

First submission

## Editor guidance

Please submit by **15 Dec 2017** for the benefit of the authors (and your \$200 publishing discount).



### Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



### Author notes

Have you read the author notes on the [guidance page](#)?



### Raw data check

Review the raw data. Download from the [materials page](#).



### Image check

Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

## Files

Download and review all files from the [materials page](#).

6 Figure file(s)

6 Table file(s)

2 Raw data file(s)



## Structure your review

The review form is divided into 5 sections.  
Please consider these when composing your review:

- 1. BASIC REPORTING**
- 2. EXPERIMENTAL DESIGN**
- 3. VALIDITY OF THE FINDINGS**

4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

## Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

### BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context.  
Literature well referenced & relevant.
- Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see [PeerJ policy](#)).

### EXPERIMENTAL DESIGN

- Original primary research within [Scope of the journal](#).
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

### VALIDITY OF THE FINDINGS

- Impact and novelty not assessed.  
Negative/inconclusive results accepted.  
*Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- Data is robust, statistically sound, & controlled.

- Conclusions are well stated, linked to original research question & limited to supporting results.
- Speculation is welcome, but should be identified as such.

# Standout reviewing tips

3



The best reviewers use these techniques

## Tip

**Support criticisms with evidence from the text or from other sources**

**Give specific suggestions on how to improve the manuscript**

**Comment on language and grammar issues**

**Organize by importance of the issues, and number your points**

**Please provide constructive criticism, and avoid personal opinions**

**Comment on strengths (as well as weaknesses) of the manuscript**

## Example

*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*

*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*

*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 - the current phrasing makes comprehension difficult.*

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*

*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

# Abundance or artefact? Explaining anomalies in long-term CPUE indices of sharks retained by pelagic longline fisheries

Gareth L Jordaan <sup>Corresp.</sup> <sup>1</sup>, Jorge Santos <sup>2</sup>, Johan C Groeneveld <sup>1,3</sup>

<sup>1</sup> Oceanographic Research Institute, 1 King Shaka Avenue, Durban, South Africa

<sup>2</sup> Norwegian College of Fishery Science, University of Tromsø, NO-9037, Tromsø, Norway

<sup>3</sup> School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal, South Africa

Corresponding Author: Gareth L Jordaan

Email address: gjordaan@ori.org.za

Pelagic longline fisheries directed mainly at tunas and swordfish frequently catch sharks, which can be retained and reported along with primary target species, or discarded overboard, mostly unreported. The assumption of a proportional relationship between catch-per-unit-effort (CPUE) data based on retained sharks, and shark abundance on fishing grounds, is therefore tenuous. We asked whether known changes in retention practices, resulting from regulatory changes and operational decisions, would be visible as anomalies in CPUE indices constructed from commercial logbook data. As a case study, we analysed data obtained from South African local and foreign-flagged longline fleets operating in the Southeast (SE) Atlantic and Southwest (SW) Indian Oceans between 2000 and 2015. A generalized linear mixed modelling (GLMM) framework was used to construct standardized CPUE indices for blue sharks *Prionace glauca* and shortfin makos *Isurus oxyrinchus* reported by the two fleets, accounting for the random effects of individual vessels (gear and fishing method), subregion and season. Shark catch rates were much higher for local- than foreign-flagged vessels, blue sharks were more abundant than shortfin makos, and both species were more abundant in the SE Atlantic than the SW Indian Ocean. A steep increase in the shortfin mako CPUE index in 2004 was ascribed to expanding fishing grounds and higher retention rates, to supply increased demand after 2003, rather than higher abundance. A second steep increase in shortfin mako and blue shark indices in 2011 coincided with a restructuring of the fishing sector, bringing formerly shark-directed vessels into the local pelagic longline fleet. Standardized CPUE indices based on retained sharks were not reliable indices of abundance, but could clearly identify increases in shark retention rates in a post hoc correlation with known operational and regulatory changes.

1 **Abundance or artefact? Explaining anomalies in long-term CPUE indices of**  
2 **sharks retained by pelagic longline fisheries**

3 **Gareth L. Jordaan<sup>a,\*</sup>, Jorge Santos<sup>b</sup> and Johan C. Groeneveld<sup>a,c</sup>**

4 *<sup>a</sup>Oceanographic Research Institute, 1 King Shaka Avenue, Durban, South Africa*

5 *<sup>b</sup>Norwegian College of Fishery Science, University of Tromsø, NO-9037, Tromsø, Norway*

6 *<sup>c</sup>School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal, South*  
7 *Africa*

8 *\*Corresponding author*

9 *Email address: jordaan.gareth@gmail.com (G.L. Jordaan)*

10 **Abstract**

11 Pelagic longline fisheries directed mainly at tunas and swordfish frequently catch sharks, which  
12 can be retained and reported along with primary target species, or discarded overboard, mostly  
13 unreported. The assumption of a proportional relationship between catch-per-unit-effort (CPUE)  
14 data based on retained sharks, and shark abundance on fishing grounds, is therefore tenuous. We  
15 asked whether known changes in retention practices, resulting from regulatory changes and  
16 operational decisions, would be visible as anomalies in CPUE indices constructed from  
17 commercial logbook data. As a case study, we analysed data obtained from South African local  
18 and foreign-flagged longline fleets operating in the Southeast (SE) Atlantic and Southwest (SW)  
19 Indian Oceans between 2000 and 2015. A generalized linear mixed modelling (GLMM)  
20 framework was used to construct standardized CPUE indices for blue sharks *Prionace glauca* and  
21 shortfin makos *Isurus oxyrinchus* reported by the two fleets, accounting for the random effects of  
22 individual vessels (gear and fishing method), subregion and season. Shark catch rates were much  
23 higher for local- than foreign-flagged vessels, blue sharks were ~~more abundant~~ than shortfin

24 makos, and both species were ~~more abundant~~ in the SE Atlantic than the SW Indian Ocean. A  
25 steep increase in the shortfin mako CPUE index in 2004 was ascribed to expanding fishing  
26 grounds and higher retention rates, to supply increased demand after 2003, rather than higher  
27 abundance. A second steep increase in shortfin mako and blue shark indices in 2011 coincided  
28 with a restructuring of the fishing sector, bringing formerly shark-directed vessels into the local  
29 pelagic longline fleet. Standardized CPUE indices based on retained sharks were not reliable  
30 indices of abundance, but could clearly identify increases in shark retention rates in a post hoc  
31 correlation with known operational and regulatory changes.

32 *Key words:* Fishery management; ICCAT; IOTC; Pelagic longline; Pelagic sharks; Reporting;  
33 Retained bycatch

## 34 **1. Introduction**

35 Pelagic (drifting) longline fisheries directed mainly at tunas and swordfish typically have high  
36 shark bycatch ratios (Oliver et al., 2015). The captured sharks are either discarded at sea, mostly  
37 unreported, or are retained and processed for their meat and fins. Drivers of retention are  
38 primarily the species of shark, as a proxy for economic value, and the regulatory environment  
39 within which a fishery operates (James et al., 2016). Commonly retained sharks with high quality  
40 meat and marketable fins include shortfin makos *Isurus oxyrinchus*, whereas blue sharks  
41 *Prionace glauca* are less valuable, and are more often discarded.

42 Pelagic sharks are vulnerable to fishing pressure, because of their life history traits and behaviour  
43 patterns (Dulvy et al., 2008). As a group, they have lower productivity than teleosts, are long-  
44 lived and slow-growing, and produce few offspring which mature late (Musick, 1999). Pelagic  
45 sharks are predatory animals, and some species are found in association with other target species  
46 of longline gear, on which they prey or compete with for food (Mejuto et al., 2008). Inevitably,

47 these sharks are caught in large numbers in areas of intensive longline fishing (Campana, 2016).  
48 Pelagic sharks migrate freely and widely over their range, often across international boundaries  
49 (Kohler et al., 2002; Block et al., 2011, Campana, 2016), thus making them vulnerable to high  
50 seas fishing fleets.

51 Blue sharks dominate the bycatch of pelagic longline fisheries in subtropical and temperate  
52 waters worldwide (Oliver et al., 2015), and in some areas, they exceed the catches of tuna and  
53 swordfish target species (Campana et al., 2009). They are faster-growing and relatively more  
54 productive than most other shark species, and are considered less vulnerable to fishing pressure  
55 (Smith et al., 1998; Aires-da-Silva and Gallucci, 2007). Shortfin makos make up a large  
56 proportion of retained bycatch of longline fisheries, and in some cases form the target of shark-  
57 directed fisheries (Francis et al., 2001; Campana et al., 2005; Petersen et al., 2009; Bustamante  
58 and Bennett, 2013). Makos are characterized by low rates of population increase and are  
59 considered to be more vulnerable to overfishing than blue sharks (Dulvy et al., 2008). Neither  
60 species are considered to be in imminent danger of collapse, although populations of one or both  
61 might be overexploited (Campana et al., 2005; Campana, 2016). For example, North Atlantic  
62 stocks of shortfin makos appear to be overfished and undergoing overfishing, whereas the status  
63 of South Atlantic stocks are highly uncertain (ICCAT, 2017a).

64 The track record for shark management worldwide has been poor, and the IUCN Red List  
65 recently reported that 17% of the species were considered threatened with extinction (critically  
66 endangered, endangered or vulnerable) (Dulvy et al., 2014). Shark landings reported to the FAO  
67 peaked in 2003, and in the decade since then have declined by almost 20% - a reflection of  
68 overfishing, rather than good management (Davidson et al., 2016). Average shark exploitation  
69 rates exceed rebound rates for many shark populations (Worm et al., 2013). Campana (2016)  
70 highlighted the risks associated with ineffective fisheries management structures, unmonitored

71 fishing mortality (particularly of discarded sharks), and the scarcity of basic information on the  
72 status of populations. Importantly, species-specific patterns and information gaps, by ocean  
73 region and individual fishery, have been identified as a critical weakness, in terms of global  
74 conservation and improved fisheries management efforts (Oliver et al., 2015).

75 Standardized catch-per-unit effort (CPUE) trends based on ~~fisher's~~ logbook data of catch and  
76 effort are widely used in fisheries management, under the assumption that they provide measures  
77 that are proportional to abundance. Potentially important biases can, however, arise from  
78 catchability fluctuations by area and season, and also as a result of changes in fishing methods  
79 and gear. Maunder and Punt (2004) reviewed methods to standardize catch and effort data, to  
80 remove the impacts of these factors from inter-annual trends. Nominal CPUE data are, however,  
81 also affected by under-reporting; in longline fisheries, sharks that are discarded overboard are  
82 infrequently reported in logbooks, and landing statistics therefore underrepresent the actual  
83 numbers of sharks caught during a fishing trip (Campana, 2016). Hence, there remains  
84 considerable uncertainty about the relationship between shark abundance, CPUE time series and  
85 total catches over the past decades (IOTC, 2016). Nevertheless, standardized CPUE trends  
86 remain an important relative measure of the abundance of sharks caught by longline gear,  
87 including for national fleets and fisheries managed by Regional Fisheries Management  
88 Organizations (RFMOs), such as the Indian Ocean Tuna Commission (IOTC) and  
89 the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Francis et al.,  
90 2001; Su et al., 2008; Petersen et al., 2009; Cortés, 2013; ICCAT, 2016; IOTC, 2016). Some of  
91 these studies have used auxiliary information collected by fisheries observers at sea to assess the  
92 levels of discarding or misreporting in logbooks (Cortés, 2013).

93 Both distant-water pelagic longline fleets and local vessels fish for tunas and swordfish in the  
94 Southeast (SE) Atlantic and the Southwest (SW) Indian Oceans, around southern Africa (Petersen

95 et al., 2009; da Silva et al., 2015). A local longline fishery for tunas first developed in South  
96 African waters during the 1960s, but it was short-lived because of a weak market for the poor-  
97 quality tuna landed by the fleet (Petersen and Goren, 2007). A local shark-directed longline  
98 fishery started in 1992, landing mainly blue sharks and shortfin makos (BCLME, 2005). Distant-  
99 water fleets, mainly from Japan and Korea, were licensed to fish in South African waters from the  
100 early 1990s, where they set deep longline gear to target tunas (Petersen and Goren, 2007). South  
101 African vessels re-entered the pelagic longline fishery in 1995, through a joint agreement with a  
102 Japanese company. The joint initiative proved to be successful, and by 1997, 30 experimental  
103 tuna permits were issued to South African-flagged vessels. This fishery was formalized in 2005,  
104 when long-term fishing rights were issued respectively for swordfish- and tuna-directed fisheries,  
105 and the shark-directed permits were abolished. Sharks continued to be targeted by some local  
106 vessels under a permit exemption, but their licenses were fully amalgamated into the tuna and  
107 swordfish fishery in 2011 (da Silva et al., 2015).

108 Based on data collected by fisheries observers, Petersen et al. (2009) found that blue sharks and  
109 shortfin makos were the most common sharks caught in longline gear set around southern Africa,  
110 and that local South African swordfish-directed vessels caught more sharks than Asian-flagged  
111 tuna-directed vessels. These authors also observed a decline in the standardized CPUE of both  
112 shark species over the 2000-2005 period, accompanied by a decline in average shark size.  
113 However, data collected by fisheries observers at sea are rarely available for long uninterrupted  
114 periods, and therefore long-term indices of abundance must often rely on commercial logbook  
115 and landings data – even though these data may be affected by targeting practices and under-  
116 reporting.

117 In the present study, we used logbook data of fishing effort and retained shark catches of two  
118 pelagic longline fleets (local and foreign-flagged) for the 2000 to 2015 period, to construct

119 standardized CPUE trends for blue sharks and shortfin makos. The influences of spatio-temporal  
120 variables and the characteristics of individual fishing vessels were accounted for within a  
121 generalised linear mixed model (Maunder and Punt, 2004). We then asked whether known  
122 changes in retention practices, resulting from market demand, changes in the regulatory  
123 environment and fleet behaviour, would be visible as anomalies in the CPUE indices. Our study  
124 provides a reference framework for the analysis and interpretation of commercial logbook data  
125 affected by unreported discards – often the only source of information that fisheries researchers  
126 have for assessments.

## 127 2. Materials and methods

### 128 2.1. Spatio-temporal stratification

129 The sampling area (South African Exclusive Economic Zone [EEZ] up to 200 nautical miles from  
130 the shore and surrounding high seas) was stratified into SE Atlantic (west of 20°E) and SW  
131 Indian Ocean regions (east of 20°E; Fig. 1). Along the South African west coast, the SE Atlantic  
132 is dominated by cool-temperate waters and highly productive upwelling systems of the  
133 northwards flowing Benguela Current (Hutchings et al., 2009). The east coast is influenced by the  
134 western boundary Agulhas Current which follows the shelf-edge southwestwards, bringing  
135 warmer subtropical waters into this moderately productive part of the SW Indian Ocean  
136 (Lutjeharms, 2006a, b; Beal et al., 2011). Cape Agulhas (~20°E) at the southernmost tip of Africa  
137 is considered an official dividing line between the Indian and Atlantic Oceans (IHO, 1953), even  
138 though the oceanographic boundary zone is dynamic across a broader geographic range, and is  
139 affected by water movements.

140 The SE Atlantic and SW Indian Ocean regions were each divided into two further subregions:  
141 West (Namibia border to 33°S; cool temperate, influenced by the Benguela Current), Southwest

142 (33°S–20°E; dynamic boundary zone, including the western Agulhas Bank), South (20–26°E;  
143 influenced by the warming lower Agulhas Current, with a narrow shelf broadening to become the  
144 eastern Agulhas Bank) and East (26°E to the Mozambique border; subtropical waters influenced  
145 by the upper Agulhas Current) (Fig. 1). This subdivision was similar to one used in a study on  
146 pelagic shark bycatches by Petersen et al., (2009).

147 Seasonal stratification was based on the average sea surface temperature (SST, °C) recorded by  
148 skippers in logbooks at the start of each longline set between 2000 and 2015. The “spatial”  
149 library of R software (Ripley et al., 2015) and geographic maps available from the “maps” and  
150 “mapsdata” libraries (Becker and Wilks, 2016a, b) were used to construct a kriging map of SST  
151 around southern Africa (R Development Core Team, 2016). Using 21°C as a reference  
152 temperature, we identified two general seasons: a cool season (June–November), when the 21°C  
153 isotherm was constrained to the northern parts of the east coast; and a warm season (December–  
154 May) when the warmer waters extended further southwards (Fig. 1). **Only two seasons were used,**  
155 **to ensure a balanced distribution of observations per category.**

156 *2.2. Data and assumptions*

157 Logbook records completed on a set-by-set (daily) basis were obtained from the Department of  
158 Agriculture, Forestry and Fisheries (DAFF) for local vessels (South African-flagged vessels) and  
159 foreign vessels (mainly Japanese and Korean flagged vessels) licensed to fish for tuna in the  
160 South African EEZ, on condition that catches are offloaded in local ports. Logbook records of  
161 foreign vessels were available for all years between 2000 and 2015, except 2006, when they did  
162 not fish. Records for local vessels were available for all years between 2000 and 2015, for fishing  
163 sets targeted at tunas, swordfish and pelagic sharks. The data comprised of daily retained catches  
164 by species by numbers, weight (after reconciliation of weights estimated at sea with landed  
165 weights, measured by Fisheries Control Officers at offloading points), numbers of hooks set, set

166 and haul positions and times, target species, depth of sets and bait type, and whether a fisheries  
167 observer was present or not.

168 The logbook data were cleaned by removing anomalous records in which setting positions, date,  
169 depth, fishing effort (number of hooks), set durations or catch composition or quantities were  
170 clearly incorrect or mismatched. Records with setting positions outside the SW Indian Ocean and  
171 SE Atlantic region were removed. Data considered to fall within acceptable ranges were dates  
172 between 2000 and 2015; 310–3 800 hooks per line; 0–1 200 blue sharks caught per set and 0–801  
173 makos caught per set. Spatio-temporally explicit catch and fishing effort of 29 019 individual sets  
174 remained (86% of initial records), which were then aggregated by fishing vessel and month,  
175 resulting in 2 488 records for further analysis. Consolidation along time (month) and geographic  
176 (region) dimensions improved tractability of the data with standard statistical software and did  
177 not corrupt their structure, because individual fishing vessels operated within the same region in  
178 any given month.

179 We assumed that blue sharks and shortfin makos were correctly identified in logbooks – these  
180 two species are commonly caught and relatively easy to identify. Longfin makos (*Isurus paucus*)  
181 have rarely been reported from the sampling region (Reardon et al., 2006), and hence all makos  
182 were assumed to be *I. oxyrinchus*. Other shark species, which made up only a small proportion of  
183 the retained catch, were not always identified to species level, and were generally grouped in  
184 logbook records, as requiem sharks (mostly *Carcharhinus* spp.), threshers (*Alopias* spp.),  
185 hammerheads (*Sphyrna* spp.) or as unidentified sharks.

186 2.3. *Data analysis*

187 Generalized Linear Mixed Models (GLMMs) are an extension of GLMs, and deal better with  
188 replicated observations and complex designs in generalized regression (Venables and Dichmont,

189 2004; Manning, 2007). Variability in blue shark and shortfin mako CPUE (numbers/1 000 hooks)  
190 by year, subregion, season, vessel and observer presence (Table 1) was explored using GLMMs  
191 in the statistical software package R, version 3.3.2 (R Development Core Team, 2016). The R-  
192 libraries “lme4” (Bates et al., 2016) and “lmtree” (Hothorn et al., 2015) were used to run the  
193 GLMM procedure. Data from 61 local South African-flagged vessels (16 810 data records) and  
194 49 foreign vessels (12 209 records) were analysed separately, because fleets differed in  
195 operational characteristics and in reporting quality.

196 The CPUE data contained many records with zero shark catches, and therefore the delta method  
197 (Pennington, 1983; Maunder and Punt, 2004; Lauretta et al., 2016) was selected for the analysis.  
198 The delta method involves fitting two submodels to the data. In the first submodel, the probability  
199 of a non-zero catch was modelled, based on presence/absence information, and assuming a  
200 binomial error distribution (Table S1a and b). In the second submodel, the positive catch numbers  
201 were modelled using the gamma continuous probability distribution. This distribution was chosen  
202 because the relationship between the logarithms of the mean and variance of non-zero CPUE  
203 records was close to two (data highly dispersed) (McCullagh and Nelder, 1989; Stefansson,  
204 1996), and the gamma provided better fits than inflated discrete distributions in preliminary tests.

205 Final models were selected based on a stepwise approach, involving modelling combinations of  
206 error structures, link functions and explanatory variables. The most parsimonious models were  
207 selected based on the lowest value of the Bayesian Information Criterion (BIC), and visual  
208 assessment of residual plots. Error back-calculation and error propagation were calculated using  
209 the conservative procedures recommended by Jørgensen and Pedersen (1998), Lindberg (2000)  
210 and Tellinghuisen (2001). Standardized CPUE trends by species and year were computed as the  
211 product of the probability of catch (binomial model) and positive catch (gamma model) obtained  
212 from the model coefficients. The expected values in the final models were the specific CPUE

213 using Year as the fixed (main) effect, as this is the factor of interest with regard to abundance  
214 trends of the whole stock (Maunder and Punt, 2004; Venables and Dichmont, 2004). Study of  
215 interactions among the random factors proved difficult. Despite the aggregation of the data, the  
216 number of realized treatment cells was just a small fraction of the potential interactions (100  
217 vessels  $\times$  4 regions  $\times$  2 seasons). Indications of the variance of the intercepts of the random  
218 effects Region, Season and Vessel are reported (Table S2), as provided in “lme4”.

219 Anomalies in the CPUE index were identified *post hoc*, as sudden increments in the scale of the  
220 index that could not be plausibly explained on biological or population dynamics grounds alone.  
221 Published and anecdotal information on the history of the fishery, management framework, and  
222 market demand were used to identify events that may have influenced the changes in shark  
223 retention practices. These were superimposed on the standardized CPUE indices.

224 **3. Results**

225 *3.1. Nominal trends in fishing effort and landings*

226 During the period 2000–2015, 52 million hooks were deployed by 110 vessels, 31 million by  
227 foreign vessels targeting tuna and 21 million by local vessels targeting mostly swordfish. Fishing  
228 effort was greatest in 2011, with a combined total of nearly 6 million hooks set by both fleets  
229 combined. Foreign vessels deployed an average of  $2.0 \pm 1.1$  million hooks per year, compared to  
230  $1.3 \pm 0.4$  million set per year by local vessels over the same period. Foreign fishing effort peaked  
231 between June and September (Fig. 2a and b), with fishing conducted throughout the South  
232 African EEZ and regularly venturing into international waters. Local vessels fished throughout  
233 the year, concentrating their effort within the EEZ. The number of hooks per year set by foreign  
234 vessels increased from 0.5 million in 2001 to a maximum of 3.9 million in 2011, when 15 vessels  
235 were active; thereafter effort declined steeply to 0.8 million hooks by 2015, set by four vessels

236 (Fig. 2a and b). The number of hooks set by local vessels increased sharply after 2004, and  
237 remained at a constant high level of 1.5–1.9 million hooks per year between 2011 and 2015,  
238 when the number of active vessels ranged from 15–17 (Fig. 2c and d).

239 Local vessels fished in all four subregions, but concentrated their effort in the West, Southwest  
240 and South subregions (63% of hooks), and in the northern part of the East subregion (37% of  
241 hooks; Fig. 3a). The geographical distribution of the local fishing grounds is influenced by  
242 distance from fishing harbours along the West Coast (Saldanha Bay), around the Cape Peninsula  
243 (Cape Town, Hout Bay), the southern Cape (Mossel Bay, Port Elizabeth) and off northern  
244 KwaZulu-Natal (Richards Bay). Foreign vessels concentrated on the SW Indian Ocean, with the  
245 bulk of hooks set in the South (58%) and East (33%) subregions, and the remainder (9%) set in  
246 the SE Atlantic (Fig. 3b).

247 A total of 682 084 sharks (10 083 t) were reported as landed by both local and foreign fleets  
248 combined between 2000 and 2015 (Fig. 4). Large increments in landings of shortfin makos  
249 occurred in 2004 and 2005, with another major year-on-year increment in 2011. Mako landings  
250 trended upwards over the last three years of the time series, to the highest level on record in 2015.  
251 The numbers of blue sharks in landings increased steeply in 2011, and peaked in 2014 and 2015.

252 By region, 63 329 (508 t) sharks were reported from the West, 298 114 (3 309 t) from the  
253 Southwest, 291 308 (5 623 t) from the South and 29 333 (644 t) from the East subregions,  
254 respectively. Sharks contributed 52% by numbers (%N) and 31% by weight (%W) of total  
255 landings reported by both fleets. By subregion, sharks contributed high proportions to the total  
256 catch, relative to tunas and swordfish, in the Southwest (77% N; 48% W), West (60% N; 22%  
257 W), and South (52% N; 42% W) subregions, but a low proportion in the East (11% N; 7% W)  
258 (Fig. 3). Local vessels landed the bulk (91% N; 88% W) of all sharks on record, with foreign  
259 vessels landing the remainder. Local vessels landed more sharks during the warm than the cool

260 season (58% versus 42% N), whereas the reverse was the case for the foreign fleet (25% versus  
261 75% N).

262 For the foreign fleet, the annual landings of sharks, as a proportion of their total landings (sharks  
263 plus tuna and swordfish), was low (11% N; 8% W on average per year) reaching a maximum in  
264 2008 (19% N; 18% W) (Fig. 5). The local fleet reported similarly low proportions of sharks up to  
265 2003, whereafter annual landings of sharks increased sharply, to roughly half of the total landings  
266 made by local vessels (Fig. 5). In the last two years of the time series, the proportion of sharks in  
267 landings made by local vessels increased even further (78% N; 63% W in 2014, and 76% N and  
268 64% W in 2015).

269 *3.2. Species composition*

270 Blue sharks dominated the combined shark landings (59% N; 38% W), followed by shortfin  
271 makos (40% N; 59% W) and other sharks (1% N; 3% W). ‘Other sharks’ comprised of four  
272 groups, which could not be confidently resolved to species level based on the landings data (Fig.  
273 3). Nearly 4 000 sharks were not identified beyond ‘Sharks nei’, 3 500 were grouped as requiem  
274 sharks (including several similar-looking Carcharhinid species, but excluding blue sharks), and  
275 neither thresher sharks (*Alopias* spp.) nor hammerheads (*Sphyraena* spp.) were identified beyond  
276 genus level. Tope sharks (*Galeorhinus galeus*) (included with the requiem shark group) were first  
277 identified in landings in 2011. Contrary to the general pattern of shark landings, which is  
278 dominated by blue sharks, landings of makos caught in the South subregion exceeded those of  
279 blue sharks caught there (see Fig. 3).

280 3.3. *Model outputs*

281 The GLMM with vessel as a random effect consistently provided the lowest BIC, indicating that  
282 vessel-to-vessel variation, which incorporates operational characteristics or fishing power, is an  
283 important factor (Table S1a and b). Most of the variance could be attributed to the individual  
284 vessels, while the remaining random effects, subregion and season, explained a small percentage  
285 of the variation in the standardized CPUE (Table S2). The resulting model provided consistently  
286 superior fits than the null models, a constant trend for both mako and blue shark models across  
287 both local and foreign fleets (Table S2a and b). The standardized CPUE trends confirmed that  
288 blue sharks had a much higher catch rate than shortfin makos, irrespective of fleet, and that local  
289 vessels had a much higher catch rate of both species, individually, than foreign vessels (Fig. 6a  
290 and b). Both these trends were based on retained catches only, and excluded sharks that were  
291 caught and discarded overboard during fishing operations, which often went unreported. Hence  
292 the standardized CPUE underestimates the actual number of sharks caught per 1 000 hooks.

293 For blue sharks, the standardized CPUE trend of local vessels indicated a period of low catch  
294 rates (1–5 blue sharks/1 000 hooks) between 2000 and 2010, followed by a sudden three-fold  
295 increase in 2011, and thereafter consistently high catch rates (15–20 sharks/1 000 hooks) between  
296 2011 and 2015 (Fig. 6a). The standardized CPUE of foreign vessels remained below 4 blue  
297 sharks/1 000 hooks over the time series, and stabilized at around 2 sharks/1 000 hooks after 2009.

298 For shortfin makos, the standardized CPUE trend of local vessels showed two sudden increases,  
299 in 2004 and again in 2011, and a gradual increase after 2013 to the highest level on record in  
300 2015 (Fig. 6b). Standardized CPUE levels fluctuated from 1–2 makos/1 000 hooks between 2000  
301 and 2003, from 3–4.5 makos/1 000 hooks between 2004 and 2010, and increased from 5.5 to 7

302 makos/1 000 hooks between 2011 and 2015. The standardized CPUE of foreign vessels  
303 fluctuated around 1 mako /1 000 hooks over the 16-year time series.  
304 We interpreted the three-fold (2004) and two-fold (2011) increases in shortfin mako standardized  
305 CPUE as implausible from biological or population dynamics viewpoints, and hence as a result  
306 of increased retention rather than increases in shark abundance. Similarly, the order of magnitude  
307 with which blue shark standardized CPUE increased in 2011 was most likely a result of increased  
308 retention rates.

309 **4. Discussion**

310 Blue sharks and shortfin makos made up the bulk of shark landings by the local South African-  
311 and foreign-flagged pelagic longline fleets operating around southern Africa, confirming a similar  
312 finding from fisheries observer data collected prior to 2006 (Petersen et al., 2009). Similarly,  
313 pelagic longline fleets from Brazil and Uruguay predominantly caught blue sharks, shortfin  
314 makos and porbeagle sharks in the South Atlantic, as bycatch or target species (Hazin et al.,  
315 2008). Portuguese longliners caught blue sharks as a main bycatch species in the equatorial  
316 Atlantic, with shortfin makos and other sharks also present in catches (Coelho et al., 2012). Fleets  
317 in the NW Atlantic (Campana et al., 2005, 2006; Cortés, 2013), NE Atlantic and Mediterranean  
318 (Megalofonou et al., 2005; Mejuto et al., 2009), North Pacific ([Walsh and Teo, 2012](#)) and South  
319 Pacific (Francis et al., 2001) also caught mainly blue sharks and varying quantities of shortfin  
320 makos. Silky sharks are sometimes a more common bycatch of pelagic longliners in equatorial  
321 regions (Kumar et al., 2015), and they are also more susceptible to purse seine fisheries than blue  
322 sharks (Hall and Roman, 2013). Nevertheless, the predominance of blue sharks and shortfin  
323 makos in landings from longline fisheries around southern Africa is consistent with trends from  
324 most other regions.

325 Several other shark species made up lesser proportions of the landings, but they were not  
326 consistently identified to species level in the data. Requiem sharks (Carcharhinidae) have similar  
327 body shape, colour, and overlapping distributions (Compagno, 1999), and large pelagic sharks of  
328 the *Carcharhinus* genus, such as dusky- (*C. obscurus*), silky- (*C. falciformes*), and copper sharks  
329 (*C. brachyurus*) may have been misidentified (pers. comm. da Silva, DAFF, 2015). Three species  
330 of thresher sharks (*Alopias* spp.) look similar, and based on DNA barcoding, Velez-Zuazo et al.  
331 (2015), found that common threshers (*A. vulpinus*) were routinely misidentified as pelagic  
332 threshers (*A. pelagicus*) in catches from the SW Pacific. Several studies have commented on the  
333 misidentification of juvenile hammerheads (*Sphyrna* spp.) in fisheries data (Abercrombie et al.,  
334 2005; Barker and Schluessel, 2005). In addition to inconsistent identification of the above taxa,  
335 the data available to our study may have been affected by a change in fishing regulations, which  
336 prohibited the retention of oceanic whitetip (*C. longimanus*), threshers and hammerhead sharks  
337 by South African fisheries since 2011, and silky sharks since 2012 (DAFF, 2014). The coarsely  
338 grouped data, combined with near absence of recent (post-2011) landings information on these  
339 species, discouraged any attempts at further analysis of species other than blue sharks and  
340 shortfin makos.

341 A key finding of this study was that the standardized CPUE of blue sharks and shortfin makos  
342 caught by longlines had increased sharply since 2010, to the highest levels on record between  
343 2011 and 2015. This result is restricted to the local South African-flagged fleet, whereas the  
344 standardized CPUE of foreign-flagged vessels remained at low levels throughout the time series.  
345 We suggest that three factors, potentially in combination, can explain the observed trends: an  
346 increase in the abundance of blue sharks and shortfin makos in the SW Indian Ocean and SE  
347 Atlantic; a change in the fishing pattern of local vessels towards targeting and retaining more

348 sharks; and changes to fishing regulations, which affected the reporting of sharks, and hence  
349 influenced the standardized CPUE trend.

350 The hypothesis of an increase in abundance is consistent with the Japanese standardized CPUE  
351 series from its longline fleet in the Indian Ocean, which suggests that shortfin mako biomass  
352 declined from 1994 to 2003, but has increased since then (Kimoti et al., 2011). Similarly, the time  
353 series of shortfin makos caught by the Portuguese longline fleet in the Indian Ocean indicated a  
354 declining trend from 1999 to 2004, but increased in more recent years up to 2012 (Coelho et al.,  
355 2013). Nevertheless, there is no quantitative stock assessment currently available for shortfin  
356 makos in the Indian Ocean, and therefore their status remains uncertain (IOTC, 2016). For blue  
357 sharks, reported catches in the Indian Ocean have continued to increase since the early 1990s  
358 (IOTC, 2016), although catch estimates are highly uncertain, and probably represent only the  
359 sharks that were retained onboard. Standardized CPUE trends were variable and sometimes  
360 conflicting among fleets reporting to the IOTC. A first quantitative assessment for the Indian  
361 Ocean region in 2015 found blue shark stock status to be close to the maximum sustainable yield,  
362 but not yet overfished (IOTC, 2016).

363 In the South Atlantic, CPUE indices of fleets that report to ICCAT suggest a relative increase in  
364 the abundance of shortfin makos, particularly since 2004, although estimates are highly variable  
365 between years and fleets (ICCAT, 2017b). Landings of shortfin makos reported to ICCAT by the  
366 South African longline fleet increased sharply in recent years, from 250 t in 2013, to 476 t in  
367 2014, and to 613 t in 2015, the highest level on record. CPUE indices for blue sharks were also  
368 variable among fleets reporting to ICCAT, but apart from the Brazilian longline fleet, trended  
369 generally upwards over the past decade (ICCAT, 2015). An assessment of data up to 2013 showed  
370 that the South Atlantic blue shark stock was not overfished, and that overfishing was probably not  
371 occurring (ICCAT, 2015). The present stock status information from both the South Atlantic and

372 the SW Indian Ocean can therefore not reject the hypothesis of increasing abundance of blue  
373 sharks and shortfin makos in the waters around southern Africa.

374 Nevertheless, uncertainty remains about the relationship between abundance, CPUE series and  
375 total catches (IOTC, 2016), and the assumption that CPUE is proportional to abundance. The  
376 standardized CPUE of shortfin makos is most likely a much better reflection of its abundance,  
377 compared to the blue sharks, because makos have a higher market value than blue sharks, and are  
378 mostly retained (and hence reported in landings data) whenever they are caught (Petersen et al.,  
379 2009). Even so, the anomalous increases in standardized CPUE, up to an order of magnitude on a  
380 year-on-year basis, are unrealistic from a biological perspective.

381 The second hypothesis, that a change in fishing pattern (or retention of more sharks) can explain  
382 the high standardized CPUE levels of local vessels in recent years, is supported by an increase in  
383 the ratio of sharks (by weight) to total landings. In the GLMMs, most of the variance was  
384 attributed to the vessel factor, which included properties of fishing operations (e.g., gear  
385 configuration) and fishing pattern (e.g., bait type, depth and timing of sets, use of light sticks, and  
386 skipper experience). This indicates the high importance of fishing pattern in determining shortfin  
387 mako and blue shark catch rates, concurring with the findings of Gilman et al. (2008) and  
388 Petersen et al. (2009). In the local fishery, hooks are set near the surface, overnight, and with gear  
389 that include lightsticks and squid for bait. Although directed mainly at swordfish, this  
390 configuration also contributes to high shark catch rates (Stone and Dixon, 2001; dos Santos et al.,  
391 2002; Ward and Myers, 2005; Gilman et al., 2008; Mejuto et al., 2008; Petersen et al., 2009).  
392 Swordfish-directed fisheries are often multi-specific (dos Santos et al., 2002; Campana et al.,  
393 2016), and may switch their effort towards targeting more pelagic sharks when swordfish are less  
394 abundant. Local longline vessels, officially licensed to catch swordfish and tuna, have a long  
395 history of also targeting shortfin makos and blue sharks, historically through a now-defunct

396 shark-directed fishery, and permit exemptions (da Silva et al., 2015). The hypothesis of a change  
397 in fishing pattern, towards targeting or retaining more shortfin makos and blue sharks, is  
398 therefore a likely scenario, based on past performance and an increased ratio of sharks in  
399 landings.

400 Whilst the occurrence or reporting of sharks, or the decision to target them, could be attributed  
401 purely to the individual vessels in the binomial model, the remaining random effects, subregion  
402 and season, explained a larger portion of the variation in the gamma model. This trend was  
403 consistent, irrespective of fleet. The local fleet operated mainly in the West, Southwest and South  
404 subregions (SE Atlantic), from where the bulk of blue shark and shortfin mako landings  
405 originated. A far greater abundance of sharks in these subregions, compared to the East (SW  
406 Indian Ocean), is supported by the logbook data, and also by data collected by fisheries observers  
407 (Petersen et al., 2009). Fewer, but larger-sized shortfin makos, have been caught in the SW Indian  
408 Ocean, and the mean fork length (FL) of captured makos decreased from east to west, with the  
409 smallest individuals, in much larger numbers, occurring near the Agulhas Bank edge, in June to  
410 November (Groeneveld et al., 2014). This suggests that the Agulhas Bank may be a feeding  
411 ground for juvenile makos, which would explain the large proportion of mako landings  
412 originating from the South and Southwest subregions – i.e., the transition zone between the SE  
413 Atlantic and SW Indian Oceans. A similar pattern has been suggested for blue sharks (da Silva et  
414 al., 2010) whereby juvenile blue sharks have been caught within the Benguela / Agulhas Current  
415 transition filaments, suggesting a parturition and nursery area for blue sharks. This area coincides  
416 with the West, Southwest and South subregions in our study, where the bulk of the local fleet  
417 operates, and from where most of the landed blue sharks originated.

418 In our study, local vessels landed far more sharks during the warmer season (December to May),  
419 which may reflect a seasonal shift towards retaining more sharks. During this season, foreign

420 vessels follow tuna schools out of the South African EEZ, suggesting a lower availability of tunas  
421 in local waters (Zagaglia et al., 2004; Block et al., 2005, 2011). Swordfish are similarly less  
422 available over the Agulhas Bank region during the warm season (pers. comm. Vessel Skippers,  
423 2015). Two asynchronous fishing seasons for swordfish and blue sharks have previously been  
424 observed in the Portuguese longline fleet in the North Atlantic, where fishing effort shifted  
425 towards targeting pelagic sharks during times of low abundance of swordfish (dos Santos et al.,  
426 2002). We suggest that a similar seasonal fishing pattern has evolved in the local South African  
427 fishery, where vessels land a greater proportion of swordfish and tunas during the cooler months  
428 (June to November), switching to blue sharks and shortfin makos during warmer months.

429 The third hypothesis, that changes to fishing regulations had affected shark landings, and hence  
430 influenced the standardized CPUE trend, is supported by two sudden increases in the  
431 standardized CPUE, which both coincide with major changes to fishing regulations. For shortfin  
432 makos, the standardized CPUE increased steeply in 2004, and again in 2011. For blue sharks, a  
433 steep increase was observed in 2011 only. Both increases were too large to be explained by  
434 changes in stock status alone. Fisheries management decisions, and their effects on fishing  
435 practices and reporting, may explain the abrupt increases in the CPUE better.

436 The low CPUE prior to 2004 can best be explained by misreporting of data. Fisheries observers  
437 found large-scale finning and discarding of carcasses in 2000 and 2001 (25–30% of blue sharks)  
438 (Petersen and Goren, 2007) and the landings of the shark-directed fishery were not reported to the  
439 IOTC in 2001 and 2002 (IOTC, 2004). The market price for pelagic sharks (especially makos)  
440 increased in 2003, leading to more sharks being landed, and an expansion of fishing grounds to  
441 the Agulhas Bank, where shortfin makos are more abundant (Smith, 2005). In 2005, the now-  
442 defunct shark-directed sector was split into a demersal component, and a large pelagic fish  
443 component, as a management attempt to reduce catches of large pelagic sharks (West and

444 Kerwath, 2015). The pelagic component of the shark fishery was incorporated into long-term  
445 commercial fishing rights allocated to 18 swordfish and 26 tuna-directed vessels (da Silva et al.,  
446 2015) – with the intention that these vessels would now target swordfish and tunas, instead of  
447 sharks. An administrative loophole, however, resulted in permit exemptions, which allowed the  
448 shark-directed vessels to continue targeting sharks, up to March 2011. The sudden increase in the  
449 standardized CPUE of shortfin makos in 2004 can therefore be explained by an expansion of  
450 fishing grounds, and increased shark landings because of higher market prices (DAFF, 2013).

451 The official incorporation of the shark exemption permit holders into the large pelagic fishery for  
452 tunas and swordfish in 2011 was expected to reduce landings of pelagic sharks (West and Smith,  
453 2012), but it had the opposite effect – with steep increases observed in the standardized CPUE of  
454 blue sharks and shortfin makos in 2011. A plausible explanation is that the formerly shark-  
455 directed vessels actively continued to target sharks, despite having permits for tunas and  
456 swordfish. These vessels now reported their landings directly to the pelagic longline fishery.  
457 Hence the observed increases in standardized CPUE in 2011 are potentially artefactual, reflecting  
458 a change in reporting practices, rather than changes in stock status. As a response, regulatory  
459 changes in 2012 included a precautionary upper catch limit of 2 000 tonne dressed weight per  
460 year (West and Smith, 2013; Anderson et al., 2015), prohibiting the retention of thresher (*Alopias*  
461 spp.), hammerhead (*Sphyrna* spp.), oceanic whitetip, and silky sharks. Shark fins had to be  
462 accompanied by trunks, with the total weight of retained fins not exceeding 8% (shortfin makos)  
463 and 13% (blue sharks) of landed weight, respectively (West and Smith, 2013). Total shark  
464 landings by pelagic longline vessels have remained well below the 2 000 tonne dressed weight in  
465 each year since 2012 (da Silva et al., 2015).

466

## 5. Conclusion

467 To conclude, the interpretation of landings data and log-book derived CPUE indices constructed  
468 for blue sharks and shortfin makos caught by the local longline fleet in South African waters is  
469 complex. The index is an unreliable indicator of shark abundance in the region, but an effective  
470 indicator of changes in shark targeting or retention practices. The scale of increments correlating  
471 with changes in retention strategies, up to an order of magnitude on a year-on-year basis, was  
472 unexpected, and highlights the strong influence of market demand on targeting and retaining  
473 sharks in fisheries where they are frequently considered as bycatch, or secondary target species.  
474 The regulatory environment within which the fishery operates was unable to reduce targeting and  
475 retention of pelagic sharks, and a continued increase in the standardized CPUE index for shortfin  
476 makos over the last years of the time series suggested that they are increasingly being targeted  
477 and retained. The index proved to be a useful tool for measuring the influence of fisheries  
478 management decisions on operational realities of fishing fleets.

479 **Acknowledgements**

480 We thank CapFish, particularly Victor Ngcongo and Willem Louw, for their advice on how the  
481 pelagic longline fishing fleet operates. Thank you to the skippers of the vessels for providing  
482 insight into various fishing strategies and techniques. Thank you to the Department of  
483 Agriculture, Forestry and Fisheries, particularly Charlene da Silva and Wendy West, for  
484 providing the landings and logbook data for the study. GJ thanks the University of KwaZulu  
485 Natal for providing a college bursary and, JG thanks the National Research Foundation for  
486 incentive funding (Grant number 96309).

487 **References**

488 Abercrombie DL, Clarke SC, Shivji MS. 2005. Global-scale genetic identification of  
489 hammerhead sharks: application to assessment of the international fin trade and law  
490 enforcement. *Conservation Genetics* 6 (5): 775-788.

491 Aires-da-Silva AM, Gallucci VF. 2007. Demographic and risk analyses applied to management  
492 and conservation of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Marine  
493 and Freshwater Research* 58 (6): 570-580.

494 Anderson R, Auerswald L, Butterworth D, Cockcroft A, Coetzee J, da Silva C, Durholtz D,  
495 Fairweather T, Geja Y, Githaiga-Mwicigi J, Kemp D, Kerwath S, Lamberth S, Leslie R,  
496 Mackenzie A, Maharaj G, Mbande S, Prochazka K, Rothman M, Singh L, Twatwa N, Van  
497 der Lingen C, West W. 2015. *Status of the South African Marine Fishery Resources 2014*.  
498 Department of Agriculture, Forestry and Fisheries. Cape Town, South Africa.

499 Animal Welfare Institute. 2017. International Shark Finning Bans and Policies. Available at  
500 <https://awionline.org/content/international-shark-finning-bans-and-policies> [accessed  
501 25/10/2017 2017].

502 Barker MJ, Schluessel V. 2005. Managing global shark fisheries: suggestions for prioritizing  
503 management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15  
504 (4): 325-347.

505 Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck  
506 G, Green P, Bolker MB. 2016. Linear Mixed-Effects Models using 'Eigen' and S4:  
507 Package 'lme4'. *CRAN Repository*.

508 BCLME (Benguela Current Large Marine Ecosystem). 2005. Ecosystem Approach to Fishery  
509 Management: South Africa Large Pelagics TROM Review. Available at  
510 <http://www.bclme.org/projects/docs/LMR-EAF-03-01.pdf>.

511 Beal LM, De Ruijter WPM, Biastoch A, Zahn R. 2011. On the role of the Agulhas system in  
512 ocean circulation and climate. *Nature* 472 (7344): 429-436.

513 Becker RA, Wilks AR. 2016a. Draw Geographical Maps: Package 'maps'. CRAN Repository.

514 Becker RA, Wilks AR. 2016b. Extra Map Databases: Package 'mapdata'. CRAN Repository.

515 Block BA, Teo SL, Walli A, Boustany A. 2005. Electronic tagging and population structure of  
516 Atlantic bluefin tuna. *Nature* 434 (7037): 1121.

517 Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG,  
518 Breed G, Harrison A. 2011. Tracking apex marine predator movements in a dynamic  
519 ocean. *Nature* 475 (7354): 86.

520 Bustamante C, Bennett MB. 2013. Insights into the reproductive biology and fisheries of two  
521 commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark  
522 (*Prionace glauca*), in the south-east Pacific Ocean. *Fisheries Research* 143 (0): 174-183.

523 Campana SE, Marks L, Joyce W. 2005. The biology and fishery of shortfin mako sharks (*Isurus*  
524 *oxyrinchus*) in Atlantic Canadian waters. *Fisheries Research* 73 (3): 341-352.

525 Campana SE, Brazner J, Marks L. 2006. *Assessment of the Recovery Potential of Shortfin Mako*  
526 *Sharks in Atlantic Canada*. Population Ecology Division, Bedford Institute of  
527 Oceanography Darmouth, Canada.

528 Campana SE, Joyce W, Manning MJ. 2009. Bycatch and discard mortality in commercially  
529 caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine*  
530 *Ecology Progress Series* 387: 241-253.

531 Campana SE. 2016. Transboundary movements, unmonitored fishing mortality, and ineffective  
532 international fisheries management pose risks for pelagic sharks in the Northwest  
533 Atlantic. *Canadian journal of fisheries and aquatic sciences* 73 (10): 1599-1607.

534 Campana SE, Joyce W, Fowler M, Showell M. 2016. Discards, hooking, and post-release  
535 mortality of porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), and blue shark  
536 (*Prionace glauca*) in the Canadian pelagic longline fishery. *ICES Journal of Marine*  
537 *Science* 73 (2): 520-528.

538 Clarke DT, Smith C. 2008. *National Report of South Africa*. Indian Ocean Tuna Commission.  
539 Report No. IOTC-2008-SC-INF17. Cape Town, South Africa.

540 Coelho R, Santos MN, Amorim S. 2012. Effects of hook and bait on targeted and bycatch fishes  
541 in an Equatorial Atlantic pelagic longline fishery. *Bulletin of Marine Science* 88 (3): 449-  
542 467.

543 Coelho R, Infante P, Santos MN. 2013. Application of Generalized Linear Models and  
544 Generalized Estimation Equations to model at-haulback mortality of blue sharks captured  
545 in a pelagic longline fishery in the Atlantic Ocean. *Fisheries Research* 145 (0): 66-75.

546 Compagno LJ. 1999. Checklist of living elasmobranchs. In: Hamlett WC (ed.) *Sharks, Skates*  
547 and *Rays: the Biology of Elasmobranch Fishes*. Baltimore, U.S.A.: John Hopkins  
548 University Press. pp. 471-498.

549 Cortés E. 2013. Standardized catch rates of mako sharks from the US pelagic longline logbook  
550 and observer programs using a generalized linear mixed model. *Collect. Vol. Sci. Pap.*  
551 *ICCAT* 69 (4): 1578-1590.

552 da Silva C, Kerwath S, Wilke C, Meyer M, Lamberth S. 2010. First documented southern  
553 transatlantic migration of a blue shark *Prionace glauca* tagged off South Africa. *African*  
554 *Journal of Marine Science* 32 (3): 639-642.

555 da Silva C, Booth AJ, Dudley SFJ, Kerwath SE, Lamberth SJ, Leslie RW, McCord ME, Sauer  
556 WHH, Zweig T. 2015. The current status and management of South Africa's  
557 chondrichthyan fisheries. *African Journal of Marine Science* 37 (2): 233-248.

558 DAFF. 2013. *National Plan of Action for the Conservation and Management of Sharks (NPOA-*  
559 *Sharks*). Department of Agriculture, Forestry and Fisheries. Report No. IOTC-2013-  
560 SC16-INF15. Cape Town, South Africa: Department of Agriculture Forestry and  
561 Fisheries.

562 DAFF. 2014. *Section C. Sector specific permit conditions: tuna longline. Fishing season: 2014.*  
563 Department of Agriculture, Forestry and Fisheries. Report No. Vol. 600 No. 38871. Cape  
564 Town, South Africa.

565 DAFF. 2016. *Permit Conditions: Large Pelagic Longline Fishery – Fishing Season: 2016/2017*.  
566 The Department of Agriculture, Forestry and Fisheries. Cape Town, South Africa

567 Davidson LN, Krawchuk MA, Dulvy NK. 2016. Why have global shark and ray landings  
568 declined: improved management or overfishing? *Fish and Fisheries* 17 (2): 438-458.

569 dos Santos MN, Garcia A, Pereira JG. 2002. A historical review of the by-catch from the  
570 Portuguese surface long-line swordfish fishery: observations on blue shark (*Prionace*  
571 *glauca*) and short-fin mako (*Isurus oxyrinchus*). *ICCAT Collective Volume of Scientific*  
572 *Papers* 54: 1333-1340.

573 Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortés E, Domingo A, Fordham S, Fowler S,  
574 Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S. 2008. You  
575 can swim but you can't hide: the global status and conservation of oceanic pelagic sharks  
576 and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18 (5): 459-482.

577 Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson  
578 LN, Fordham SV, Francis MP. 2014. Extinction risk and conservation of the world's  
579 sharks and rays. *eLife* 3: e00590.

580 Francis MP, Griggs LH, Baird SJ. 2001. Pelagic shark bycatch in the New Zealand tuna longline  
581 fishery. *Marine and Freshwater Research* 52 (2): 165-178.

582 Gilman E, Clarke S, Brothers N, Alfaro-Shigueto J, Mandelman J, Mangel J, Petersen S, Piovano  
583 S, Thomson N, Dalzell P, Donoso M, Goren M, Werner T. 2008. Shark interactions in  
584 pelagic longline fisheries. *Marine Policy* 32 (1): 1-18.

585 Groeneveld JC, Cliff G, Dudley S, Foulis A, Santos J, Wintner S. 2014. Population structure and  
586 biology of shortfin mako, *Isurus oxyrinchus*, in the south-west Indian Ocean. *Marine and*  
587 *Freshwater Research* 65 (12): 1045-1058.

588 Hall M, Roman M. 2013. Bycatch and non-tuna catch in the tropical tuna purse seine fisheries of  
589 the world. *FAO fisheries and aquaculture technical paper* 568.

590 Hazin FH, Broadhurst MK, Amorim AF, Arfelli CA, Domingo A. 2008. Catches of pelagic sharks  
591 by subsurface longline fisheries in the South Atlantic Ocean during the last century: A

592 review of available data with emphasis on Uruguay and Brazil. In: Camhi MD, Pikitch  
593 EK, Babcock EA (eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*.  
594 Oxford, UK: Blackwell Publishing Ltd. pp. 213-229.

595 Hothorn T, Zeileis A, Farebrother RW, Cummins C, Millo G, Mitchell D, Zeileis MA 2015.  
596 Testing Linear Regression Models: Package 'lmtest'. CRAN.

597 Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheyen HMS, Bartholomae CH,  
598 van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T,  
599 Coetze J, Shillington F, Veitch J, Currie JC, Monteiro PMS. 2009. The Benguela  
600 Current: An ecosystem of four components. *Progress in Oceanography* 83 (1-4): 15-32.

601 ICCAT. 2015. *Report of the 2015 ICCAT blue shark stock assessment session (Lisbon, Portugal)*.  
602 International Commission for the Conservation of Atlantic Tunas. Madrid, Spain.  
603 [https://www.iccat.int/Documents/.../Docs/2015\\_BSH%20ASSESS\\_REPORT\\_ENG.pdf](https://www.iccat.int/Documents/.../Docs/2015_BSH%20ASSESS_REPORT_ENG.pdf)

604 ICCAT. 2016. *Report for biennial period, 2014-15 Part II (2015) - Vol. 1* International  
605 Commission for the Conservation of Atlantic Tunas. Madrid, Spain.

606 ICCAT 2017a. *Report of the 2017 ICCAT shortfin mako assessment meeting*. International  
607 Commission for the Conservation of Atlantic Tunas. Madrid, Spain.  
608 [https://www.iccat.int/Documents/Meetings/Docs/2017\\_SMA\\_ASS\\_REPORT\\_ENG.pdf](https://www.iccat.int/Documents/Meetings/Docs/2017_SMA_ASS_REPORT_ENG.pdf)

609 ICCAT. 2017b. *Report of the 2017 ICCAT shortfin mako data preparatory meeting*. International  
610 Commission for the Conservation of Atlantic Tunas. Madrid, Spain.  
611 [https://www.iccat.int/Documents/Meetings/Docs/2017\\_SMA\\_DATA\\_PREP\\_ENG.pdf](https://www.iccat.int/Documents/Meetings/Docs/2017_SMA_DATA_PREP_ENG.pdf)

612 IHO. 1953. *International Hydrographic Organization Special Publication: Limits of Oceans and  
613 Seas*. International Hydrographic Organization.

614 IOTC. 2004. *South Africa National Report*. Indian Ocean Tuna Commission. Report No. IOTC-  
615 2004-SC-INF06. Mahe, Seychelles.

616 IOTC. 2016. *Report of the 19th Session of the IOTC Scientific Committee*. Report No. IOTC-  
617 2016-SC19-R[E]. Seychelles, 1-5 December 2016.

618 James KC, Lewison RL, Dillingham PW, Curtis KA, Moore JE. 2016. Drivers of retention and  
619 discards of elasmobranch non-target catch. *Environmental Conservation* 43 (1): 3-12.

620 Jørgensen E, Pedersen AR. 1998. *How to obtain those nasty standard errors from transformed*  
621 *data—and why they should not be used.* Department of Biometry and Informatics, Danish  
622 Institute of Agricultural Science. Tjele, Denmark.

623 Kimoto A, Hiraoka Y, Ando T, Yokawa K. 2011. Standardized CPUE of shortfin mako shark  
624 (*Isurus oxyrinchus*) caught by Japanese longliners in the Indian Ocean in the period  
625 between 1994 and 2010. *IOTCWPEB07-34. 8pp.*

626 Kohler NE, Turner PA, Hoey JJ, Natanson LJ, Briggs R. 2002. Tag and recapture data for three  
627 pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*),  
628 and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. *Collective Volume of Scientific*  
629 *Papers - ICCAT* 54 (4): 1231-1260.

630 Kumar KVA, Pravin P, Meenakumari B, Khanolkar PS, Baiju MV. 2015. Shark bycatch in the  
631 experimental tuna longline fishery in Lakshadweep Sea, India. *Journal of Applied*  
632 *Ichthyology* 31: 301-307.

633 Lauretta MV, Walter JF, Christman MC. 2016. Some considerations for CPUE standardization;  
634 variance estimation and distributional considerations. *Collective Volume of Scientific*  
635 *Papers - ICCAT* 72 (9): 2304-2312.

636 Lindberg V. 2000. *Manual on Uncertainties, Graphing and the Vernier Caliper, Part I:*  
637 *Uncertainties and error propagation.* Rochester Institute of Technology. New York, USA.

638 Lutjeharms J. 2006a. *The Agulhas Current.* New York: Springer.

639 Lutjeharms JRE. 2006b. The Coastal Oceans of South-Eastern Africa (15,W). In: Robinson AR,  
640 Brink KH (eds.), *The Sea.* Cambridge: Harvard University Press. pp. 783-834.

641 Manning C. 2007. Generalized Linear Mixed Models (illustrated with R on Bresnan et al.'s  
642 datives data).

643 Maunder MN, Punt AE. 2004. Standardizing catch and effort data: a review of recent approaches.  
644 *Fisheries Research* 70 (2-3): 141-159.

645 McCullagh P, Nelder JA. 1989. Generalized Linear Models, no. 37 in Monograph on Statistics  
646 and Applied Probability. Chapman & Hall.

647 Megalofonou P. 2005. Incidental catch and estimated discards of pelagic sharks from the  
648 swordfish and tuna fisheries in the Mediterranean Sea. *Fishery Bulletin* 103 (4): 620-634.

649 Mejuto J, García-Cortés B, Ramos-Cartelle A. 2008. Trials using different hook and bait types in  
650 the configuration of the surface longline gear used by the Spanish swordfish (*Xiphias*  
651 *gladius*) fishery in the Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT* 62 (6): 1793-1830.

652 Mejuto J, García-Cortés B, Ramos-Cartelle A, De la Serna J. 2009. Scientific estimations of by-  
653 catch landed by the Spanish surface longline fleet targeting swordfish (*Xiphias gladius*) in  
654 the Atlantic Ocean with special reference to the years 2005 and 2006. *Collect. Vol. Sci.*  
655 *Pap. ICCAT* 64 (7): 2455-2468.

656 Musick JA. 1999. Criteria to define extinction risk in marine fishes: the American Fisheries  
657 Society initiative. *Fisheries* 24 (12): 6-14.

658 Oliver S, Braccini M, Newman SJ, Harvey ES. 2015. Global patterns in the bycatch of sharks and  
659 rays. *Marine Policy* 54: 86-97.

660 Parker D, West W, Mketsu Q, Kerwath S. 2016. *South African National Report to the Scientific*  
661 *Committee of the Indian Ocean Tuna Commission, 2016*. Indian Ocean Tuna Commission.  
662 Cape Town, South Africa.

663 Pennington M. 1983. Efficient estimators of abundance, for fish and plankton surveys.  
664 *Biometrics* 39 (1): 281-286.

665 Petersen S, Goren M. 2007. South Africa Pelagic Lingline Tuna and Swordfish Fishery: Industry  
666 Practices and Attitudes towards Shark Depredation and Unwanted Bycatch. In: Gilman E,  
667 Clarke S, Brothers N, Alfaro-Shigueto-J., Mandelman J, Mangel J, Petersen S, Piovano S,  
668 Thomson N, Dalzell P, et al. (eds.). *Shark Depredation and Unwanted Bycatch in Pelagic*

669       *Longline Fisheries: Industry Practices and Attitudes, and Shark Avoidance Strategies.*  
670       Honolulu, U.S.A.: Western Pacific Regional Fishery Management Council.

671       Petersen S, Honig M, Ryan P, Underhill L, Compagno LJ. 2009. Pelagic shark bycatch in the  
672       tuna-and swordfish-directed longline fishery off southern Africa. *African Journal of*  
673       *Marine Science* 31 (2): 215-225.

674       R\_Development\_Core\_Team. 2016. R: A language and environment for statistical computing.  
675       Vienna, Austria.: R Foundation for Statistical Computing.

676       Reardon MB., Gerber L, Cavanagh RD. 2006. *Isurus paucus*. The IUCN Red List of Threatened  
677       Species 2006: e.T60225A12328101. <http://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T60225A12328101.en>. Downloaded on 18 October 2017.

679       Ripley B, Bivand R, Venables B. 2015. Functions for Kriging and Point Pattern Analysis:  
680       Package 'spatial'. CRAN.

681       Smith C. 2005. *National Report of South Africa*. Indian Ocean Tuna Commission. Cape Town.

682       Smith SE, Au DW, Show C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks.  
683       *Marine and Freshwater Research* 49 (7): 663-678.

684       Stefánsson G. 1996. Analysis of groundfish survey abundance data: combining the GLM and  
685       delta approaches. *ICES Journal of Marine Science* 53 (3): 577-588.

686       Stone HH, Dixon LK. 2001. A comparison of catches of swordfish, *Xiphias gladius*, and other  
687       pelagic species from Canadian longline gear configured with alternating monofilament  
688       and multifilament nylon gangions. *Fishery Bulletin* 99 (1): 210-216.

689       Su N-J, Yeh S-Z, Sun C-L, Punt AE, Chen Y, Wang S-P. 2008. Standardizing catch and effort data  
690       of the Taiwanese distant-water longline fishery in the western and central Pacific Ocean  
691       for bigeye tuna, *Thunnus obesus*. *Fisheries Research* 90 (1): 235-246.

692       Tellinghuisen J. 2001. Statistical error propagation. *The Journal of Physical Chemistry A* 105  
693       (15): 3917-3921.

694 Velez-Zuazo X, Alfaro-Shigueto J, Mangel J, Papa R, Agnarsson I. 2015. What barcode  
695 sequencing reveals about the shark fishery in Peru. *Fisheries Research* 161: 34-41.

696 Venables WN, Dichmont CM. 2004. GLMs, GAMs and GLMMs: an overview of theory for  
697 applications in fisheries research. *Fisheries Research* 70 (2-3): 319-337.

698 Walsh W, Teo S. 2012. *Catch statistics, length data and standardized CPUE for blue shark*  
699 *Prionace glauca taken by longline fisheries based in Hawaii and California.*

700 Ward P, Myers RA. 2005. Inferring the depth distribution of catchability for pelagic fishes and  
701 correcting for variations in the depth of longline fishing gear. *Canadian Journal of*  
702 *Fisheries and Aquatic Sciences* 62 (5): 1130-1142.

703 West W, Kerwath S. 2015. *National Report of South Africa*. Indian Ocean Tuna Commission.  
704 Report No. IOTC-2015-SC16-NR33. Cape Town.

705 West W, Smith C. 2012. *National Report of South Africa*. Indian Ocean Tuna Commisison.  
706 Report No. IOTC-2012-SC15-NR33. Cape Town.

707 West W, Smith C. 2013. *National Report of South Africa*. Indian Ocean Tuna Commisison.  
708 Report No. IOTC-2013-SC16-NR33. Cape Town.

709 Worm B, Davis B, Kettner L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber  
710 SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine*  
711 *Policy* 40: 194-204.

712 Zagaglia CR, Lorenzetti JA, Stech JL. 2004. Remote sensing data and longline catches of  
713 yellowfin tuna (*Thunnus albacares*) in the equatorial Atlantic. *Remote Sensing of*  
714 *Environment* 93 (1): 267-281.

715 **Figure titles:**

716 **Fig 1.** Average sea surface temperatures (SST C°) for cool (June to November) and warm  
717 (December to May) seasons as reported in logbooks. Interpolation performed by kriging. The  
718 four subregions are shown in plot a) as W – West, SW – South West, S – South, and E – East.  
719 Towns and ports are abbreviated as follows: CT = Cape Town, CA = Cape Agulhas, PE = Port  
720 Elizabeth, DBN = Durban, RB = Richards Bay.

721 **Fig 2.** Fishing effort (numbers of hooks set) by month and year by foreign- (a & b) and local  
722 pelagic longline vessels (c & d) between 2000 and 2015. The distribution of the data by area and  
723 season is shown in supplementary Table S3.

724 **Fig 3.** Average fishing effort (numbers of hooks set) and landings by weight by subregion for  
725 local and foreign pelagic longline fleets, based on DAFF landings data (2000-2015). Bubble size  
726 is proportional to the numbers of hooks set. Sharks nei (not elsewhere included) include thresher,  
727 hammerhead, requiem, and unknown sharks.

728 **Fig 4.** Annual landings (in numbers) of shortfin mako and blue sharks reported by local and  
729 foreign pelagic longline fleets.

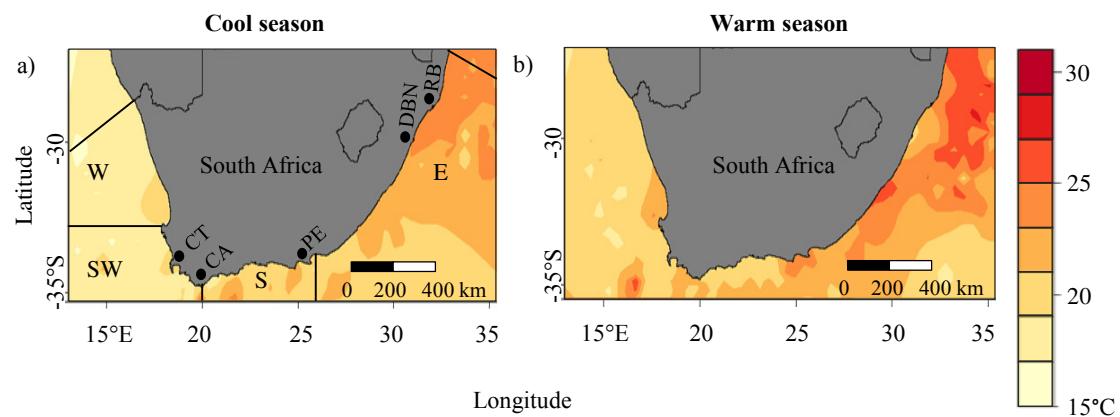
730 **Fig 5.** The ratio of shark landings (blue sharks + shortfin makos) to total landings (all species,  
731 including tunas, swordfish, blue sharks and shortfin makos) for local and foreign pelagic longline  
732 fleets.

733 **Fig 6.** The standardized CPUE ( $\pm$ SE) trends for blue sharks and shortfin makos landed by local  
734 and foreign pelagic longline fleets.

**Figure 1**(on next page)

Average sea surface temperatures (SST C°) for cool (June to November) and warm (December to May) seasons as reported in logbooks. Interpolation performed by kriging.

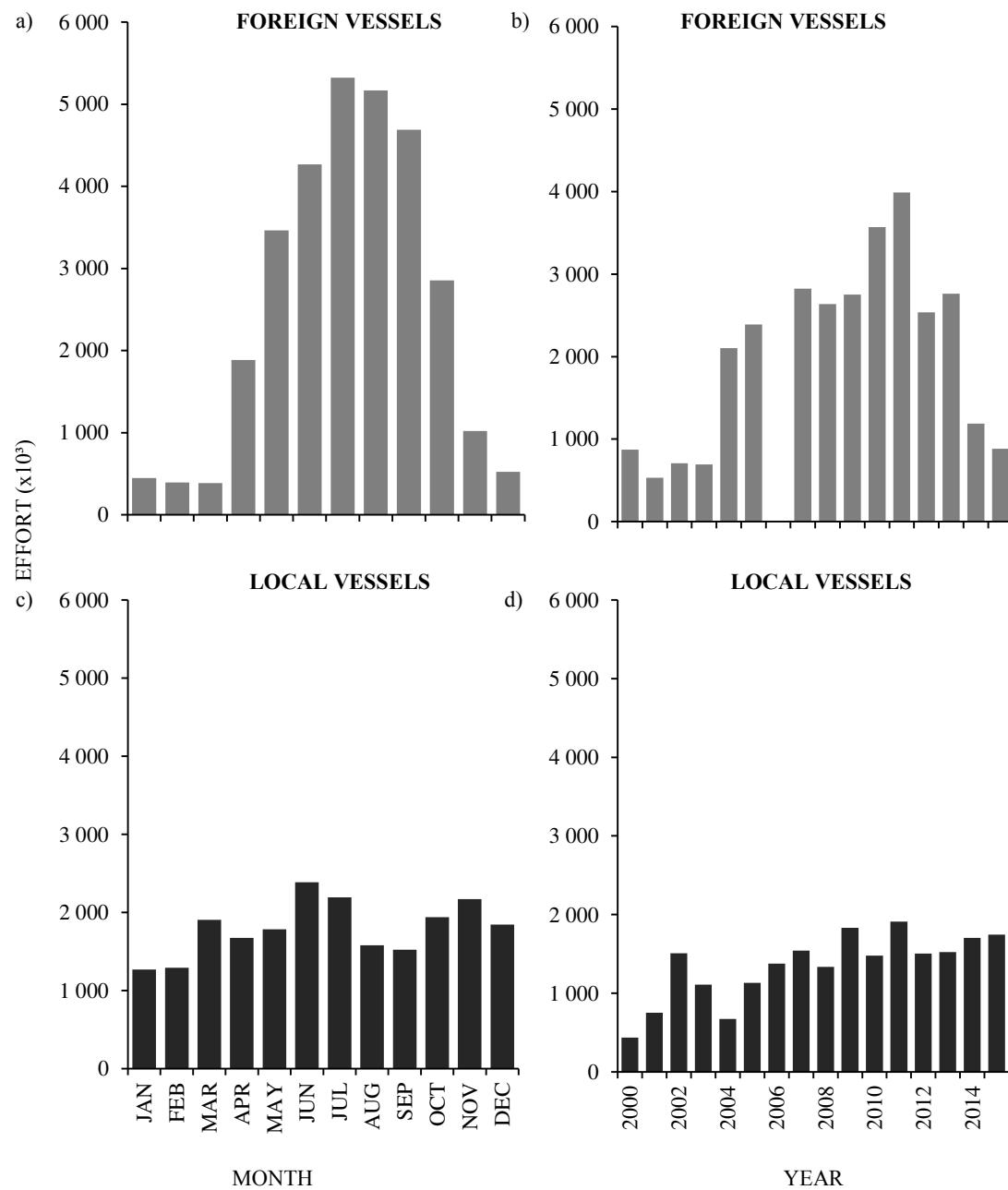
The four subregions are W = West, SW = South West, S = South, and E = East. Towns and ports are abbreviated as follows: CT = Cape Town, CA = Cape Agulhas, PE = Port Elizabeth, DBN = Durban, RB = Richards Bay. Source: DAFF landings data (2000 - 2015).



**Figure 2**(on next page)

Fishing effort (numbers of hooks set) by month and year by foreign- (a & b) and local pelagic longline vessels (c & d) between 2000 and 2015.

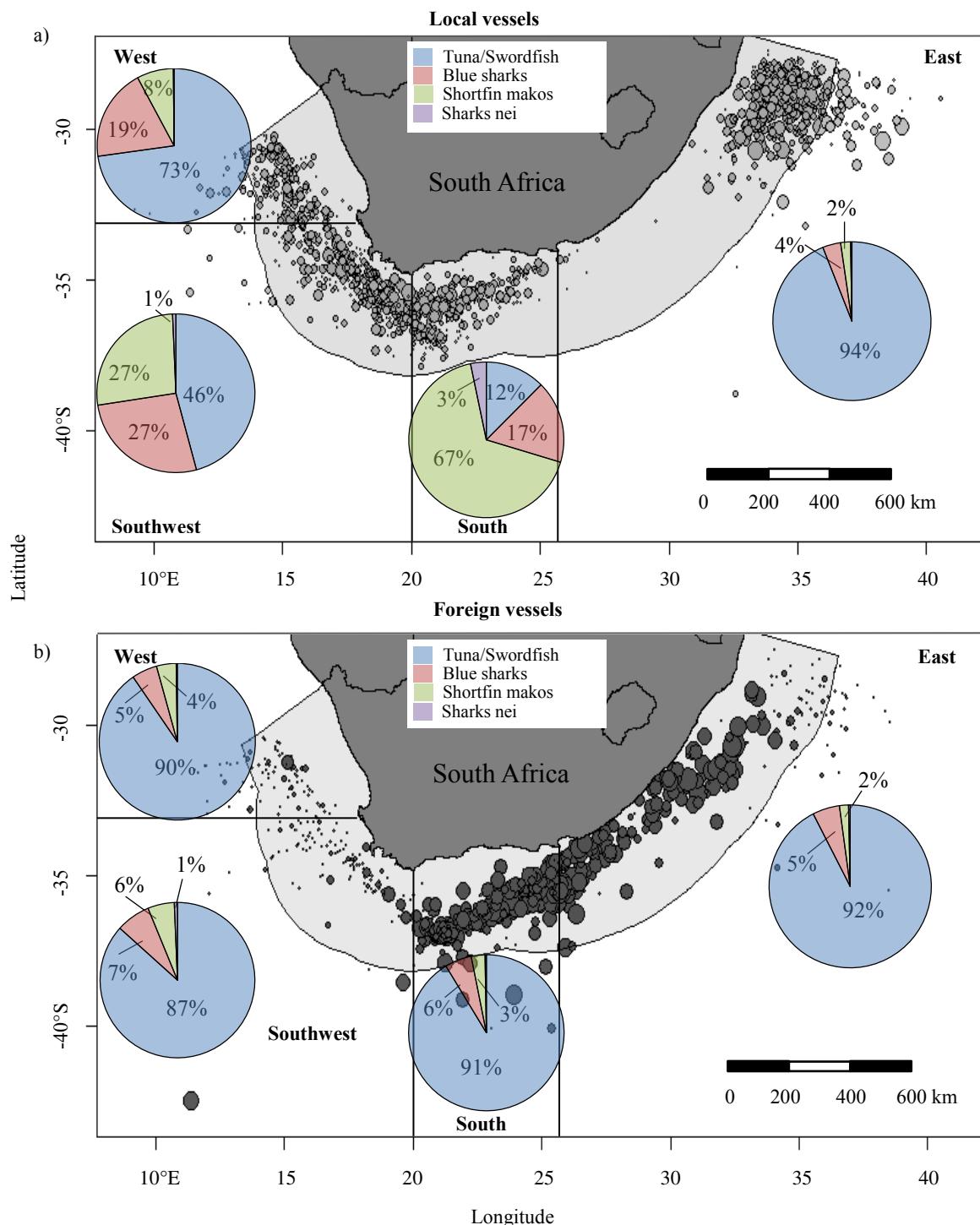
The distribution of the data by area and season is shown in supplementary Table S3.



**Figure 3**(on next page)

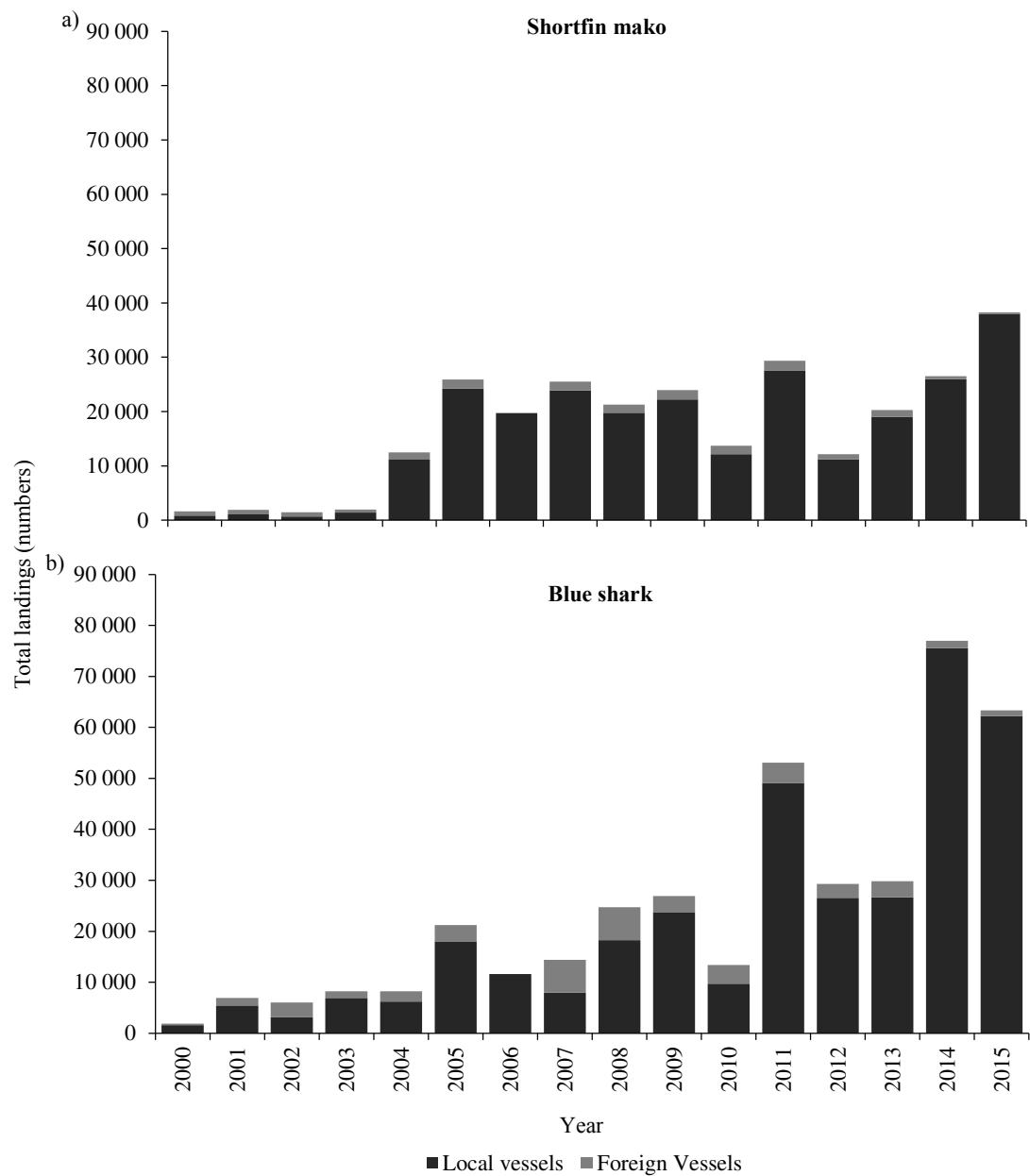
Fig 3. Average fishing effort (numbers of hooks set) and landings by weight by subregion for local and foreign pelagic longline fleets, based on DAFF landings data (2000-2015).

Bubble size is proportional to the numbers of hooks set. Sharks nei (not elsewhere included) include thresher, hammerhead, requiem, and unknown sharks.



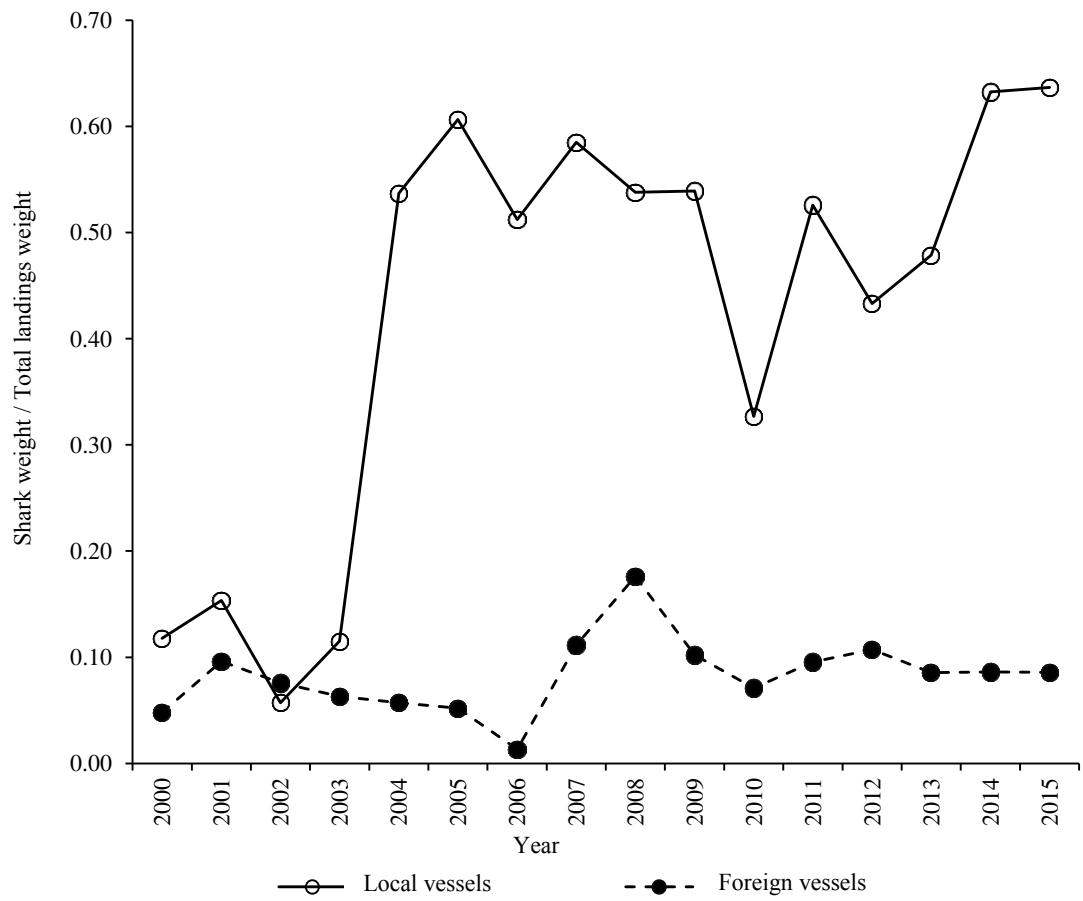
**Figure 4**(on next page)

Annual landings (in numbers) of shortfin mako and blue sharks reported by local and foreign pelagic longline fleets.



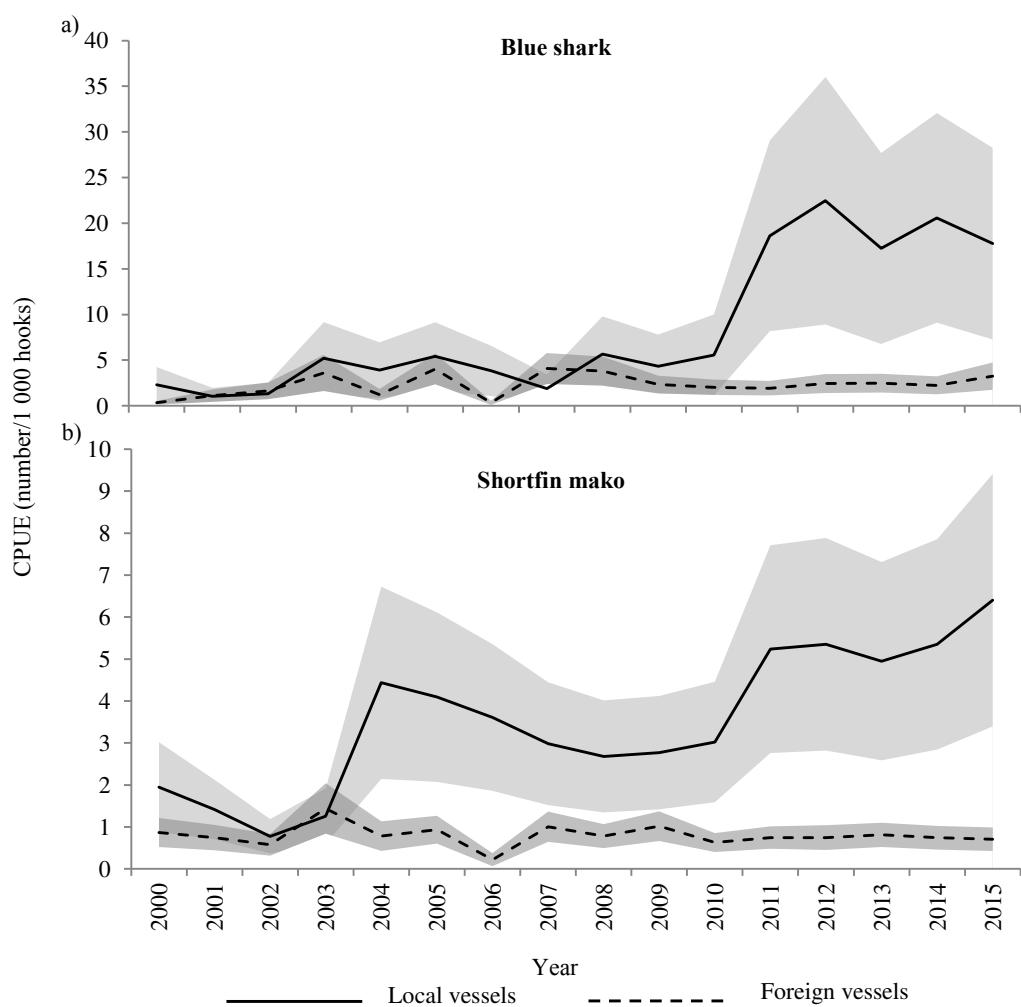
**Figure 5**(on next page)

The ratio of shark landings (blue sharks + shortfin makos) to total landings (all species, including tunas, swordfish, blue sharks and shortfin makos) for local and foreign pelagic longline fleets.



**Figure 6**(on next page)

The standardized CPUE ( $\pm$ SE) trends for blue sharks and shortfin makos landed by local and foreign pelagic longline fleets.



**Table 1**(on next page)

Explanatory variables hypothesised to affect the CPUE of blue sharks and shortfin makos caught by local and foreign pelagic longline fishing vessels from 2000-2015.

“Year” was the only fixed effect in the model.

Variable	Type	Description
Year	Categorical	2000–2015
Region	Categorical	West, Southwest, South, East
Season	Categorical	Warm = December–May Cool = June–November
Vessel	Categorical	Local: 61 individual vessels represented by 16 810 longline records  Foreign: 41 individual vessel represented by 12 209 longline records
<u>Observer present</u>	Categorical	Yes, No