean=3.8, S.D.=2.0) and 19 of the 25 sharks tagged in the
261 metropolitan region were also located inside Cockburn Sound or adjacent waters.

262

263 **Figure 5.**

264

265 Pooled multi-year detection data indicated that *C. carcharias* may be present off the lower-
266 West and South coasts of WA throughout the year, although the number of sharks detected
267 and mean detection periods differed seasonally (Figure 6). Sharks were sporadically
268 detected at Ningaloo Reef in winter (June-August) and late spring (November) to summer
269 (December- January) but too few sharks were detected to suggest these detections might
270 represent a consistent pattern of occurrence in the region. Off metropolitan Perth, the
271 numbers of recorded sharks and detection rate increased through winter, before peaking in
272 spring (October). While relatively high numbers of sharks were also detected off Perth in
273 November and December, the steep decline in detection rates over those months indicated
274 that the amount of time sharks spent within monitored areas in the region was much lower.
275 To the South, the mode of detected shark frequency in Geographe Bay and Cape Leeuwin
276 was December, although the peak in monthly detection rates was slightly earlier in
277 October. The number of sharks detected off the western South coast (Chatham and Bald
278 Islands) was slightly more consistent throughout most months, although there were distinct
279 troughs in the numbers of sharks detected by these arrays between April and July and
280 February to June, respectively. Although pooled monthly detection rates also suggested
281 relatively low levels of shark activity in the Recherche Archipelago between December
282 and February, detections were highly variable and monthly monitoring effort was uneven
283 due to the 18 month data collection period (Nov 2014 - Apr 2016, Table 1). Thus, seasonal
284 patterns of shark activity remain unclear in this region.

285

286 Including data from first and last detections by South Australian receivers and sharks'
287 known release and recapture locations, a total of 293 inter-array and inter-regional
288 movement vectors were estimated for 73 individual sharks. Cumulatively, all estimated
289 movement vectors totalled 186,387km. The maximum individual movement distance
290 (between the Neptune Islands and Ningaloo Reef before arrays were installed off the South
291 and South-West coasts of WA) was estimated to be 3,375 km. However, nearly half of the
292 estimated individual movements (n=145) were between adjacent receiver arrays or release
293 and recapture locations, over distances of less than 300km (Figure 7A). Of the other 148
294 movements, 67 exceeded 1,000km, 18 were over 2,000km and 6 were over distances of
295 more than 3,000km. Multiple inter-regional movements were recorded for most tagged
296 sharks (n=47) and individuals were recorded travelling cumulative distances of up to
297 6,986km (mean=2,553km; S.D.=1,733km, Figure 7B). Four South Australian-tagged

298 sharks made return trips between the Neptune Islands and WA (two to Perth, one to
299 Ningaloo and one made two trips to Cape Leeuwin). Following removal of the CSIRO
300 VR4G at the Neptune Islands, an additional 11 SA-tagged sharks were detected at
301 Ningaloo (n=3), Perth (n=7) and Cape Leeuwin (n=1) before being detected travelling
302 back towards SA by Bald Island and Recherche arrays. However, due to the lack of
303 consistent receiver coverage in SA and cryptic tag-shedding issues, it is impossible to
304 determine whether those sharks eventually returned to SA. Only one WA-tagged shark was
305 detected (by IMOS receivers in Gulf St. Vincent, Figure 3A), before being recaptured in
306 the Recherche Archipelago.

307

308 The maximum Rate of Movement (RoM) was estimated at 5.6kmh^{-1} for a 1.8m estimated
309 TL male shark that travelled between receivers off Bald and Chatham Islands (orthodromic
310 distance of 193km) in less than 35h (Figure 7C). Twenty five other sharks were estimated
311 to have maintained ROMs in excess of 3kmh^{-1} over distances of between 103 and 3,362km
312 (Figure 7D), suggesting that rapid and possibly direct, long-distance movements are
313 relatively common for this species.

314

315 There was very limited evidence that white sharks regularly returned to the same WA
316 locations. One of the four sharks that undertook return movements into WA from the
317 Neptune Islands (an 5.0m estimated TL male) apparently travelled briefly to the South-
318 West corner of WA (between Cape Leeuwin and metropolitan Perth arrays) in August to
319 September 2012 and again in August 2013. In the most intensively-monitored region off
320 metropolitan Perth, seven white sharks (five males and 2 females, 2.42m-3.92m FL) were
321 re-detected in the region more than one year after their first detection (or tagging). Two of
322 these (a 3.86m FL female and 3.5m estimated TL male) were redetected after more than 2
323 years. Five of the seven sharks were tagged in metropolitan region, one was tagged 30km
324 east of Albany and one at the Neptune Islands. All seven of these sharks were detected in
325 the region at least once during spring but also at other times of year.

326

327 Apart from six sharks detected off Perth as they travelled south after detection at Ningaloo
328 Reef, all of the inter-regional movements into the metropolitan arrays were from the South.
329 Movements into the region occurred from the South in all months and from the North in
330 January, March, July and December (Figure 8A), without any clear seasonal patterns.

331 South of Perth (Figure 8B-E), shark movements were generally bi-directional in most
332 months and there were also no clear indications of seasonal patterns in movement
333 directions. While there were general increases in the frequency of detected movements
334 between the South-West (Cape Leeuwin and Geographe Bay) and South coast (Chatham
335 Island, Bald Island and Recherche Archipelago) arrays, during winter and spring months,
336 directions of those movements were approximately equal. The only suggestion of distinct
337 seasonal travel was from eight of the 11 sharks that travelled to Ningaloo, which were first
338 detected there between November and January. However, those detections were composed
339 of separate detections of two groups of three sharks that were tagged within a month of
340 each other at the Neptune Islands and off Perth and then within days to weeks of each
341 other at Ningaloo. It is unclear whether these unusually coordinated or coincidental
342 movements are representative of all of the sharks that travel as far North as Ningaloo.

343

344 **Discussion**

345 Understanding the ecological factors influencing encounters with *C. carcharias* in Western
346 Australia has previously been hampered by the paucity of data describing the species'
347 apparently sporadic occurrence around the extensive Western Australian coastline (Anon.
348 2004). Satellite telemetry data from four sharks (Bruce and Stevens, 2004; Bruce et al.,
349 2006) and occasional but inconsistent records of white shark captures, sightings and bites
350 (McAuley et al., 2016) were of little value in explaining how the probability of human
351 encounters with this species changes with time and location. In lieu of reliable empirical
352 data to explain these rare and unpredictable events, there has been considerable speculation
353 about the reasons for apparent increases in white shark encounters and bites and many
354 theories and opinions have instead gained popular acceptance (Anon., 2012).

355

356 Tag detection data collected since 2009 have revealed that white sharks may be
357 encountered off the lower West and South coasts of WA at any time of year. Apart from
358 brief reductions in tagged sharks' abundance off Cape Leeuwin and Chatham Island in
359 winter, Albany/Bald Island in autumn and the Recherche Archipelago in late summer-early
360 autumn, the data indicate that *C. carcharias* abundance is more seasonally consistent off
361 the South coast of WA than off the lower West coast. As suggested by the number of
362 sharks detected off Perth and concurrent peak in mean duration of detection periods, it
363 appears that the probability of encountering the species off the metropolitan coast is

364 highest between September and December and lowest (but never zero) between February
365 and May. This peak detection period in metropolitan and SW regions, corresponds to a
366 relative increase in the frequency of *C. carcharias* bites to people in spring and early
367 summer, with 43% of incidents having occurred in these regions between October and
368 December (ASAF, 2015). However, because the probability of human-shark encounters is
369 confounded with peoples' participation rates in aquatic activities, which increase with
370 improving weather and ocean conditions during spring, the disproportionately high rate of
371 shark bite incidents in the region at this time of year cannot solely be attributed to changes
372 in white shark abundance.

373

374 Despite the seasonal patterns in their occurrence, the direction and timing of individual
375 sharks' movements were found to be highly variable throughout the study area. Apart from
376 the specific examples of concurrent movements to Ningaloo Reef and in some of those
377 cases, back to Perth and the South-West WA, *C. carcharias* were recorded travelling past
378 each monitored region in both directions at most times of the year. Such asynchronous
379 movements do not support one popular theory (Sprivulis, 2014) that white sharks follow
380 humpback whales (*Megaptera novaeangliae*) as they predictably migrate northwards along
381 the WA coast during winter (June-August) and southwards in spring (August-November;
382 Jenner et al., 2001; Kent et al., 2012). Given the extent of tagged sharks' movements off
383 the WA coast, however, it is apparent that they co-occur along much of the *M.*
384 *novaeangliae* migration route. Although *C. carcharias* is not known to actively predate
385 great whales, they have frequently been observed scavenging carcasses (Bruce and
386 Stevens, 2004) and eleven of the WA-tagged sharks, including all nine tagged in 2009-10
387 were located in vicinity of humpback, southern right (*Eubalaena australis*) and sperm
388 (*Physeter macrocephalus*) whale carcasses. This association was opportunistically
389 investigated when five sharks were monitored at the site of a beached humpback carcass in
390 Two Peoples Bay (25km East of Albany) between June and September 2010. Detections
391 by a temporary 6-receiver array deployed in the area, revealed that tagged sharks
392 continued to visit the bay for up to 17 days (mean=6.6d) after the carcass had come ashore.
393 However, their visits were typically brief (mean detection periods of 7h per day) and
394 declined in frequency and duration, presumably, as sharks' interest diminished after
395 repeated unsuccessful scavenging attempts and/or scent from the carcass dissipated.

396

397 Another popular theory for explaining the increasing rate of *C. carcharias* bites in WA is
398 that sharks have been attracted to the increasing number and densities of long-nosed fur
399 seal (*Arctocephalus forsteri*) colonies off the South and lower West coasts of the State
400 (Campbell et al., 2014). Although receiver arrays were not designed to monitor sharks'
401 behaviour around pinniped colonies, detection rates from receivers in close proximity to
402 WA seal colony and haul-out sites, were noticeably lower than those of receivers further
403 offshore of those locations. As nearshore patrolling is a consistent feature of white sharks'
404 predatory behaviour at pinniped colonies in South Australia and California (Strong et al.,
405 1992; Goldman and Anderson, 1999; Bruce et al., 2005a; Domier et al., 2012), higher
406 detection rates close to WA colonies would logically be expected if sharks were actively
407 targeting seals at those locations. However, detection rates of white sharks by receivers
408 within 2km of a large new *A. forsteri* colony at Chatham Island were between 0.00-1.35
409 detections 100d⁻¹, compared to an average rate of 11.41 detections 100d⁻¹ (S.D.=16.42) by
410 receivers further off Chatham Island. Similarly, detection rates by OTN receivers within
411 2km of the West End of Rottnest Island, where an expanding fur seal colony has been
412 blamed for perceived increases in shark activity in the metropolitan area and a fatal bite
413 near the colony in October 2011, were also an order of magnitude lower (0.00-0.27
414 detections 100d⁻¹) than the average detection rate of OTN receivers further offshore (2.33
415 detections 100d⁻¹, S.D.=1.88).

416

417 Given the asynchrony observed in sharks' movements throughout the study region, the two
418 instances of coordinated or coincidental movements to north-western WA were unusual
419 and the ecological or social drivers for them, if any, remain uncertain. When reporting a
420 tagged 380cm TL female's return migration between South Africa and North West Cape,
421 Bonfil et al. (2005) suggested that this region might be an area of inter-breeding between
422 geographically-separated African and Australian populations. However, as all of the white
423 sharks detected at Ningaloo during the current study were juveniles and sub-adults (2.0-
424 3.5m estimated TL), reproductive migration is an unlikely reason for these sharks to visit
425 the region. As there are multiple relatively abundant sources of prey between Ningaloo
426 Reef and the Neptune Islands, where most (n=8) of these sharks were tagged, prey
427 availability also does not seem to be a likely explanation. As yet undescribed features of *C.*
428 *carcharias* foraging behaviour, therefore, provide the most likely explanation for these
429 movements.

430

431 The lack of receivers between metropolitan Perth and Ningaloo Reef and between
432 monitored sites in South Australia and off Esperance resulted in obvious gaps in the data
433 recorded from large portions of tagged sharks' ranges. Although sharks' movements and
434 behaviour may have differed in those areas from the patterns observed in the more-
435 intensively monitored region between Perth and Albany, the primary focus of this study
436 was to investigate movements along the most heavily-populated part of the Western
437 Australian coastline. With the exception of Geraldton on the mid-West coast (28.79°S
438 114.60°E, population *c.* 40,000), monitoring arrays were situated close to all of the major
439 coastal population centres around white sharks' known Western Australian distribution
440 (Last and Stevens, 2009). Thus, these data gaps are not thought to have compromised our
441 interpretation of shark movements in the most heavily-populated part of the State or at a
442 broader scale and how these dynamics might relate to the risks of shark bites.

443

444 Movements of SA-tagged sharks into WA (n=46) waters were relatively common and their
445 visits were sometimes prolonged. By contrast, only two WA-tagged sharks were detected
446 in SA: a 2.7m (FL) female shark that was detected by AATAMS receivers in Gulf St.
447 Vincent in February-March 2014 and an as yet unidentified WA-tagged shark that was
448 photographed at the Neptune Islands in June 2015. Despite the small number of acoustic
449 receivers installed at the Neptune Islands, these have been in nearly-continuous operation
450 around the Islands since 2008 (Bradford et al., 2011; Rogers et al., 2014). Given that
451 identical external tagging methods were employed in South and Western Australia and that
452 an increasing number of sharks were tagged with internal transmitters in WA since 2012,
453 avoiding uncertainties caused by uncertain rates of external tag shedding, the paucity of
454 detections at the Neptune Islands suggests that WA-tagged sharks may not be frequent
455 visitors to this specific location. Although there are several other possible explanations for
456 the lack of WA-tagged shark detections in SA (e.g. low levels of receiver coverage, tag
457 shedding, cryptic mortality, etc.), previous studies have noted fine-scale spatial sexual and
458 ontogenetic segregation of sharks over relatively small geographic areas (Anderson and
459 Pyle, 2003; Robbins and Booth, 2012; Kock et al., 2013). It may therefore be that
460 movements of WA-tagged sharks into South Australian waters were more common than
461 indicated by detections by Neptune Islands and IMOS Gulf St. Vincent receivers.

462 In WA, detections by cross-shelf receiver arrays were characterised by short detection
463 periods, punctuated by relatively rapid movements between adjacent arrays, suggesting

464 that sharks generally only occurred within and between monitored areas for brief periods.
465 However, data from the more thoroughly monitored metropolitan region, included
466 examples of more prolonged localised detection periods, with 10 of the 52 sharks recorded
467 in the region, detected in three or more consecutive months, five of them twice. Eleven of
468 these sharks' 15 extended metropolitan detection periods included detections in either
469 October or November, implying that ecologically-favourable local conditions might have
470 existed during those months. Although four of these sharks were disproportionately
471 responsible for the majority (94%) of detections by receivers in and around Cockburn
472 Sound, where the highest regional detection rates were recorded, extended occurrences of
473 seven other sharks in southern metropolitan waters suggest that the area is particularly
474 attractive to *C. carcharias* at that time of year. In addition to the high detection rates
475 recorded by receivers in southern Perth waters, relatively large numbers of different sharks
476 were detected in the southern part of the region. For example, on average nearly twice as
477 many sharks (9-12, mean=10 receiver⁻¹) were detected by receivers around north-eastern
478 Cockburn Sound than at beachside locations (2-7, mean=4.2 receiver⁻¹).

479

480 The high abundance and persistence of tagged sharks in southern metropolitan waters
481 during spring and early summer coincided with the seasonal formation of locally-
482 significant spawning aggregations of snapper (*Chrysophrys auratus*) in Cockburn Sound,
483 which nearly half (n=9) of the 21 *C. carcharias* tagged in the metropolitan region were
484 caught in close proximity to. Extensive commercial and recreational fishery management
485 actions have been introduced over the last decade to rebuild previously over-exploited
486 demersal teleost stocks in the metropolitan region and recent assessments now indicate that
487 these stocks are recovering (Fairclough et al., 2014). Snapper are thought to be a relatively
488 important component of white sharks' diets across southern Australia and tagged sharks
489 have previously been associated with pre-spawning and spawning schools of *C. auratus* in
490 various areas including Spencer Gulf (SA) and off eastern Victoria (Bruce et al., 2006;
491 Sims et al., 2012). Thus, the regular seasonal occurrence of spawning aggregations of
492 demersal teleost species off the metropolitan coast provides at least a circumstantial
493 explanation for the observed increase in seasonal abundance of tagged white sharks and
494 their prolonged detection periods at this time of year.

495

496 Observed occurrences of *C. carcharias* off the metropolitan coast were not, however,
497 restricted to those predictable seasonal prey availability events. For example, four male
498 and female sharks (3.0-4.5m estimated TL) were tagged whilst scavenging whale carcasses
499 in May and July 2009. Another three males and three females (2.1–3.9m FL) were caught
500 around a highly unseasonal school of Australian salmon (*Arrips truttaceus*) 8km North of
501 Cockburn Sound during 3 (non-consecutive) days in August 2015. Even sharks that were
502 tagged around *C. auratus* schools in Cockburn Sound were detected away from Cockburn
503 Sound for periods of over several days. For example, during their extended periods of
504 detection in Cockburn Sound during October and November 2012, two female sharks
505 (2.6m and 3.0m FL) were concurrently detected over consecutive 3-5 day periods by
506 receivers in the central and northern-most extents of the metropolitan arrays, respectively.
507 Real-time investigations of local ecological conditions during those detection periods
508 revealed large schools of unidentified baitfish and in the latter case, skipjack tuna
509 (*Katsuwonis pelamis*), Australian sea lions (*Neophoca cinerea*), bottlenose dolphins
510 (*Tursiops aduncus*) and various seabirds were also present. Once these transient conditions
511 subsided, one of the sharks returned to Cockburn Sound for a month before departing to
512 Ningaloo Reef where the other shark was also next detected.

513

514 Although accurately predicting when and where individual white sharks might occur off
515 any particular part of the WA coast remains an unrealistic aspiration at this time, the data
516 collected during these ambitious continental-scale international collaborative projects have
517 rapidly and substantially improved understanding of white sharks' movement ecology in
518 south-western Australian waters. Although data suggest that the abundance, distribution
519 and movements of white sharks around WA vary between southern Australian government
520 jurisdictions from one year to another, they have identified periods and locations where
521 white sharks are more likely to occur and have begun to identify the range of ecological
522 factors that may influence the probability of encountering this species off the WA coast.
523 More detailed analyses of these data in relation to specific local environmental variables
524 (e.g. ocean temperatures, circulation patterns, Southern Oscillation Indices, etc.), may
525 provide additional explanations of the patterns observed in this study.

526

527 Notwithstanding further analyses, the observed patterns of tagged sharks' occurrence and
528 movements provide useful insights into how *C. carcharias* abundance and movements

529 influence probabilities of human encounters with the species. In particular these results
530 indicated that although white shark movements appear asynchronous and uncoordinated,
531 peak activity periods differed around the WA coast. It is hoped that results from this study
532 might offer an important empirical basis for developing effective and defensible methods
533 for identifying and responding to locally-important white shark hazards (eg. seasonal and
534 transient fish schools and whale carcasses). As such, the authors hope that the results of
535 this study might provide a useful basis for reducing risks of human encounters with white
536 sharks in WA and other regions where such interactions are an issue of concern.

537

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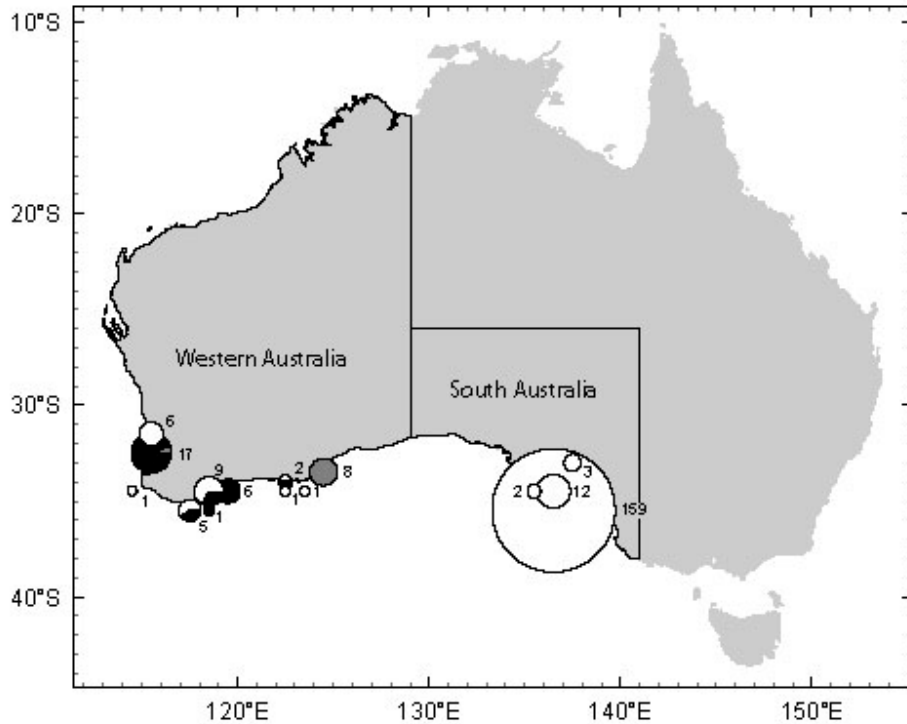
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814
815 West, J. G. (2011). Changing patterns of shark attacks in Australian waters. *Marine and*
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817

818 **Table 1.** Summary of WA-located acoustic receiver arrays characteristics. Modifications
819 to arrays' configuration are indicated by: ^a reduced to 17 in 2011; ^b reduced to 27 in 2015;
820 ^c inshore section of cross-shelf array was moved from mainland-Rottneest Is. to mainland-
821 Garden Is.-Rottneest Is. in February 2014; ^d5 receivers were installed in 2013-2014 before
822 being removed and replaced by a partial cross-shelf line between Nov 2014 and April
823 2016.

Array	Configuration	Receivers	No.	Data collection period
IMOS Ningaloo	Cross-shelf (partial)	VR2W	42	Jan 2008 – Mar 2016
SMN Perth	Along-shore/gate	VR2W	19 ^a	Jan 2009 – Feb 2016
	Location-specific	VR4G	19	Jan 2009 – May 2016
DoF snapper	Mixed (gate/cluster)	VR2W	52 ^b	Jan 2009 – Feb 2016
OTN	Cross-shelf	VR2W	53 ^c	Jan 2009 – Feb 2016
SMN SW/Albany	Location-specific	VR4G	6	Oct 2013 – May 2016
SMN Cape Leeuwin	Cross-shelf	VR2W	48	Apr 2012 – Jun 2015
SMN Chatham Is.	Cross-shelf	VR2W	44	Apr 2012 – Jun 2015
Two Peoples Bay	Along-shore	VR2W	6	Jul 2010 – Nov 2010
SMN Bald Is.	Cross-shelf	VR2W	33	Apr 2012 – Apr 2016
SMN Recherche	Cross-shelf (partial)	VR2W	17 ^c	Feb 2013 – Apr 2016

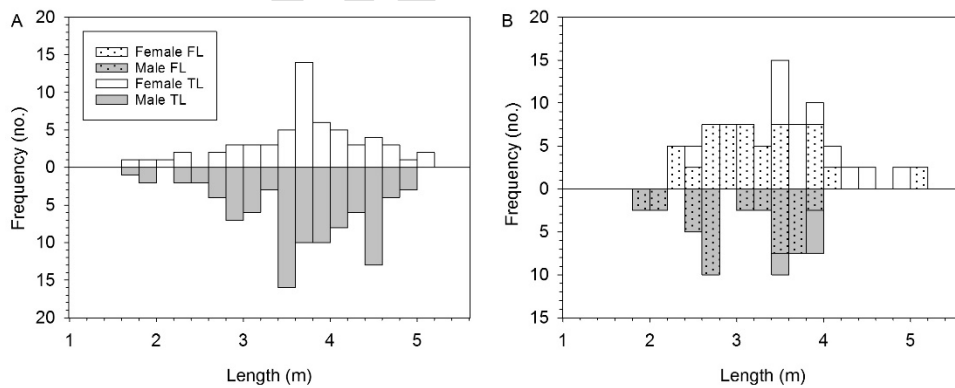
824



825

826 **Figure 1.** Spatial distribution of acoustic transmitters (tags) deployed on 234 *C.*
827 *carcharias*, between December 2007 and December 2015. Pie charts illustrate the numbers
828 of sharks tagged externally (white segments), internally (grey segments) and with dual
829 internal and external transmitters (black segments) by 1 degree latitude and longitude
830 blocks. Numbers indicate the total number of sharks tagged in each block.

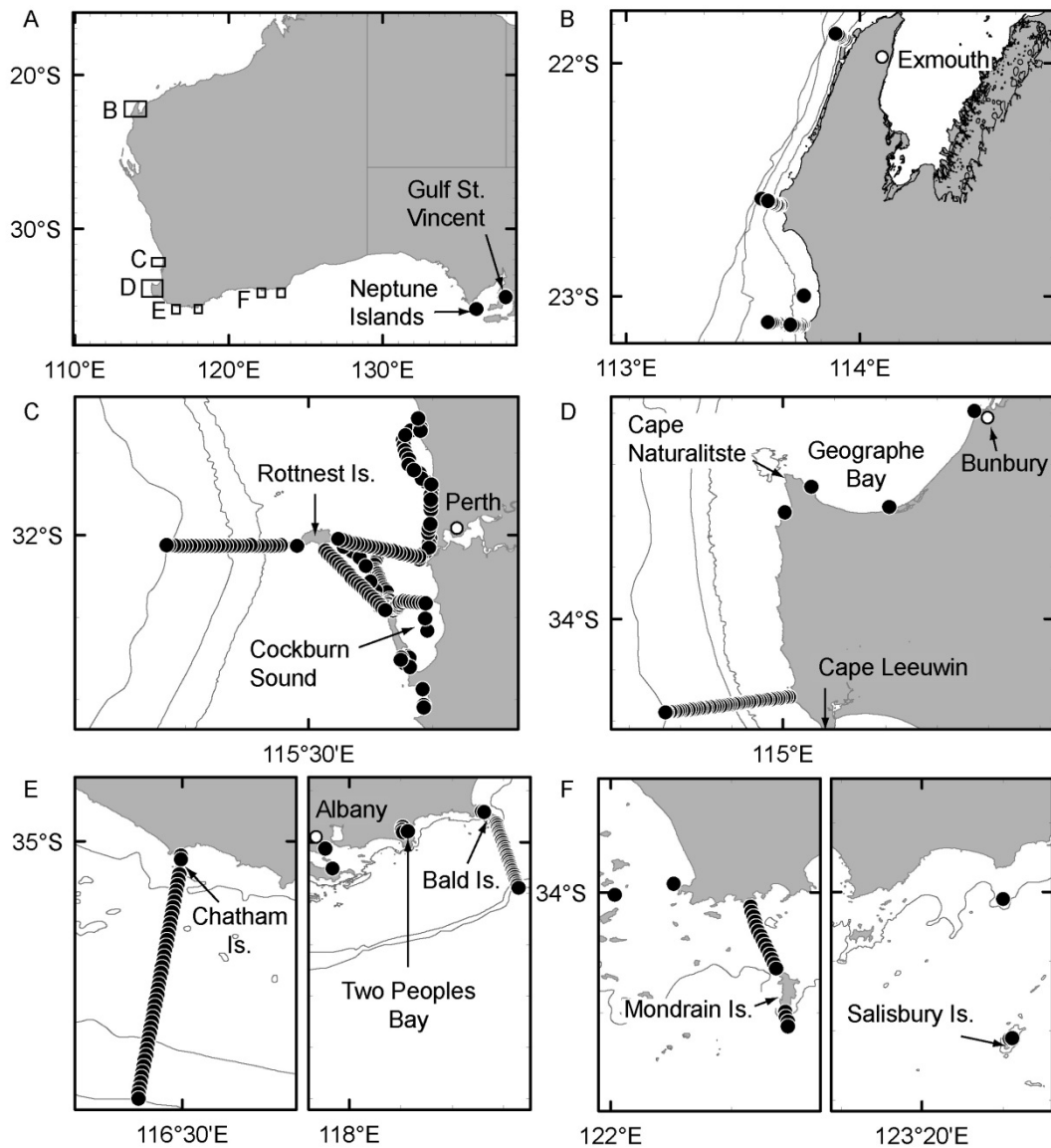
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832

833 **Figure 2.** Size frequencies of *C. carcharias* tagged in (A) South Australia (n=156) and (B)
834 Western Australia (n=54). Plain bars show estimated Total Lengths (TL) of externally-
835 tagged sharks; dotted bars show measured Fork Lengths (FL) of internally-tagged sharks.
836 N.B. size or sex was not recorded for 24 sharks.

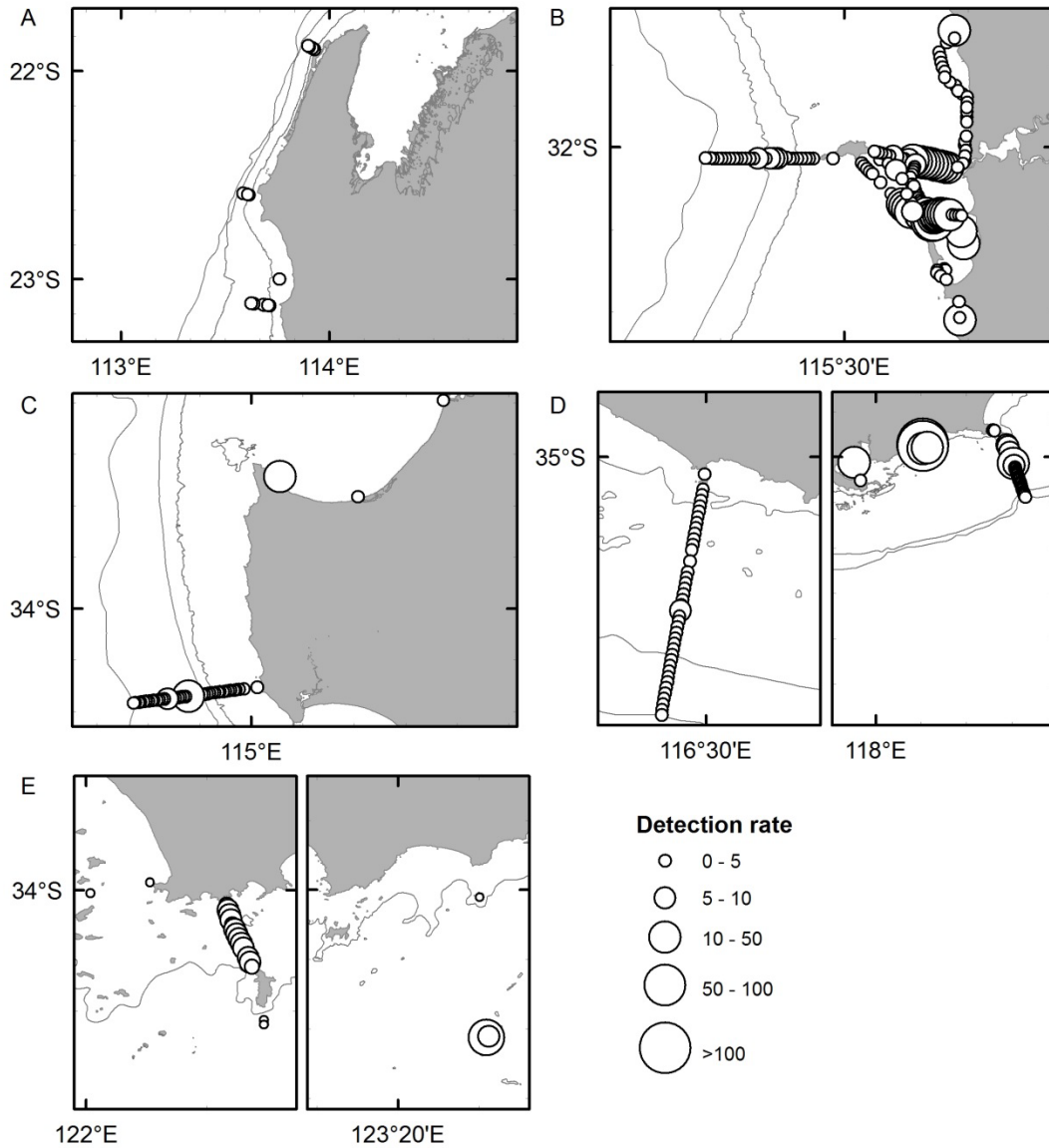
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838

839 **Figure 3.** (A) Distribution of acoustic receiver arrays that provided data for this study and
840 individual receiver locations (filled black circles) in the (B) IMOS Ningaloo array; (C)
841 combined metropolitan Perth arrays; (D) South-West arrays; (E) Chatham Island (left
842 panel) and Albany, Two Peoples Bay and Bald Island arrays (right panel) arrays and (F)
843 Recherche Archipelago array. Locations include all permanent, temporary and re-located
844 receiver stations between December 2008 and May 2016. Isobaths are shown at 50m,
845 100m and 200m intervals.

846



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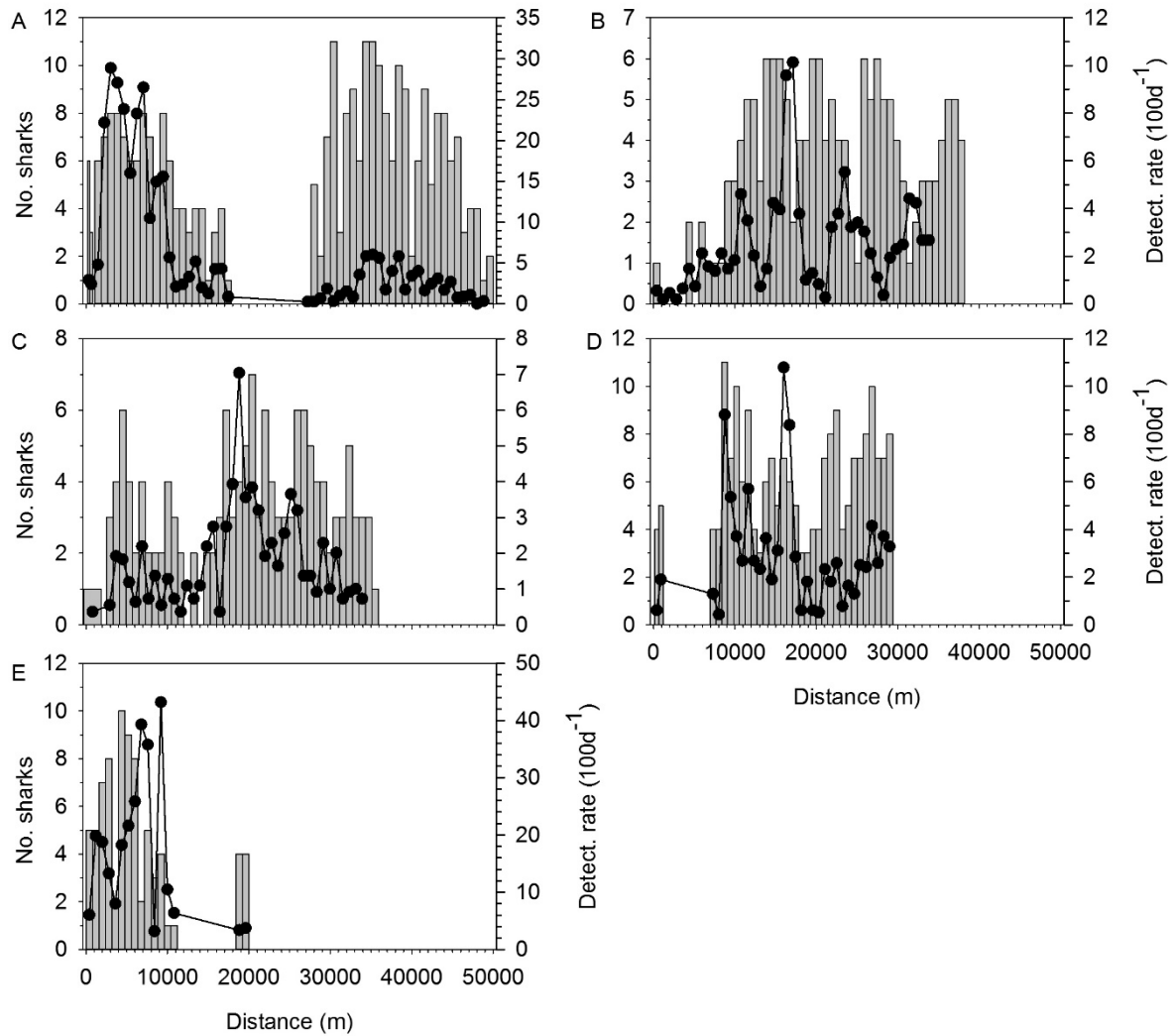
848 **Figure 4.** Individual receivers' detection rates (detections 100d⁻¹) of tagged *C. carcharias*

849 in the (A) Ningaloo; (B) metropolitan Perth arrays; (C) South-West; (D) Chatham Island,

850 Albany and (E) Recherche Archipelago regions. Isobaths are shown at 50m, 100m and

851 200m depths.

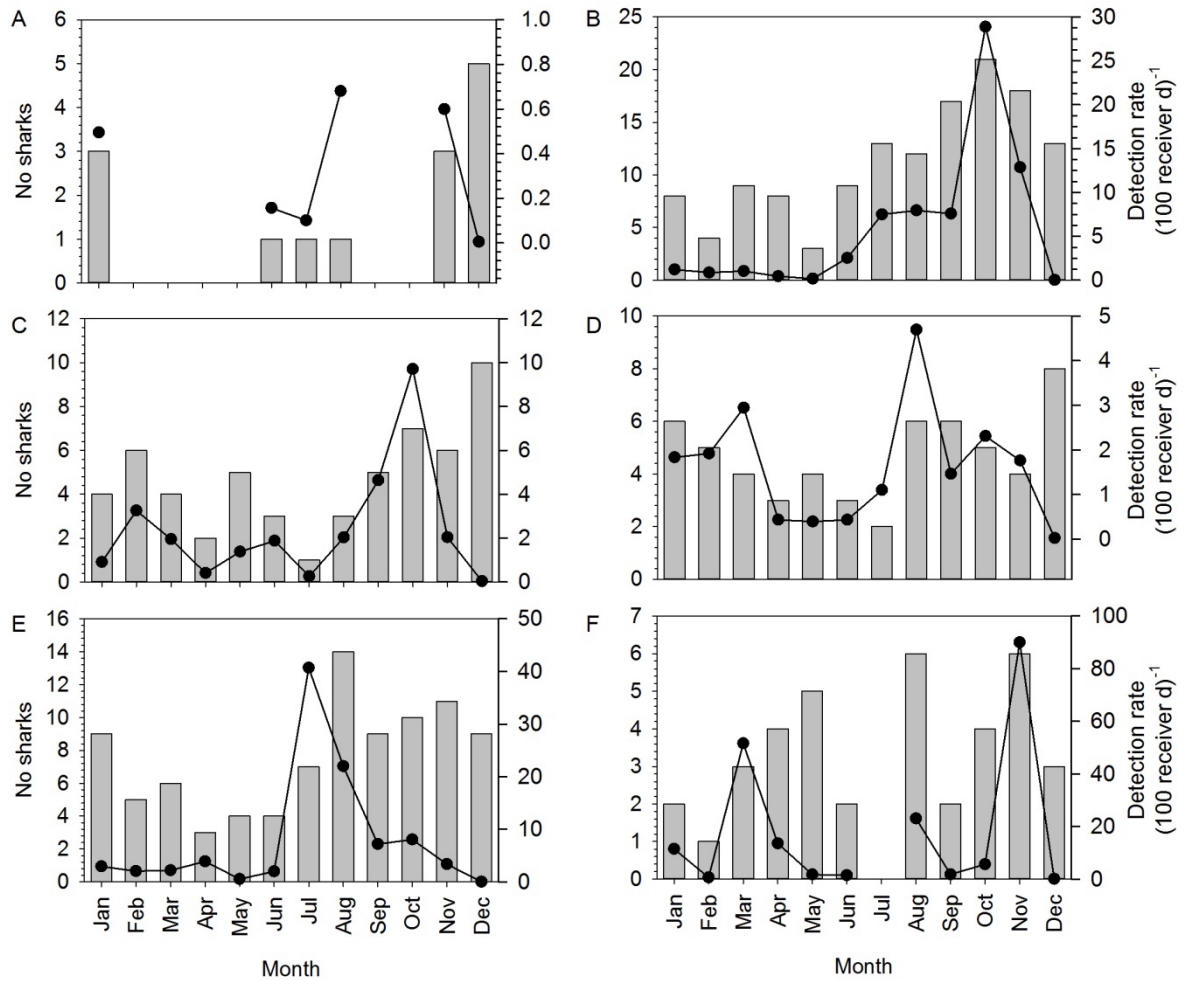
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853

854 **Figure 5.** Frequency of tagged *C. carcharias* (grey bars) detected and tag detection rates
855 (detections 100d⁻¹; black line) by cross-shelf receiver arrays off (A) metropolitan Perth
856 (Ocean Tracking Network); (B) Cape Leeuwin; (C) Chatham Island; (D) Bald Island and
857 (E) Recherche Archipelago.

858

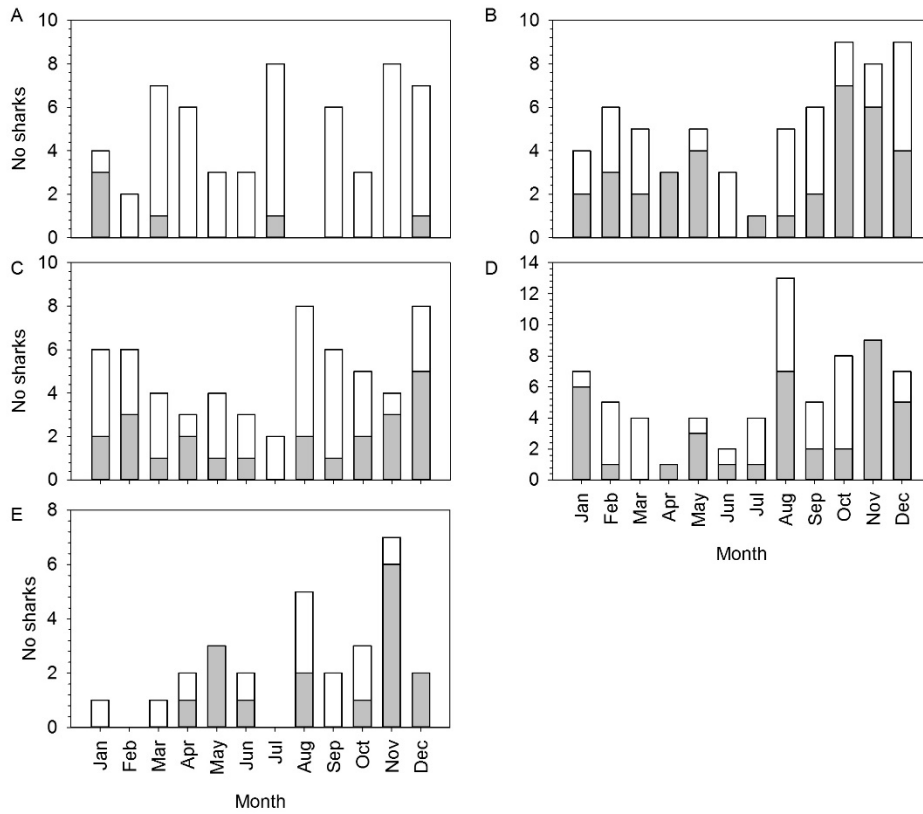


859

860 **Figure 6.** Monthly detections of tagged *C. carcharias*. Grey bars are the number of sharks
861 detected (left axes) and black lines indicate the number of detections (right axes) by pooled
862 calendar months in: (A) Ningaloo, (B) combined metropolitan, (C) South-West; (D)
863 Chatham Island; (E) Albany and (F) Recherche Archipelago arrays.

864

865
866 **Figure 7.** Frequency distributions of estimated (A) movement distances (n=293) and (B)
867 individual sharks' cumulative movement distances (n=73); (C) Rate of Movement (ROM)
868 vs. distance and (D) frequency distribution of estimated ROM.
869



870

871 **Figure 8.** Pooled monthly movements of *C. carcharias* into the (A) metropolitan, (B)
872 South-West; (C) Chatham Island; (D) Albany and (E) Recherche Archipelago regions.
873 Grey bars indicate eastward/southward movements and white bars indicate
874 westward/northward movements.