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The importance of environment and life stage on interpretation of silky shark relative abundance indices for the equatorial Pacific Ocean

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Abstract

Recent large fluctuations in an index of relative abundance for the silky shark in the eastern Pacific Ocean have called into question its reliability as a population indicator for management. To investigate whether these fluctuations were driven by environmental forcing rather than true changes in abundance, a Pacific-wide approach was taken. Data collected by observers aboard purse-seine vessels fishing in the equatorial Pacific were used to compute standardized trends in relative abundance by region, and where possible, by shark size category as a proxy for life stage. These indices were compared to the Pacific Decadal Oscillation (PDO), an index of 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 (<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 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 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 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 trends.

KEYWORDS

Carcharhinus falciformis, ENSO, FAD, Pacific Ocean, PDO, purse-seine, silky shark

1 | 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, Joseph, & Squires, 2010), is based only on trends in indices of relative abundance estimated from data collected observers aboard large (vessels with fish carrying

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capacity > 363 t) tuna purse-seine vessels. Data available from other fisheries operating in the EPO that catch silky sharks (bycatch or targeted) are either incomplete with respect to fishing effort or with respect to catch by species (Siu & Aires-da-Silva, 2016). In the Western and Central Pacific Ocean (WCPO) there is long-term observer coverage for the longline fishery, but the sample size is small and may be unrepresentative of the fishery as a whole. Observer coverage for the purse seine fishery is higher but only in the years since 2010 (Clarke, 2017). Management of the silky shark in the WCPO is primarily through a no retention rule adopted subsequent to a WCPO silky shark stock assessment, which concluded that the species is severely over-fished (Rice & Harley, 2013).

The first exploration of trends in Pacific silky shark populations began in 2007 in the EPO, and interpretation of these trends, which continue to be updated annually, has proved to be an ongoing challenge. Of concern was the initial decline that began in the late 1990s (Minami, Lennert-Cody, Gao, & Román-Verdesoto, 2007), which may have been related to expansion of the purse-seine fishery on floating objects in the EPO (Lennert-Cody & Hall, 1999). However, other interpretations are also possible and the processes driving change in the index have continued to be debated (Aires-da-Silva, Lennert-Cody, Maunder, & Román-Verdesoto, 2014). Since the mid 2000s, 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 recent increases in the EPO indices from 1 year to the next, especially in the northern EPO, are in many cases too rapid to be due exclusively to population growth (Lennert-Cody, Clarke, Aires-da-Silva, Maunder, & Román, 2017). 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 that processes behind the recent changes in the index are not specific to aspects of the fishery on tunas associated with floating objects.

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 associated with floating-objects in the equatorial Pacific: silky shark bycatch in purse-seine fisheries primarily occurs in floating-object (associated) sets (Clarke, 2017; Román-Verdesoto & Orozco-Zöller, 2005), and the silky shark is a tropical species, preferentially inhabiting 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. Relative abundance indices for the silky shark were computed from bycatch-perset data by area within the equatorial Pacific and compared to an index of Pacific Ocean climate variability, the Pacific Decadal Oscillation (PDO). Where possible, indices also were computed by shark size categories that reflect life stages.

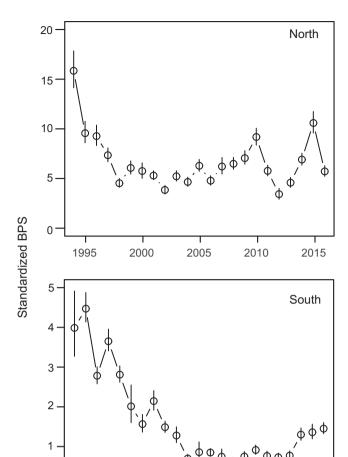


FIGURE 1 Standardized bycatch-per-set (BPS, in numbers of silky sharks per set) for floating-object sets in the north (top panel) and south (bottom panel) EPO, with approximate point-wise 95% confidence intervals. From Lennert-Cody et al. (2017)

2005

2010

2015

2000

1.1 Data

n

1995

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 different management agencies, the IATTC and the Western and Central Pacific Fisheries Commission (WCPFC). Although the data collected under these two management agencies largely represent different fleets, both data sets were collected by observers aboard purseseine vessels setting on tunas associated with floating objects (also referred to as "floating-object" or "associated" sets). Floatingobject sets include sets on tunas associated with fish aggregating devices (FADs) and with natural and anthropogenic drifting debris (e.g., tree trunks, metal 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 because FADs used in the EP are drifting FADs.

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 & Orozco-Zöller, 2005). These size categories roughly correspond to animals of age <1 year, 1–3 or 4 years, and >3 or 4 years, respectively (Oshitani, Nakano, & Tanaka, 2003; Sánchez-de-Ita, Quiñónez-Velázquez, Galván-Magaña, Bocanegra-Castillo, & Félix-Uraga, 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, Lennert-Cody, Gao, & Roman-Verdesoto, 2006).

Based on the spatial and temporal distributions of floating-object sets in the EP (Lennert-Cody et al., 2017), eight areas were defined in the EP equatorial region from the coast of the Americas to 180°W between 10°S to 8°N: four areas north of the equator and four areas south of the equator (Figure 2). After data processing, and excluding sets outside of the equatorial zone, data on 63,768 sets were available for analysis, which represents over 80% of largevessel floating-object sets of trips sampled by IATTC observers (numbers of sets by area are shown in Figure 3). In the post-processed IATTC dataset, there were no floating-object sets west of 180°W. IATTC coverage of large-vessel trips originating in the Americas and fishing within the IATTC management area (coast to 150°W; Allen et al., 2010) was typically 60% or greater, depending on the country and the year (the remaining trips are covered by national observer programs of various countries, see e.g., Table 1 (IATTC, 2017) REF). Because of the expansion of the EP floatingobject set fishery in the mid-1990s (Lennert-Cody & Hall, 1999), the areas farthest to the west within the EP, Areas 3-4 and 7-8 (Figure 2), only contain data beginning in 1995 and 1996, respectively. Areas 4 and 8 fall outside the IATTC management area.

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 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 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 throughout the 12 year period. Although WP silky shark bycatch data were not recorded by shark size category, samples of the size composition of the bycatch were collected. The vast majority (~96%) of lengths in those samples from the WP post-processed data set were equivalent to the EP small or medium size categories. The data for the WP provided by the WCPFC included vessel trips that extended into the EP (i.e., to the east of 180°W). The WCPFC data east of 180°W were not included in this analysis because duplicate data (i.e., sets covered by both IATTC and WCPFC observer programmes) could not be easily identified.

The monthly PDO index for 1950–2017 was obtained from the website of the Joint Institute for the Study of Atmosphere and Ocean (http://research.jisao.washington.edu/pdo/) at the University of Washington. The PDO is an index of interannual-to-interdecadal variability of the Pacific Ocean climate (Mantua & Hare, 2002) that has been shown to correspond to many facets of variability in the ecological dynamics of the eastern North Pacific Ocean (Francis, Hare, Hollowed, & Wooster, 1998; Franks et al., 2013; Mantua, Hare, Zhang, Wallace, & Francis, 1997). It is the first principal component of sea surface temperature (SST) variability for latitudes north of 20°N, after removing a globally-integrated trend. The PDO

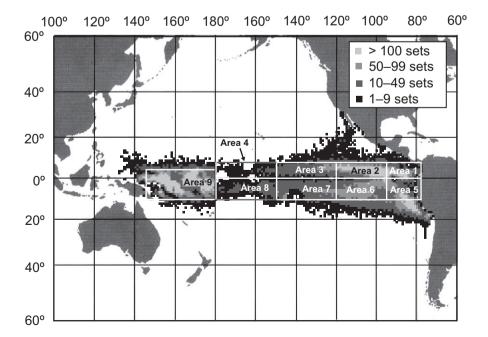


FIGURE 2 Areas used in the analysis and number of floating-object (associated) sets by 1° area after data processing, but including sets outside Areas 1–9 (see text for details)

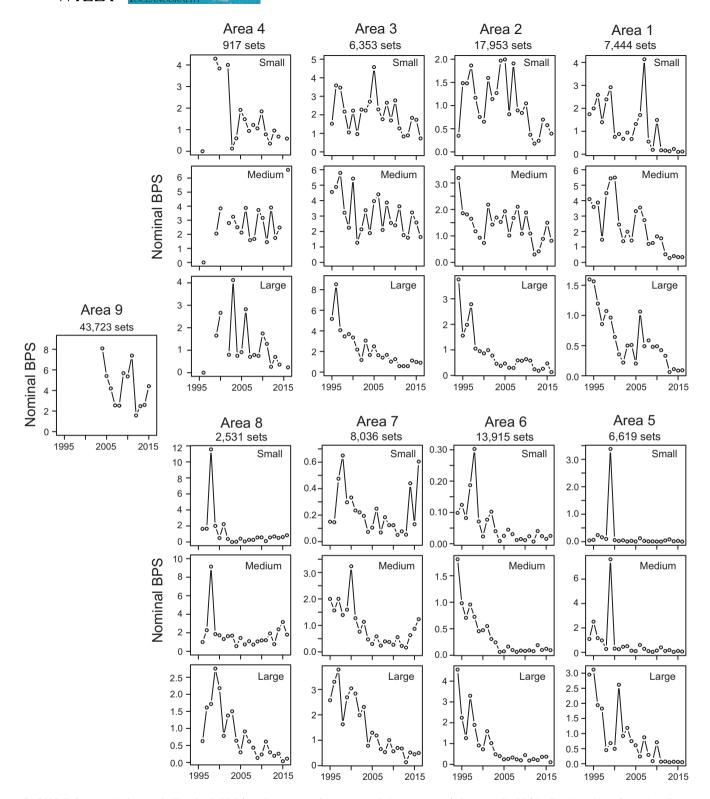


FIGURE 3 Nominal annual silky shark BPS (numbers per set) by area and size category (where applicable) in floating-object (associated) sets. The numbers of sets by area used in the analysis is shown at the top of each panel

has a strong El Niño component (Franks et al., 2013; Mantua & Hare, 2002) along with other lower-frequency oceanic signals in both the tropics and subtropics (e.g., Newman et al., 2016). As such, the PDO is a single mode of complex North Pacific variability that is only partly related to tropical processes.

2 | MATERIALS AND METHODS

Standardized bycatch-per-set (BPS) indices, by area and shark size category (where available), were estimated in order to model effects of factors other than interannual oceanographic variability that may

TABLE 1 Percent deviance explained by the logistic and negative binomial regression components of the ZINB GAM models, by area and shark size category (where applicable)

	Logistic component S; M; L	Negative binomial component 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%

S, small; M, medium; L, large.

influence trends in shark abundance. These standardized indices were 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 distribution that is commonly used to model count data with a high proportion of zerovalued observations and also large count values (e.g., Zuur, leno, Walker, Saveliev, & Smith, 2009), which is the case for silky shark bycatch in purse-seine fisheries in the Pacific Ocean and elsewhere (Amandè, Chassot, Chavance, & Piante, 2008; Clarke, 2017; Minami et al., 2007). All ZINB GAMs were fitted to the set-by-set data using an EM algorithm (e.g., Minami et al., 2007). For modelling the EP BPS data, the same covariates were used as those of Minami et al. (2007) for each component of the ZINB GAM: year (a categorical variable), linear terms for fishing gear characteristics (depth of the purse-seine net, depth of the floating-object below the surface of the water), for proxies for local community biomass (natural logarithm of the amount of tuna catch, natural logarithm of the amount of other bycatch 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), latitude and longitude (to capture temporallyinvariant spatial gradients), and time of the set. The model used for the WP BPS data was somewhat different, in part because less covariate information was available: year (factor), month (factor), country of vessel registry and type of 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 of the set. No interaction terms were included in the models.

From the estimated ZINB GAM coefficients a standardized index of relative abundance was computed on a monthly time step. With exception of the time step (year and day of the year at 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 (categorical variables). The medians and most common values were determined separately for the north EP, the south EP and the WP. The standardized index was the predicted BPS in each 1° square of an area at a time step, summed over all 1° squares in the area. A monthly time step was selected to be

consistent with the time step of the PDO (see below). Finally, a 12 month symmetric moving average was applied to each standardized time series to remove seasonal pattern in the predicted trend.

For each area and shark size category, approximate pointwise 95% confidence intervals were 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), 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 could be computed; a value of 500 was selected as a compromise between the typical number of simulation runs used to compute confidence intervals (1,000s) and the time required to run each simulation. Pointwise confidence intervals were computed at each time step from the 500 simulated index values using the percentile method (Efron, 1982).

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 the same moving average filter as was applied to the standardized BPS indices. Because the two 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 respective standard deviations to facilitate visual comparison. The Spearman rank correlation coefficient was computed between these normalized indices (the rank correlation is unaffected by normalization). Approximate 95% confidence intervals for the correlation coefficient were computed for each area and shark size category (where applicable) using the 500 simulated index values described above.

3 | RESULTS

Nominal (unstandardized) annual silky shark BPS was generally greater in the equatorial WP 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 1–4) 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 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 silky sharks south of the equator. North of the equator, a decrease in the BPS trends for small and medium silky sharks is only pronounced in the northern inshore area (Area 1).

Standardized BPS indices could not be obtained for some areas and/or shark size categories 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 computed for Area 8 due to model instability, probably because of the low numbers of data observations before 2007 and

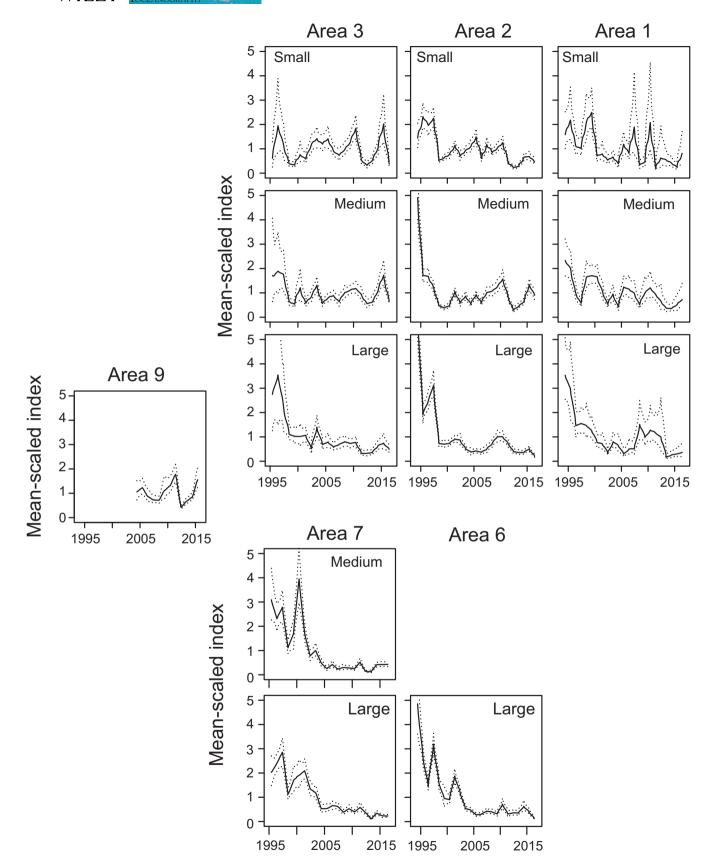


FIGURE 4 Mean-scaled standardized BPS indices, by area and shark size category (where applicable). In some panels, the y-axis range was truncated to show detail. Dashed lines are the approximate 95% confidence intervals

after 2012; about 67% of the data in Areas 4 and 8 corresponded to years 2007–2012. Standardized indices were not computed for small sharks in Areas 5–6 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 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 due to data gaps.

For those areas where standardized BPS indices could be computed, trends varied by area and shark size category (Figure 4). As with the nominal indices, the standardized trends for large sharks within the equatorial EP were dominated by a pronounced decrease in the late 1990s that continued into the early 2000s south of the equator. In contrast, the standardized trends for small and medium sharks within the EP do not show this pronounced decrease except for medium silky sharks in Areas 2 and 7, and the decrease in Area 2 occurred only at the beginning of the time series. In the offshore north EP (Area 3) there is no decreasing trend for either small or medium sharks. The standardized medium silky trend was most similar to the standardized large silky 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 indices in the inshore Area 1 (Figures 4 and 5). However, the peak in the WP index around 2011 lags that for small and medium sharks in Area 1, which occurred in 2010.

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

The primary effect of the standardization process was the reduction of high bycatch rates in some years (cf., Figures 3 and 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.

4 | DISCUSSION

In this study it has been demonstrated that the level of correlation of silky shark relative abundance indices for the equatorial Pacific

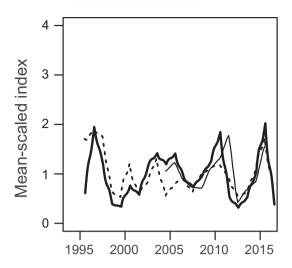


FIGURE 5 Mean-scaled standardized BPS indices for small (thick solid line) and medium (dashed line) silky sharks in Area 3, and for Area 9 (thin solid line), all from Figure 4

with the PDO differs by geographical region and life stage. The highest correlations identified between the PDO and shark indices by size category were for small and medium silky sharks from the western region of the equatorial EP and from the equatorial WP. It was demonstrated that this significant correlation for juvenile sharks (i.e., 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 PDO and juvenile silky shark indices in the equatorial WP and western region of the equatorial EP implies that during warm (El Niño-like) conditions the shark indices increase whereas cold (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 juveniles across the Pacific as the Indo-Pacific Warm Pool shifts location with ENSO event characteristics that influence the PDO index.

Movement of juvenile silky sharks within the equatorial Pacific Ocean could be non-directional 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 favourable habitat (e.g., a preferred 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, Deser, Yu, DiNezio, & Clement, 2016). Silky 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 individuals of age <1 year, 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 result of directed swimming, a cruising speed of 0.5 m/s (Filmalter, Cowley, Forget, & Dagorn, 2015; Ryan, Meeuwig, Hemmi, Collin, & Hart, 2015), for example, over a 1 year period would equate to more than 15,000 km/year, which at the equator would be about 142 degrees of longitude-more than enough to

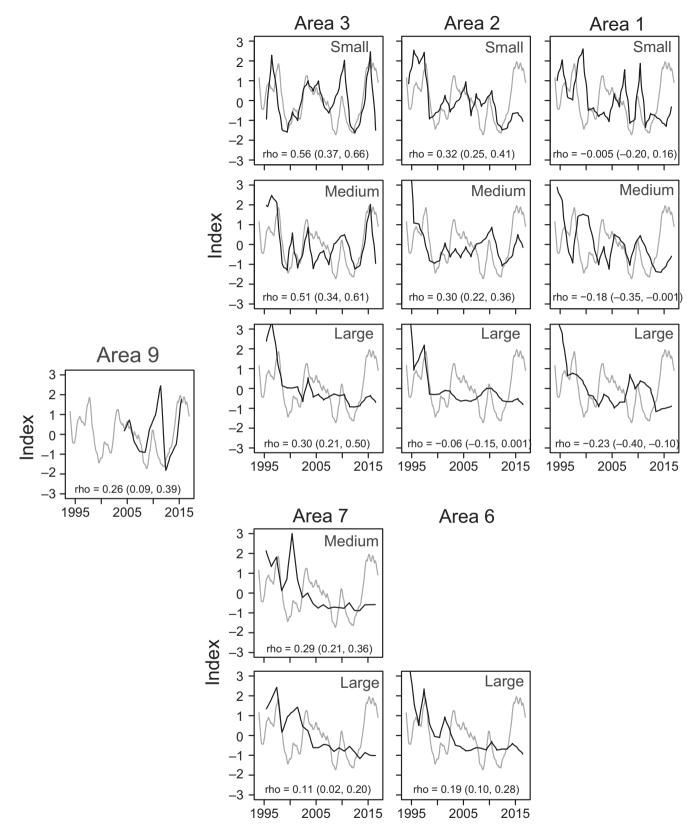


FIGURE 6 Normalized standardized BPS indices (black lines; from Figure 4) and the PDO (grey lines), by area and shark size category (where applicable). "rho": Spearman rank correlation coefficient (approximate 95% confidence intervals are shown in parentheses). In some panels, the y-axis range was truncated to show detail

move from the western margin of the WP into Area 3 of the EP (Figure 2).

For non-directional movement to be a plausible mechanism, however, there would need to be an 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 Pacific is not known, and locations of silky shark pupping grounds within the Pacific are not known. Nonetheless, assuming that bycatch-per-set is related to absolute abundance, the difference between the average nominal bycatchper-set of the WP and that in the EP is consistent with such a gradient. The average nominal bycatch-per-set for the WP was greater than that of the juvenile silky sharks in the western EP in a number of years, including in 2010-2011 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 145°E within the Pacific. Available data from the western edge of the WP are not consistent with this hypothesis (Clarke, 2017; Lawson, 2011) and instead indicate areas of high abundance in the 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 poorly represented in the available WP observer data. Thus, the non-directional movement hypothesis cannot be adequately evaluated with existing data.

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.

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, Thorson, Piner, & Maunder, 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 northern extreme of the fishery (Lennert-Cody et al., 2017); environmentally mediated changes in catchability (e.g., vertical distribution) associated with thermocline fluctuations; biological factors that may fluctuate with environmental changes, such as survival and maturity; and, environmentally mediated change in the spatial distribution and abundance of prey. Given its recent CITES listing (https://cites.org/eng/cop/17/ prop/index.php), expanding data collection for the silky shark and other shark species is of importance because fishery-dependent data are the main source of information on shark distributions and status. Unfortunately, those data can be biased even when sample sizes are large (Maunder et al., 2006).

The lack of correlation of the small silky shark index with the PDO in the north EP inshore area (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 inshore area of the north EP (Area 1) (Siu & Airesda-Silva, 2016). Thus, any increase in silky shark abundance with El Niño warming might be removed as bycatch and catch in fisheries other 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 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 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 offshore equatorial EP (Figure 6).

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 Niño, of which the 1997–1998 event is an example, and a warm pool, or Modoki El Niño (Johnson, 2013), which might lead to a different response in the WP.

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

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REFERENCES

- Aires-da-Silva, A., Lennert-Cody, C. E., Maunder, M. N., & Román-Verdesoto, M. (2014). Stock status indicators for silky sharks in the Eastern Pacific Ocean. IATTC Document SAC-05-11a. Retrieved from http://www.iattc.org/Meetings/Meetings2014/May/_English/SAC-05-11a-Indicators-for-silky-sharks.pdf
- Allen, R., Joseph, J., & Squires, D. (2010). Managing world tuna fisheries with emphasis on right-based management. In R. Quentin, R. Hilborn, D. Squires, M. Tait & M. Williams (Eds.), Handbook of marine fisheries conservation and management (pp. 698–712). New York, NY: Oxford University Press.
- Amandè, M.-J., Chassot, E., Chavance, P., & Piante, R. (2008). Silky shark (Carcharhinus falciformis) bycatch in the French tuna purse-seine fishery of the Indian Ocean. IOTC WPEB – 2008/16. Retrieved from http://iotc.org/sites/default/files/documents/proceedings/2008/ wpeb/IOTC-2008-WPEB-16.pdf
- Bonfil, R. (2008). The biology and ecology of the silky shark, Carcharhinus falciformis. In M. Camhi, E. Pikitch & E. Babcock (Eds.), Sharks of the open ocean (pp. 114–127). Oxford: Blackwell Science. https://doi.org/ 10.1002/9781444302516
- Capotondi, A., Wittenberg, A. T., Newman, M., Di Lorenzo, E., Yu, J.-Y., Braconnot, P., ... Yeh, S.-W. (2015). Understanding ENSO diversity. Bulletin of the American Meteorological Society, 96, 921–938. https://doi.org/10.1175/BAMS-D-13-00117.1
- Clarke, S. (2017). Summary of progress on data preparation for an updated, Pacific-wide silky shark (*Carcharhinus falciformis*) assessment. Document WCPFC-SC13-2017/SA-IP-12, Western and Central Pacific Fisheries Commission Scientific Committee 13th Regular Session, 9–17 August, 2017, Rarotonga, Cook Islands.
- Clarke, S., Coelho, R., Francis, M., Kai, M., Kohin, S., Liu, K. M., ... Smart, J. (2015). Report of the Pacific Shark Life History Expert Panel Workshop, 28–30 April 2015. WCPFC-SC11-2015/EB-IP-13. Retrieved from https://www.wcpfc.int/system/files/EB-IP-13%20Workshop% 20Shark%20Life%20History%20Expert%20Panel%202.pdf
- Efron, B. (1982). The Jackknife, the Bootstrap and Other Resampling Plans. SIAM #38. 92 pp. CBMS-NSF Regional Conference Series in Applied Mathematics. Philadelphia, PA: Society for Industrial and Applied Mathematics.
- Filmalter, J., Cowley, P., Forget, F., & Dagorn, L. (2015). Fine-scale 3-dimensional movement behaviour of silky sharks Carcharhinus falciformis associated with fish aggregating devices (FADs). Marine Ecology Progress Series, 539, 207–223. https://doi.org/10.3354/meps11514
- Francis, R. C., Hare, S. R., Hollowed, A. B., & Wooster, W. S. (1998). Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Ocenanography*, 7, 1–21.
- Franks, P. J. S., Di Lorenzo, E., Goebel, N. L., Chenillat, F., Rivière, P., Edwards, C. A., & Miller, A. J. (2013). Modeling physical-biological responses to climate change in the California Current System. *Oceanography*, 26, 26–33. https://doi.org/10.5670/oceanog
- IATTC. (2010). Tunas and billfishes in the eastern Pacific Ocean in 2008.
 IATTC Fishery Status Report 7. Retrieved from http://www.iattc.org/PDFFiles/FisheryStatusReports/_English/FisheryStatusReport7ENG.pdf

- IATTC. (2016). Tunas and billfishes in the eastern Pacific Ocean in 2015. IATTC Fishery Status Report 14. Retrieved from http://www.iattc.org/PDFFiles2/FisheryStatusReports/FisheryStatusReport14.pdf
- IATTC. (2017). Report on the International Dolphin Conservation Program. Inter-American Tropical Tuna Commission Document MOP-36-05. http://www.iattc.org/Meetings/Meetings2017/AIDCP-36/PDFs/Docs/_English/MOP-36-05_Report-on-the-International-Dolphin-Conservation-Program.pdf
- Johnson, N. C. (2013). How many ENSO flavors can we distinguish? Journal of Climate, 26, 4816–4827. https://doi.org/10.1175/JCLI-D-12-006491
- Kai, M., Thorson, J. T., Piner, K. R., & Maunder, M. N. (2017). Predicting the spatio-temporal distributions of pelagic sharks in the western and central North Pacific. *Fisheries Oceanography*, 26, 569–582. https://d oi.org/10.1111/fog.12217
- Kessler, W. S. (2006). The circulation of the eastern tropical Pacific: A review. Progress in Oceanography, 69, 181–217. https://doi.org/10. 1016/i.pocean.2006.03.009
- Lawson, T. (2011). Estimation of catch rates and catches of key shark species in tuna fisheries of the Western and Central Pacific Ocean using observer data. WCPFC-SC7-2011/EB-IP-02. Retrieved from https://www.wcpfc.int/node/2777
- Lennert-Cody, C. E., Clarke, S. C., Aires-da-Silva, A., Maunder, M. N., & Román, M. H. (2017). Updated stock status indicators for silky sharks in the eastern Pacific Ocean (1994-2016), with oceanographic considerations. IATTC Scientific Advisory Committee Document SAC-08-08a(i). Retrieved from http://www.iattc.org/Meetings/Meetings2017/SAC-08/PDFs/Docs/_English/SAC-08-08a(i)_Updated-purse-seine-indicators-for-silky-sharks-in-the-EPO.pdf
- Lennert-Cody, C. E., & Hall, M. A. (1999). The development of the purse seine fishery on drifting fish aggregating devices in the eastern Pacific Ocean: 1992–1998. In J.-Y. Le Gall, P. Cayré & M. Taquet (Eds.), Pêche thonière et dispositifs de concentration de poisons, Colloque Caraïbe-Martinique, Trois-Îlets, 15–19 Octobre 1999. Issy-les-Moulineaux, France: IFREMER.
- Mantua, N. J., & Hare, S. R. (2002). The Pacific Decadal Oscillation. *Journal of Oceanography*, 58, 35–44. https://doi.org/10.1023/A: 1015820616384
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78, 1069–1079. https://doi.org/10.1175/1520-0477(1997)078<1069: APICOW>2.0.CO;2
- Maunder, M. N., Silbert, J. R., Fonteneau, A., Hampton, J., Kleiber, P., & Harley, S. J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science, 63, 1373–1385. https://doi.org/10.1016/j.icesjms.2006.05.008
- Minami, M., Lennert-Cody, C. E., Gao, W., & Roman-Verdesoto, M. H. (2006). Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. ISM Research Memorandum, 978.
- Minami, M., Lennert-Cody, C. E., Gao, W., & Román-Verdesoto, M. (2007). Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. Fisheries Research, 845, 210–221. https://doi.org/10.1016/j.fishres.2006.10.019
- Musyl, M. K., Brill, R. W., Curran, D. S., Fragoso, N. M., McNaughton, L. M., Nielsen, A., ... Moyes, C. D. (2011). Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fishery Bulletin, 109, 341–368.
- Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Di Lorenzo, E., ... Smith, C. A. (2016). The Pacific Decadal Oscillation, revisited. *Journal of Climate*, 29, 4399–4427. https://doi.org/10.1175/JCLI-D-15-0508.1
- Oshitani, S., Nakano, H., & Tanaka, S. (2003). Age and growth of the silky shark Carcharhinus falciformis from the Pacific Ocean. Fisheries

- FISHERIES OCEANOGRAPHY

- Science, 69, 456–464. https://doi.org/10.1046/j.1444-2906.2003. 00645.x
- Rice, J., & Harley, S. (2013). Updated Stock assessment of silky shark in the western and central Pacific Ocean. WCPFC -SC9-2013/SA-WP-03. Retrieved from https://www.wcpfc.int/node/3685
- Román-Verdesoto, M., & Orozco-Zöller, M. (2005). Bycatches of sharks in the tuna purse-seine fishery of the eastern Pacific Ocean reported by observers of the Inter-American Tropical Tuna Commission, 1993–2004. Data Report 11. http://www.iattc.org/PDFFiles/DataRe ports/_English/No.11-2005-Marlon%20Román-Verdesoto%20and% 20Mauricio%20Orozco-Zöller_Bycatches%20of%20sharks%20in% 20the%20tuna%20PS%20fishery%20of%20the%20EPO%20reported %20by%20observers%20of%20the%20IATTC.%201993-2004.pdf
- Ryan, L. A., Meeuwig, J. J., Hemmi, J. M., Collin, S. P., & Hart, N. S. (2015). It is not just size that matters: Shark cruising speeds are species-specific. *Marine Biology*, 162, 1307–1318. https://doi.org/10.1007/s00227-015-2670-4
- Sánchez-de-Ita, J. A., Quiñónez-Velázquez, C., Galván-Magaña, F., Bocanegra-Castillo, N., & Félix-Uraga, R. (2011). Age and growth of the silky sharks *Carcharhinus falciformis* from the west coast of Baja California Sur, Mexico. *Journal of Applied Ichthyology*, 27, 20–24. https://doi.org/10.1111/j.1439-0426.2010.01569.x
- Siu, S., & Aires-da-Silva, A. (2016). An inventory of sources of data in Central America on shark fisheries operating in the eastern Pacific Ocean: Metadata Report. IATTC Document SAC-07-06b(ii). Retrieved

- from http://www.iattc.org/Meetings/Meetings2016/SAC-07/PDFs/Docs/_English/SAC-07-06b(ii)_Results-of-FAO-GEF-shark%20project-1 ndf
- Wang, C., Deser, C., Yu, J.-Y., DiNezio, P., & Clement, A. (2016). El Niño-Southern Oscillation (ENSO): A review. In P. Glynn, D. Manzello & I. Enochs (Eds.), Coral reefs of the Eastern Pacific (pp. 85–106). Dordrecht, Netherlands: Springer Science. https://doi.org/10.1007/978-94-017-7499-4
- Wood, S. N. (2006). *Generalized additive models, an introduction with R* (391 pp.). Boca Raton, FL: Chapman & Hall/CRC.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions with R (574 pp.). New York, NY: Springer. https://doi.org/10.1007/978-0-387-87458-6

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