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5	Article type : Original Article
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8	Running title: silky shark relative abundance
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10	The importance of environment and life stage on interpretation of silky shark relative
11	abundance indices for the equatorial Pacific Ocean
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	This is the author manuscript accepted for publication and has undergone full peer review but has

not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u>. Please cite this article as <u>doi:</u> <u>10.1111/fog.12385</u>

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### 31 Abstract

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Recent large fluctuations in an index of relative abundance for the silky shark in the eastern 32 Pacific Ocean have called into question its reliability as a population indicator for management. 33 To investigate whether these fluctuations were driven by environmental forcing rather than true 34 changes in abundance, a Pacific-wide approach was taken. Data collected by observers aboard 35 purse-seine vessels fishing in the equatorial Pacific were used to compute standardized trends in 36 relative abundance by region, and where possible, by shark size category as a proxy for life 37 stage. These indices were compared to the Pacific Decadal Oscillation (PDO), an index of 38 39 Pacific Ocean climate variability. Correlation between silky indices and the PDO was found to differ by region and size category. The highest correlations by shark size category were for small 40 41 (< 90 cm total length (TL)) and medium (90-150 cm TL) sharks from the western region of the equatorial eastern Pacific (EP) and from the equatorial western Pacific. This correlation 42 43 disappeared in the inshore EP. Throughout, correlations with the PDO were generally lower for large silky sharks (> 150 cm TL). These results are suggestive of changes in the small and 44 45 medium silky indices being driven by movement of juvenile silky sharks across the Pacific as the eastern edge of the Indo-Pacific Warm Pool shifts location with ENSO events. Lower correlation 46 47 of the PDO with large shark indices may indicate that those indices were less influenced by environmental forcing and therefore potentially less biased with respect to monitoring population 48 49 trends.

- 50
- 51 Keywords: silky shark; *Carcharhinus falciformis*; Pacific Ocean; purse-seine; PDO; ENSO;
  52 FAD
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# 54 Introduction

Assessment and management of the silky shark (*Carcharhinus falciformis*) in the Pacific Ocean has been complicated by a lack of information about both the ecology of the silky shark and the amount of fishery removals. Management of the silky shark east of 150°W (EPO), in the Inter-American Tropical Tuna Commission (IATTC) management area (Allen *et al.*, 2010), is based 59 only on trends in indices of relative abundance estimated from data collected by observers aboard large<sup>1</sup> tuna purse-seine vessels. Data available from other fisheries operating in the EPO 60 that catch silky sharks (bycatch or targeted) are either incomplete with respect to fishing effort or 61 with respect to catch by species (Siu and Aires-da-Silva, 2016). In the Western and Central 62 Pacific Ocean (WCPO) there is long-term observer coverage for the longline fishery but the 63 sample size is small and may be unrepresentative of the fishery as a whole. Observer coverage 64 for the purse seine fishery is higher but only in the years since 2010 (Clarke, 2017). 65 Management of silky shark in the WCPO is primarily through a no-retention rule adopted 66 subsequent to a WCPO silky shark stock assessment, which concluded that the species is 67 severely over-fished (Rice and Harley, 2013). 68

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The first exploration of trends in Pacific silky shark populations began in 2007 in the EPO, and 70 interpretation of these trends, which continue to be updated annually, has proved to be an 71 72 ongoing challenge. Of concern was the initial decline that began in the late 1990s (Minami et al., 73 2007), which may have been related to expansion of the purse-seine fishery on floating objects in 74 the EPO (Lennert-Cody and Hall, 1999). However, other interpretations are also possible and the processes driving change in the index have continued to be debated (Aires-da-Silva et al., 2014). 75 76 Since the mid 2000's, the index for the silky shark in the EPO north of the equator has fluctuated considerably (Figure 1), raising further questions as to the processes driving the index. The 77 78 recent increases in the EPO indices from one year to the next, especially in the northern EPO, are 79 in many cases too rapid to be due exclusively to population growth (Lennert-Cody et al., 2017). 80 Similar fluctuations are found in indices computed for other types of purse-seine sets (sets on dolphin-associated tunas and unassociated tuna schools; Lennert-Cody et al., 2017), suggesting 81 82 that processes behind the recent changes in the index are not specific to aspects of the fishery on tunas associated with floating-objects. 83

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Other processes that might contribute to fluctuations in the index include environmentally mediated changes in availability of silky sharks to fishing gear and/or east-west/north-south movement. Here we investigate the potential for recent fluctuations in the EPO index to be driven by environmental forcing. We focus on data from purse-seine vessels fishing on tunas

<sup>&</sup>lt;sup>1</sup> Vessels with fish-carrying capacity >363 t.

associated with floating-objects in the equatorial Pacific: silky shark bycatch in purse-seine 89 fisheries primarily occurs in floating-object (associated) sets (Román-Verdesoto and Orozco-90 Zöller, 2005; Clarke, 2017), and the silky shark is a tropical species, preferentially inhabiting 91 92 temperatures over 23°C (Bonfil, 2008; Musyl et al., 2011). In addition, the purse-seine fishery is the only gear type with adequate observer coverage in both the eastern and western Pacific. 93 94 Relative abundance indices for the silky shark were computed from by catch-per-set data by area within the equatorial Pacific and compared to an index of Pacific Ocean-climate variability, the 95 Pacific Decadal Oscillation (PDO). Where possible, indices also were computed by shark size 96 categories that reflect life stages. 97

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- 99 **D**a



100 Two silky shark data sets were used in this analysis, one from the coast of the Americas to 180°W (EP) and the other from 180°W to the west (WP). The data were collected under two 101 102 different management agencies, the IATTC and the Western and Central Pacific Fisheries Commission (WCPFC). Although the data collected under these two management agencies 103 104 largely represent different fleets, both data sets were collected by observers aboard purse-seine vessels setting on tunas associated with floating objects (also referred to as "floating-object" or 105 "associated" sets). Floating-object sets include sets on tunas associated with fish aggregating 106 devices (FADs) and with natural and anthropogenic drifting debris (e.g., tree trunks, metal 107 108 drums). Since the mid-1990s floating-object sets in the EP have been dominated by sets on FADs (IATTC, 2010; 2016). Sets made in the WP on anchored FADs were excluded from this analysis 109 110 because FADs used in the EP are drifting FADs.

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The EP data were collected by IATTC observers aboard large purse-seiners during 1994-2016. Collection of quantitative data on non-mammal bycatch by observers began in 1993 but data were not complete for that year. Observers recorded bycatch of silky sharks in three size categories: small (< 90 cm total length (TL)), medium (90-150 cm TL), and large (>150 cm TL)) (Román-Verdesoto and Orozco-Zöller, 2005). These size categories roughly correspond to animals of age < 1 yr, 1 – 3 or 4 yrs, and > 3 or 4 yrs, respectively (Oshitani *et al.*, 2003;

118 Sanchez de Ita *et al.*, 2011). Post-processing of the data was done to remove sets that may have

been unusual with respect to fishing practices, such as repeat sets on the same floating-object and
sets with no tuna catch (Minami *et al.*, 2006).

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Based on the spatial and temporal distributions of floating-object sets in the EP (Lennert-Cody et 122 al., 2017), eight areas were defined in the EP equatorial region from the coast of the Americas to 123 180°W between 10°S to 8°N: four areas north of the equator and four areas south of the equator 124 (Figure 2). After data processing, and excluding sets outside of the equatorial zone, data on 125 63,768 sets were available for analysis, which represents over 80% of large-vessel floating-126 object sets of trips sampled by IATTC observers (numbers of sets by area are shown in Figure 3). 127 In the post-processed IATTC dataset, there were no floating-object sets west of 180°W. IATTC 128 coverage of large-vessel trips originating in the Americas and fishing within the IATTC 129 management area (coast to 150°W; Allen et al., 2010) was typically 60% or greater, depending 130 on the country and the year<sup>2</sup>. Because of the expansion of the EP floating-object set fishery in the 131 mid-1990s (Lennert-Cody and Hall, 1999), the areas farthest to the west within the EP. Areas 3-4 132 and 7-8 (Figure 2), only contain data beginning in 1995 and 1996, respectively. Areas 4 and 8 133 134 fall outside the IATTC management area.

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136 The WP data were collected by onboard observers of national observer programs that participated in the WCPFC observer program during 2004-2015 (Clarke, 2017). Data prior to 137 138 2004 were considered unreliable for shark species identifications. Post-processing of the WP data was done to remove data of countries that were not active over the full 12-year period and 139 140 sets that may have been faulty as they did not catch any tuna. The data (Figure 2) were further limited to the region from 145°E - 180°W and 10°S - 5°N as this area had fishing activity 141 142 throughout the 12-year period. Although WP silky shark by catch data were not recorded by shark size category, samples of the size composition of the bycatch were collected. The vast 143 majority (~96%) of lengths in those samples from the WP post-processed data set were 144 equivalent to the EP small or medium size categories. The data for the WP provided by the 145 WCPFC included vessel trips that extended into the EP (*i.e.*, to the east of 180°W). The WCPFC 146

<sup>&</sup>lt;sup>2</sup> The remaining trips are covered by national observer programs of various countries, see *e.g.*, Table 1 of: <u>http://www.iattc.org/Meetings/Meetings2017/AIDCP-36/PDFs/Docs/\_English/MOP-36-05\_Report-on-the-International-Dolphin-Conservation-Program.pdf</u>

147 data east of 180°W were not included in this analysis because duplicate data (*i.e.*, sets covered by
148 both IATTC and WCPFC observer programs) could not be easily identified.

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The monthly Pacific Decadal Oscillation index (PDO) for 1950 to 2017 was obtained from the 150 website of the Joint Institute for the Study of Atmosphere and Ocean<sup>3</sup> at the University of 151 Washington. The PDO is an index of inter-annual-to-interdecadal variability of the Pacific Ocean 152 climate (Mantua and Hare, 2002) that has been shown to correspond to many facets of variability 153 in the ecological dynamics of the eastern North Pacific Ocean (Mantua et al., 1997; Francis et 154 al., 1998; Franks et al., 2013). It is the first principal component of sea surface temperature 155 (SST) variability for latitudes north of 20°N, after removing a globally-integrated trend. The 156 PDO has a strong El Niño component (Mantua and Hare, 2002; Franks et al., 2013) along with 157 other lower-frequency oceanic signals in both the tropics and subtropics (e.g., Newman et al., 158 2016). As such, the PDO is a single mode of complex North Pacific variability that is only partly 159 related to tropical processes. 160

161

# 162 Methods

Standardized bycatch-per-set (BPS) indices, by area and shark size category (where available), 163 164 were estimated in order to model effects of factors other than inter-annual oceanographic variability that may influence trends in shark abundance. These standardized indices were 165 166 constructed by fitting a zero-inflated negative binomial (ZINB) generalized additive model (GAM) to the BPS data following the method of Minami et al. (2007). The ZINB is a 167 distribution that is commonly used to model count data with a high proportion of zero-valued 168 observations and also large count values (e.g., Zuur et al., 2009), which is the case for silky 169 170 shark bycatch in purse-seine fisheries in the Pacific Ocean and elsewhere (Minami et al., 2007; Amandè et al., 2008; Clarke, 2017). All ZINB GAMs were fitted to the set-by-set data using an 171 EM algorithm (e.g., Minami et al., 2007). For modelling the EP BPS data, the same covariates 172 were used as those of Minami et al. (2007) for each component of the ZINB GAM: year (a 173 categorical variable), linear terms for fishing gear characteristics (depth of the purse-seine net, 174 175 depth of the floating-object below the water's surface), for proxies for local community biomass (natural logarithm of the amount of tuna catch, natural logarithm of the amount of other bycatch 176

<sup>&</sup>lt;sup>3</sup> <u>http://research.jisao.washington.edu/pdo/</u>

177 species), and for two proxies for local floating-object density and for SST (measured by the observer at the time of the set), and smooth terms for the day of the year (to capture seasonality), 178 latitude and longitude (to capture temporally-invariant spatial gradients), and time of the set. The 179 model used for the WP BPS data was somewhat different, in part because less covariate 180 information was available: year (factor), month (factor), country of vessel registry and type of 181 182 associated set (both factors), linear terms for the natural logarithm of tuna catch and natural logarithm of a proxy for object density, and smooth terms for latitude, longitude and time of day 183 of the set. No interaction terms were included in the models. 184

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From the estimated ZINB GAM coefficients a standardized index of relative abundance was 186 computed on a monthly time step. With exception of the time step (year and day of the year at 187 188 the mid-point of each month for EP, or month for WP) and latitude and longitude, all other covariates were fixed at their median value (continuous variables) or most common value 189 190 (categorical variables). The medians and most common factors were determined separately for the north EP, the south EP and the WP. The standardized index was the predicted BPS in each 1° 191 192 square of an area at a time step, summed over all 1° squares in the area. A monthly time step was 193 selected to be consistent with the time step of the PDO (see below). Finally, a 12-month 194 symmetric moving average was applied to each standardized time series to remove seasonal pattern in the predicted trend. 195

196

For each area and shark size category, approximate pointwise 95% confidence intervals were 197 198 computed for the standardized BPS index by resampling from a multivariate normal distribution with means, variances and covariances of the estimated ZINB GAM coefficients (Wood, 2006), 199 200 assuming known GAM smoothing parameters and negative binomial scale parameters. Five hundred indices were simulated in this manner for each area and size category for which a trend 201 202 could be computed; a value of 500 was selected as a compromise between the typical number of simulation runs used to compute confidence intervals (1000's) and the time required to run each 203 204 simulation. Pointwise confidence intervals were computed at each time step from the 500 205 simulated index values using the percentile method (Efron, 1982).

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207 To evaluate the correlation between the PDO and the standardized BPS indices, the Spearman rank correlation coefficient was computed. For consistency, the PDO index was first filtered with 208 209 the same moving average filter as was applied to the standardized BPS indices. Because the two 210 indices are on different scales, both the filtered PDO and the filtered standardized BPS indices were then each centered and scaled by subtracting their respective means and dividing by their 211 212 respective standard deviations to facilitate visual comparison. The Spearman rank correlation coefficient was computed between these normalized indices (the rank correlation is unaffected 213 by normalization). Approximate 95% confidence intervals for the correlation coefficient were 214 computed for each area and shark size category (where applicable) using the 500 simulated index 215 values described above. 216

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#### 218 **Results**

Nominal (unstandardized) annual silky shark BPS was generally greater in the equatorial WP 219 220 than in the equatorial EP, and varied by area and shark size category within the equatorial EP (Figure 3). The magnitude of small silky BPS was typically greater north of the equator (Areas 1 221 222 - 4) than south of the equator (Areas 5-8), whereas that of large silky sharks were similar throughout the equatorial EP. Temporal trends in large silky BPS also were similar across the 223 224 equatorial EP, showing an overall decreasing trend over the 23 year period. In contrast, temporal trends for small and medium silky sharks varied by area and were most similar to those of large 225 226 silky sharks south of the equator. North of the equator, a decrease in the BPS trends for small and 227 medium silky sharks is only pronounced in the northern inshore area (Area 1).

228

Standardized BPS indices could not be obtained for some areas and/or shark size categories 229 230 within the equatorial EP. Standardized indices for Area 4 were not computed due to a lack of data in some years, in particular prior to 1999 and in 2015. Standardized indices were not 231 computed for Area 8 due to model instability, probably because of the low numbers of data 232 observations before 2007 and after 2012; about 67% of the data in Areas 4 and 8 corresponded to 233 years 2007-2012. Standardized indices were not computed for small sharks in Areas 5 - 6 234 235 because of the very low level of bycatch (Figure 3) and for Areas 5 - 6 (medium sharks) and Area 7 (small sharks) because of a lack of convergence of the EM algorithm within 100 236 237 iterations. Also, the fit of the ZINB GAM to the silky shark BPS data was better for the EP than

for the WP (Table 1), possibly because fewer covariates could be included in the WP model dueto data gaps.

240

For those areas where standardized BPS indices could be computed, trends varied by area and 241 shark size category (Figure 4). As with the nominal indices, the standardized trends for large 242 243 sharks within the equatorial EP were dominated by a pronounced decrease in the late 1990s that continued into the early 2000's south of the equator. In contrast, the standardized trends for small 244 and medium sharks within the EP do not show this pronounced decrease except for medium silky 245 sharks in Areas 2 and 7, and the decrease in Area 2 occurred only at the beginning of the time 246 series. In the offshore north EP (Area 3) there is no decreasing trend for either small or medium 247 sharks. The standardized medium silky trend was most similar to the standardized large silky 248 249 trend in Area 2, both indices highest in 1995. In addition, the small and medium shark indices of Area 3 appear more similar to the WP trend in Area 9 over the 2004-2015 period than to the EP 250 251 indices in the inshore Area 1 (Figures 4, 5). However, the peak in the WP index around 2011 lags that for small and medium sharks in Area 1, which occurred in 2010. 252

253

There was considerable spatial and life-stage related variability in the correlation between the 254 255 PDO and the standardized silky BPS indices (Figure 6). The highest correlation with the PDO 256 was found in the offshore north equatorial EP for small and medium sharks (Area 3). The 257 similarity between the small silky index in Area 3 and the PDO is striking. Higher correlation 258 was found between small/medium silky indices and the PDO in Areas 2-3 and 7, than between 259 the large shark index and the PDO in the same areas. Within a shark size category, the 260 correlation decreases to the east within the equatorial EP (*i.e.*, Area 3 correlation > Area 2 261 correlation > Area 1 correlation), and the correlation low or not significant in the north equatorial 262 EP inshore area (Area 1). The correlation coefficient is low for the PDO and the WP silky index 263 (Area 9), despite the good visual agreement, perhaps in part because the WP index only spans a 12-year period. 264

265

The primary effect of the standardization process was the reduction of high bycatch rates in some years (*cf.*, Figure 3 and Figure 4). For example, for 2005 and 2014, Area 3 for small and medium silky sharks, the peaks in the nominal indices are not apparent in the standardized indices. Also changed by the standardization process was the relative level of the bycatch rates for small silky
sharks in Areas 1-2 between 2001-2006 relative to the 1995-1997 period.

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#### 272 **Discussion**

In this study it has been demonstrated that the level of correlation of silky shark relative 273 abundance indices for the equatorial Pacific with the PDO differs by geographical region and life 274 stage. The highest correlations identified between the PDO and shark indices by size category 275 were for small and medium silky sharks from the western region of the equatorial EP and from 276 the equatorial WP. It was demonstrated that this significant correlation for juvenile sharks (i.e., 277 278 small and medium sharks) disappears in the inshore area of the EP, and that the correlation with the PDO is weaker for adult (large) silky sharks throughout the EP. The correlation between the 279 PDO and juvenile silky shark indices in the equatorial WP and western region of the equatorial 280 EP implies that during warm (El Niño-like) conditions the shark indices increase whereas cold 281 282 (La Niña-like) conditions lead to a decrease in the silky shark indices. Although correlation is not synonymous with causation, we hypothesize that this correlation may be driven by movement of 283 284 juveniles across the Pacific as the Indo-Pacific Warm Pool shifts location with ENSO event characteristics that influence the PDO index. 285

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Movement of juvenile silky sharks within the equatorial Pacific Ocean could be non-directional 287 288 and/or due to directed swimming. Non-directional swimming would be movement that is not ontogenetic, such as might be the case for individuals seeking favorable habitat (e.g., a preferred 289 290 temperature range). The warming of the central Pacific during an El Niño is believed to be in part due to advection of warm water from the WP (Kessler, 2006; Wang et al., 2016). Silky 291 292 sharks are born at about 65 – 81 cm TL (Oshitani et al., 2003; see also summary in Clarke et al., 2015), and therefore the spatial distribution of the EP small shark size category, which represents 293 294 individuals of age < 1 yr, might be more likely to be influenced by movement of water masses than the spatial distribution of adults. Alternatively, if juvenile silky shark movement were the 295 result of directed swimming, a cruising speed of 0.5 m s<sup>-1</sup> (Filmalter *et al.*, 2015; Ryan *et al.*, 296 2015), for example, over a one year period would equate to more than 15,000 km per year, which 297 at the equator would be about 142 degrees of longitude – more than enough to move from the 298 western margin of the WP into Area 3 of the EP (Figure 2). 299

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301 For non-directional movement to be a plausible mechanism, however, there would need to be an 302 increasing gradient in the abundance of silky sharks, in particular juvenile silky sharks, from the western EP into the far western part of the WP. The abundance of silky sharks in the equatorial 303 Pacific is not known, and locations of silky shark pupping grounds within the Pacific are not 304 305 known. Nonetheless, assuming that by catch-per-set is related to absolute abundance, the difference between the average nominal bycatch-per-set of the WP and that in the EP is 306 consistent with such a gradient. The average nominal bycatch-per-set for the WP was greater 307 than that of the juvenile silky sharks in the western EP in a number of years, including in 2010-308 309 2011 and 2015 (Figure 3). However, given the overall similarity between the western EP and WP silky index trends (Figure 5), there would also need to be greater abundance to the west of 310 311 145°E within the Pacific. Available data from the western edge of the WP are not consistent with this hypothesis (Lawson, 2011; Clarke, 2017) and instead indicate areas of high abundance in the 312 313 waters of Papua New Guinea, the Solomon Islands, and various parts of the Central Pacific, depending on year. It is important to consider, however, that these areas farther to the west are 314 315 poorly represented in the available WP observer data. Thus, the non-directional movement hypothesis cannot be adequately evaluated with existing data. 316

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If directed swimming were occurring, Pacific-wide spatial gradients in shark abundance would not be necessary to produce an increase in abundance in the EP. In general, if juvenile silky shark movement were directed towards a particular region, then directed swimming to that region would result in an increase in local abundance. It is unknown whether such directed (ontogenetic) movement occurs for the silky shark.

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Cleary, any movement hypothesis is speculative given the state of knowledge about the ecology of the silky shark in the Pacific Ocean, and more data collection and studies would be necessary to evaluate such mechanisms. Other shark species show ontogenetic, seasonal and environmentally based movement (Kai *et al.*, 2017). At present, more data are collected on the oceanography of the Pacific Ocean than are collected and/or available for analysis of the ecology of at-risk species such as the silky shark. Other alternative hypotheses that could explain the correlation been oceanographic conditions and juvenile silky sharks include: north and south

movement of the juveniles or the purse-seine fleet, given that the highest catch rates are on the 331 northern extreme of the fishery (Lennert-Cody et al., 2017); environmentally mediated changes 332 333 in catchability (e.g., vertical distribution) associated with thermocline fluctuations; biological factors that may fluctuate with environmental changes, such as survival and maturity; and, 334 environmentally mediated change in the spatial distribution and abundance of prey. Given its 335 recent CITES listing<sup>4</sup>, expanding data collection for the silky shark and other shark species is of 336 importance because fishery-dependent data are the main source of information on shark 337 distributions and status. Unfortunately, those data can be biased even when sample sizes are 338 large (Maunder et al., 2006). 339

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The lack of correlation of the small silky shark index with the PDO in the north EP inshore area 341 342 (Area 1) may be due to a combination of increased fishing activity and different oceanographic forcing. A greater diversity of fisheries that catch the silky shark is believed to operate in the 343 344 inshore area of the north EP (Area 1) (Siu and Aires-da-Silva, 2016). Thus, any increase in silky shark abundance with El Niño warming might be removed as bycatch and catch in fisheries other 345 346 than the purse-seine fishery. In addition, the warming of the far eastern Pacific during an El Niño is due to a reduction in upwelling of cooler waters, rather than eastward advection of warmer 347 348 west-central Pacific waters (Kessler, 2006). Thus, eastward movement of juveniles with warmer water might not be expected to have as much of an effect on silky abundance in inshore regions 349 350 of the EP. The net result may be that the purse-seine indices for the silky shark in the inshore north equatorial EP may not be expected to correlate with the PDO to the extent seen in the 351 offshore equatorial EP (Figure 6). 352

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The lag in the timing of the peak in the WP silky index around 2011 relative to the peak in the EP small and medium silky indices in Area 3 around 2010 (Figure 5), would seem to contradict our hypothesis about movement of juveniles into the western EP from the WP. Movement from west to east would be expected to produce a lag in the opposite direction. Unfortunately, the only strong El Niño event for which there is silky data in both the WP and the EP is the 2009-2010 El Niño. There is a range of characteristics associated with El Niño events (Capotondi *et al.*, 2015) and the 2009-2010 El Niño has been hypothesized to be a hybrid of a classical cold tongue El

<sup>&</sup>lt;sup>4</sup> <u>https://cites.org/eng/cop/17/prop/index.php</u>

Niño, of which the 1997-1998 event is an example, and a warm pool, or Modoki El Niño

362 (Johnson, 2013), which might lead to a different response in the WP.

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Our results suggest that for EPO management purposes, a relative abundance index for large 364 silky sharks may be the only reliable index that can be generated from these purse-seine data. We 365 366 have demonstrated that inter-annual fluctuations in the indices for small and medium silky sharks in the offshore region of the north EP correlate with inter-annual variability in oceanographic 367 conditions. In contrast, the trend in the index of relative abundance for large silky sharks was 368 shown to be more consistent across areas within the EP and showed less or no correlation with 369 370 the PDO, suggesting the large shark index is less influenced by fluctuations in the environment of the EP. 371

372

### 373 Acknowledgements

374 The authors express their appreciation to the Secretariat and members of the Western and Central Pacific Fisheries Commission which made available the WCPFC Regional Observer Programme 375 376 purse seine observer data for this project. This analysis was partially supported by the Common 377 Oceans (Areas Beyond National Jurisdiction) Tuna Project by agreement with the United 378 Nations Food and Agriculture Organization. The authors also thank Nickolas Vogel for data base assistance, Christine Patnode for help with graphics, and two anonymous reviewers whose 379 380 comments improved this manuscript. AJM thanks the National Science Foundation (OCE1419306) and the National Oceanic and Atmospheric Administration (NOAA-MAPP; 381 NA17OAR4310106) for support. 382

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- 488
- 489 **Table 1**. Percent deviance explained by the logistic and negative binomial regression
- 490 components of the ZINB GAM models, by area and shark size category (where applicable). S:
- 491 small; M: medium; L: large.
- 492

	Logistic component	Negative binomial
	S; M; L	component
<b>T</b>		S; M: L
Area 1	19%; 19%; 15%	38%; 33%; 34%
Area 2	22%; 19%; 16%	33%; 27%; 24%
Area 3	17%; 16%; 15%	20%; 29%; 25%
Area 6	;; 27%	;; 31%
Area 7	; 19%; 23%	; 29%; 26%
Area 9	7%	17%

493

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Standardized BPS









