

# Patterns of long-term climate variability and predation rates by a marine apex predator, the white shark *Carcharodon carcharias*

R. A. Skubel<sup>1,2,\*</sup>, B. P. Kirtman<sup>1,3</sup>, C. Fallows<sup>4</sup>, N. Hammerschlag<sup>1,2</sup>

<sup>1</sup>Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA

<sup>2</sup>Abess Center for Ecosystem Science & Policy, University of Miami, Miami, FL 33146, USA

<sup>3</sup>Cooperative Institute for Marine and Atmospheric Science, University of Miami, FL, 33149, USA

<sup>4</sup>Apex Expeditions, Cape Town, South Africa

**ABSTRACT:** Understanding potential responses of aquatic animals to climate variability is important, given the wide-ranging implications of current and future climatic change scenarios. Here, we used long-term data from natural predator–prey interactions between white sharks *Carcharodon carcharias* and Cape fur seals *Arctocephalus pusillus pusillus* in False Bay, South Africa, paired with environmental monitoring to examine potential relationships between temperature variability and shark predation rates on seals. Based on generalized linear modelling of a dataset of 941 shark attacks on seals collected over 15 years (1999–2013) during the austral winter (May–September) season, we found water temperature was included as a significant predictor of daily and monthly variability in predation rates. However, the signal of temporal variability over the season emerged as a more predominant predictor. Moreover, inter-annual variability in predation rate appeared linked to other environmental factors (wind, water visibility, and the occurrence of El Niño and La Niña events) rather than water temperature. These data suggest that water temperatures on an intra-annual scale might contribute to predation patterns in white sharks either directly or indirectly (e.g. due to associated changes in prey availability), but do not implicate water temperature as a primary driver in this scenario, or at an interannual scale. It is possible that (1) the metabolic demand of white sharks may be modulated against temperature variability by their partially endothermic nature, and (2) the predation patterns of white sharks on seals are the result of a complex interplay between ambient physical conditions and broader oceanographic, biological, and ecological factors.

**KEY WORDS:** Predator ecology · Climate variation · El Niño · Shark · Seal · Temperature

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## INTRODUCTION

The world's aquatic habitats are experiencing significant physiochemical shifts due to human-induced climate change. Warming, deoxygenation, and acidification associated with rising atmospheric CO<sub>2</sub> can impose physiological stressors on aquatic animals that, in turn can increase extinction risk at the local and global scales (Hoegh-Guldberg & Bruno 2010). Therefore, understanding the potential effects on

species in response to climate variability is critical at this time (Sunday et al. 2012), especially with respect to higher trophic-level predators, such as many large sharks, which can play an important role in regulating ecosystem structure and health (Ruppert et al. 2013, Barley et al. 2017).

While a variety of climate variables can impact the biology and physiology of fish, arguably the most significant on diurnal to interannual timescales is ambient water temperature. For instance, a species'

movements may be limited to water temperatures within a fundamental thermal range defined by physiological tolerance (Kearney & Porter 2009, Allen-Ankins & Stoffels 2017) and, among elasmobranchs, individuals may behaviorally thermoregulate by moving among different water temperatures to optimize hunting, digestion, and gestation (Hight & Lowe 2007, Di Santo & Bennett 2011, Ketchum et al. 2014, Papastamatiou et al. 2015). Experimental exposure of sharks and other aquatic predators to warmer water temperatures in the laboratory have shown increased hunting effort and feeding rate (Dowd et al. 2006, Miller et al. 2014, Pistevos et al. 2015); however, comparative studies in the wild involving large mobile fish are lacking due to logistical and technological challenges. Moreover, most experiments have been over relatively short durations (weeks to months) and have not been able to provide insight into how long-term (years to decades) climate variability may directly impact ecological processes, such as predation intensity. Thus, it remains unknown how long-term climate cycles and temperature variability may impact the biology and ecology of aquatic top predators.

As with other members of the lamnidae family, white sharks *Carcharodon carcharias* are partially endothermic elasmobranch fish, with stomach temperatures measured up to 14.3°C higher than that of the surrounding water (Goldman 1997). Given that white sharks can modulate their body temperature to some extent, within a narrow range (e.g. 23.4–26.7°C, Goldman 1997), recurrent predation patterns are likely due to behavioral optimization of predation for energy intake rather than for a need to maintain optimal body temperature (as opposed to teleost fishes (Pink et al. 2016)). False Bay, South Africa, is the location of a long-term monitoring program on the predation rates of white sharks on Cape fur seals *Arctocephalus pusillus pusillus* (Martin et al. 2005, 2009, Hammerschlag et al. 2006, 2012, 2017, Fallows et al. 2012, 2013, 2016, Martin & Hammerschlag 2012) as well as a site of ongoing climate and temperature monitoring (Dufois & Rouault 2012). Accordingly, the system provides an opportunity to investigate for possible relationships between climate-driven temperature variability and predation rates by a marine apex predator.

The climate of the study region is influenced by sea-surface temperature (SST) leakage from the Agulhas current (known as Agulhas leakage), which transports warm and saline waters from the Indian Ocean (Gordon & Haxby 1990, de Ruijter et al. 1999, van Sebille et al. 2009, Beal et al. 2011). However, recent climate

modeling has revealed that El Niño-Southern Oscillation (ENSO) can influence interannual variability of Agulhas leakage SST with a 2 yr time lag, which subsequently affects regional climate variability (Putrasahan et al. 2016), including ENSO effects on water temperatures in False Bay (Dufois & Rouault 2012). Here, we compared changes in white shark predation patterns, in terms of successful and unsuccessful predation attempts on seals, in relation to environmental and temporal variability and ENSO events, over a 15 yr period. In our analysis, explanatory environmental and temporal variables tested against shark predation rates included water temperature and visibility at the site, and the variables day of year (DOY), month, and year to account for change over time

## MATERIALS AND METHODS

### Predation events

Seal Island (35° 8' 6" S, 18° 35' 00" E) in False Bay, South Africa, is inhabited by approx. 60 000 Cape fur seals (Fig. 1). White sharks *Carcharodon carcharias* aggregate here during the winter to actively hunt Cape fur seals *Arctocephalus pusillus pusillus* when they leave and return from Seal Island (Martin et al. 2005, 2009). The seals forage in False Bay or up to 30 km (or greater) offshore, returning to Seal Island at irregular intervals (Martin et al. 2005, Fallows et al. 2012). Seals travel to and from the island via porpoising at the surface (Fallows et al. 2012). Thus, white shark attacks on seals occur at the water surface, where they can be documented (Hammerschlag et al. 2006, Martin & Hammerschlag 2012). Attacks are concentrated on the southern side of the island, close to shore (within 2 km). Thus, by positioning at the south end of Seal Island where most predatory activity occurs, a single vessel can survey at least 270° uninterrupted to a distance of at least 3.5 km (Hammerschlag et al. 2006, Martin et al. 2009). Observations were made at Seal Island each month, by 1 boat, between 1999 and 2013. At least part of the research team averaged some 200 d per year on the water, although the majority of observation occurred during austral winter months (May–September), when most predatory activity occurs (Hammerschlag et al. 2006). The research vessel arrived and began observations at Seal Island at about 07:00 h (~1.5 h before sunrise), sea conditions permitting. Although multiple people were on the observation boat each day, the data in this study was restricted to that gathered by a trained observer (C. Fallows) onboard.

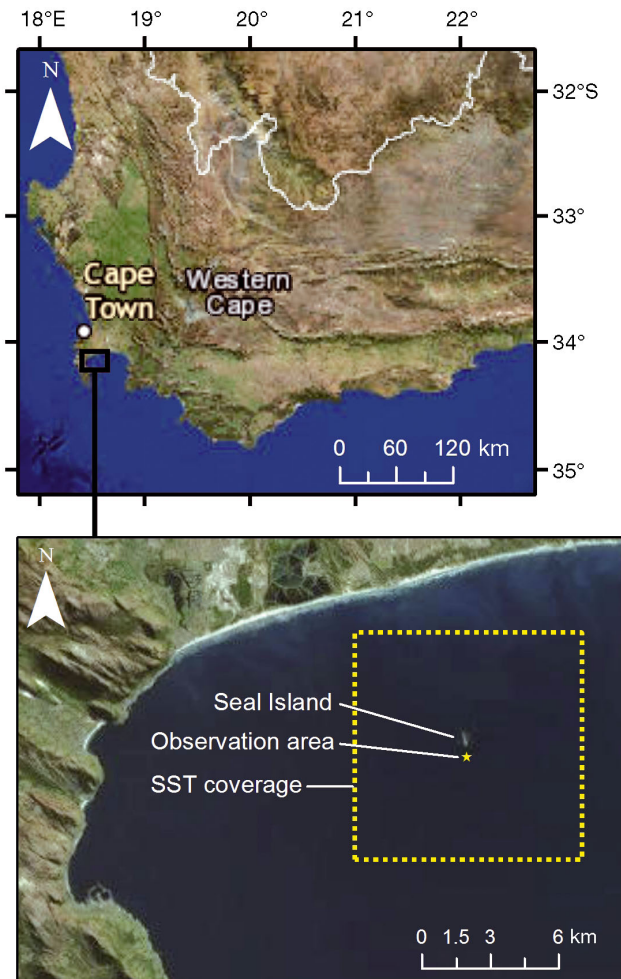


Fig. 1. Study area of Seal Island in False Bay, South Africa. The area indicated by the dashed square is the  $10 \times 10$  km grid over which sea surface temperature was evaluated ( $-34.09^\circ$  to  $-34.18^\circ$  N,  $18.53^\circ$  to  $18.64^\circ$  E). The observation area south of Seal Island is indicated. Imagery is provided by ESRI

As described in Fallows et al. (2012), predatory events were detected from the surface by one or more of the following: (1) white shark breach with a seal in its mouth or a seal leaping away from its mouth; (2) a sudden change in the travel behavior of seals, switching from directional porpoising to zigzag evasive maneuvers with a shark in pursuit; (3) a splash accompanied by a blood stain, oil slick, a distinctive odor, and by any of the following indicators such as a floating seal head or entrails floating on the surface or trailing from the gill openings of a white shark in the immediate vicinity and/or highly localized plunge-diving black-backed kelp gulls *Larus dominicanis vetula* picking up and feeding on seal entrails. Any subsurface kills could be detected by the appearance of a bloodstain at the surface and floating seal entrails (Martin et al. 2005). Observed

predatory events were recorded and classified as unsuccessful, in which the seal escaped, or successful, in which the seal was consumed (Hammerschlag et al. 2006).

While observations were made year-round, there were more frequent trips during the winter months when white sharks aggregate at Seal Island to actively hunt juvenile Cape fur seals (Hammerschlag et al. 2006). To standardize data analyses when predation activity peaked and observational effort was consistent, we restricted our analysis to predation data collected between 1999 and 2013, from 07:00 h to 09:30 h, for the months of May to September. Following Fallows et al. (2016), we considered this 120–150 min observational period (approx.  $\pm 1$  h of sunrise) per day as a sample. Upon arrival at the study site, water temperature was recorded each day using the vessel's onboard temperature sensor (Furuno model 1870). Wind speed observational estimates were determined daily from windfinder.com for measurements taken at Muizenberg (8 km from Seal Island), then, once arriving at Seal Island, wind speed in 5 knot bins was estimated and recorded. Water visibility was estimated daily using an anchor line suspended into the water column as a reference.

### SST and ENSO status

Monthly daytime SSTs for the study period were retrieved from Pathfinder Version 5.0 ([www.nodc.noaa.gov/SatelliteData/pathfinder4km/](http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/)) for 1999–2002 and MODIS Aqua for 2003–2013 (NASA JPL) as there was not one contiguous data set available for the study period. Both Pathfinder and MODIS provided 4 km resolution daytime SST, which was preferred to a continuous coarser resolution source for SST (e.g. ERSSTv4; Huang et al. 2015). For Pathfinder SST, the quality of a measurement when considering pixel clouding ranges from 0 to 7, with 4 the minimum quality considered acceptable (Kilpatrick et al. 2001); following convention, we only used SST measurements with a quality of 4 or greater. The area included in this analysis is indicated in Fig. 1. The SST grid extended 5 km from the viewing area at the south point of Seal Island, to encompass the 3.5 km visual range of the observers. Monthly ENSO status was obtained via the Multivariate ENSO Index (MEI) maintained by the National Oceanic and Atmospheric Administration's Earth System Research Laboratory (NOAA ESRL). The MEI is a bimonthly index extending from 1950 to present, reflecting the first unrotated principal component of 6 variables (sea

level pressure, zonal and meridional components of surface wind, sea surface temperature, surface air temperature, and cloudiness fraction of the sky) (Wolter & Timlin 1993, 1998). ENSO classification was based on historically ranked MEI values (1 through 67), with the upper quartile (54–67) indicating an El Niño and lower quartile (1–14) indicating a La Niña.

### Data analysis

For each day, kills ( $K$ ) and unsuccessful attempted predations ( $AP$ ) by white sharks upon seals were averaged over the sample period of 07:00–09:30 h to calculate an hourly rate of kills and total predations. This yielded a single value of kill rate ( $K\text{ h}^{-1}$ ) and total predation rate ( $K+AP\text{ h}^{-1}$ ) for each day of observation within the standardized sampling period. The broader ( $K+AP$ )  $\text{h}^{-1}$  metric showed hunting effort, while the  $K\text{ h}^{-1}$  metric indicated presumed seal consumption by the animal, and putatively, some extent of metabolic demand fulfilment. Given that each of  $K\text{ h}^{-1}$  and ( $K+AP$ )  $\text{h}^{-1}$  were assigned on a daily basis, it was not feasible to directly compare the 2 metrics as a direct measure of relative predation success. Rather, each was considered independently as a measure of general predation patterns. Daily, monthly, and annual scale generalized linear models (GLMs) were used to explore relationships of kill rates and total predation rates with environmental variability. For the daily GLM, explanatory variables tested were water temperature ( $T_w$ , °C) and water visibility (Vis, m) measured at the site, and the variables day of year (DOY), mo, and yr to account for change over time. For the monthly GLM, explanatory variables tested were monthly means of  $T_w$ , Vis, and wind speed (wind, knots), and an indication of ENSO status via the MEI. GLMs were constructed in Matlab using a stepwise procedure with interactions, using the default method of 'sse' to determine model criterion. Here, the function 'stepwiseglm' begins with an initial model containing all terms, then uses forward and backward stepwise regression to construct the final model, comparing the explanatory power of these smaller or larger models via the p-value of an  $F$ -test of change in sum of squared error (SSE) with addition or removal of terms. Terms themselves are added or removed based on whether the term would have a zero coefficient once added to the model (or the term is removed from the model if it has a zero coefficient when included, e.g. in the initial model or with successive steps). Interaction terms are not added unless

both constituent terms are in the model, after which point the single terms may be removed. For the annual GLM, explanatory variables tested were annual means of  $T_w$ , Vis, and wind, the standard deviation of annual  $T_w$  to look for effects of variability, and whether an El Niño or La Niña event had occurred that year from May–September (indicated by a binary 0 for no, and 1 for yes). Putrasahan et al. (2016) indicated a 2 yr lag in thermal impacts found for the region; however, comparison of 2 yr-lagged  $T_w$  from our dataset with MEI did not show a significant trend, so a second iteration of the annual GLM run with 2 yr-lagged El Niño or La Niña event occurrence was not included in the results. Wind was not included in the daily model as there was insufficient data coverage, reducing the number of observations in the model to 185 of 1085 observation days. Variables were judged as significant in the model if they were significant at  $p < 0.05$  ( $t$ -statistic versus the constant model). All analyses were performed in Matlab (Mathworks). Although SST was initially considered in the monthly GLMs, models produced for both  $K\text{ h}^{-1}$  and ( $K+AP$ )  $\text{h}^{-1}$  were over-parameterized and had lower performance than those fitted without SST, so SST was excluded from the final GLMs.

### RESULTS

Over the study period from 1999–2013, SST and  $T_w$  measured during the observational period showed overall similar seasonal and interannual variability (Fig. 2a). When the Furono record of  $T_w$  (monthly mean) from the study site and remotely-sensed SST for the region were compared, the 2 data sets demonstrated consistent monthly variations in temperature trends. However, a 2-way  $t$ -test comparing the monthly means of the 2 data sets revealed statistical difference ( $p = 9.04 \times 10^{-5}$ ), reflecting differences in the spatial and temporal coverage of the 2 data sets. While Furono measured daily temperatures at Seal Island, the remotely sensed SST encompassed a broader regional area. Further,  $T_w$  captured water temperature at the time of predation observation expeditions (morning) versus the more encompassing daytime SST which was capable of capturing warmer temperatures over the course of the entire diel period. Although SST tended to be higher than  $T_w$ , temporal trends were generally similar among the 2 datasets, supporting the use of the daily water temperature measurements from the predation observation expeditions. El Niño conditions based on the MEI occurred in 2002, 2005, 2006, 2009, and

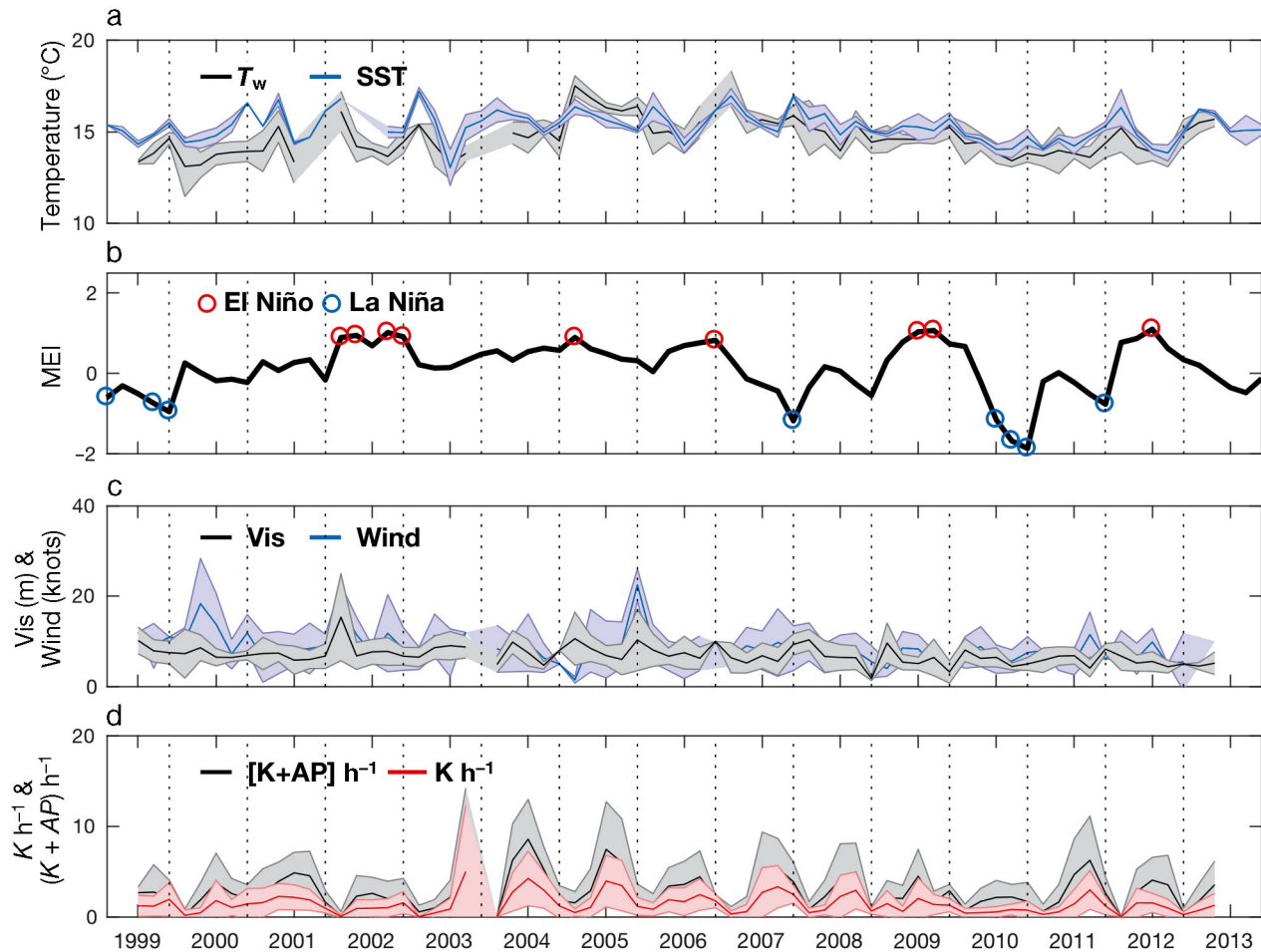


Fig. 2. Monthly trends in (a) daily water temperature ( $T_w$ ) and sea surface temperature (SST) measured during predation observation expeditions, (b) multivariate ENSO index (MEI) and El Niño/La Niña status, (c) daily wind speed and visibility (Vis) measured during predation observation expeditions, and (d) daily kills per hour ( $K h^{-1}$ ) and total predations (kills plus attempted predations per hour,  $(K+AP) h^{-1}$ ) measured during predation observation periods. Standard deviation is indicated by the shaded area around the main trendline in panels a, c and d

2012, while La Niña conditions occurred in 1999, 2007, 2010, and 2011 (Fig. 2b).

From 1999 through 2013 from May through September, a total of 1085 observation periods occurred between 07:00 and 09:30 h, 941 of which featured successful and/or unsuccessful predations of white sharks *Carcharodon carcharias* upon Cape fur seals *Arctocephalus pusillus pusillus* and 801 of which featured successful attacks. A comparison of daily, monthly, and annual  $(K+AP) h^{-1}$  and  $K h^{-1}$  showed consistently strong and significant Pearson correlation coefficients ( $r = 0.875, 0.934, 0.957$  and  $p = 0, 1.19 \times 10^{-31}, 2.32 \times 10^{-8}$  for daily, monthly, and annual scales respectively), while a  $t$ -test showed the 2 metrics to be significantly different ( $p = 7.73 \times 10^{-43}, 2.91 \times 10^{-7}, 7.73 \times 10^{-43}$  for daily, monthly, and annual scales respectively). Predation intensity peaked in the austral winter, with the greatest  $K h^{-1}$  and  $(K+AP) h^{-1}$

from June through September (Fig. 2d). Years 2003, 2004, 2005, and 2007 exhibited the greatest magnitude peaks in  $(K+AP) h^{-1}$  during this season (Figs. 2a & 3). Frequency distributions of  $T_w$  for all daily observational periods, and those days with either  $K h^{-1}$  or  $(K+AP) h^{-1}$  greater than zero, show that most predation effort, successful and otherwise peaked at 14–14.5°C (10.8% of all observations), although this may have been an artefact of the distribution of observation effort (Fig. 3).

GLMs constructed for daily  $K h^{-1}$  and  $(K+AP) h^{-1}$  had significant yet weak fits (adjusted  $r^2$  for the model and  $p$ -value for the  $F$ -statistic = 0.173 and  $6.97 \times 10^{-20}$  and 0.222 and  $1.14 \times 10^{-26}$  for  $K h^{-1}$  and  $(K+AP) h^{-1}$ , respectively). Model fit for monthly GLMs of  $K h^{-1}$  and  $(K+AP) h^{-1}$  had similarly weak fits, with lower significance (adjusted  $r^2$  for the model and  $p$ -value for the  $F$ -statistic = 0.245 and 0.00221 and 0.139 and

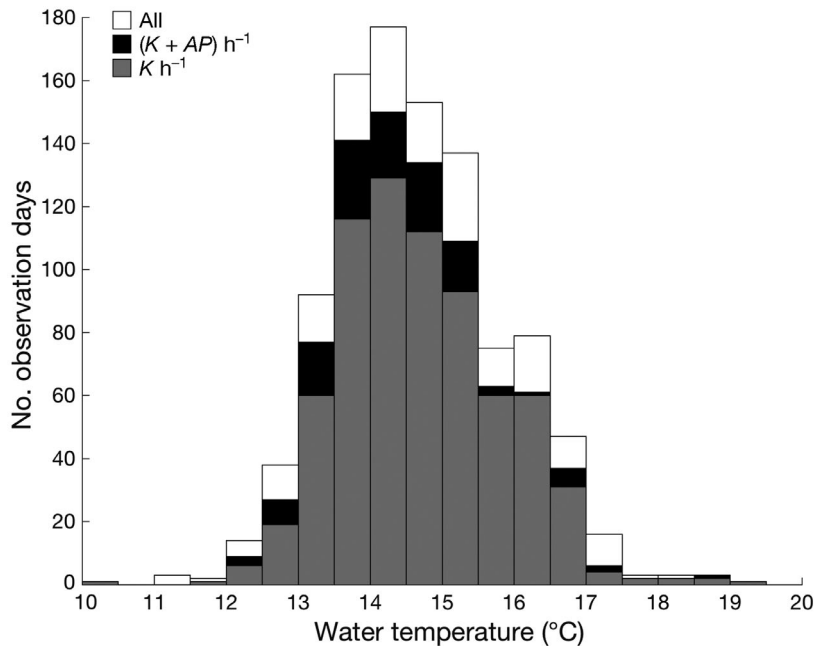


Fig. 3. Frequency distribution of water temperature measured during predation observation periods, for all days, for days when  $(K+AP) h^{-1} > 0$ , and for days when  $K h^{-1} > 0$ . See Fig. 2 for abbreviations

0.0291 for  $K h^{-1}$  and  $(K+AP) h^{-1}$ , respectively). Both daily and monthly GLMs indicated the importance of temporal variability through the inclusion of DOY and monthly terms, and of temperature variability through the inclusion of  $T_w$ . The daily GLM of  $K h^{-1}$  indicated  $T_w * \text{Month}$  as the highest magnitude coefficient (positive), with the model of  $(K+AP) h^{-1}$  including  $T_w * \text{DOY}$  as a lower magnitude (positive) coefficient (Table 1 a,b).  $\text{Vis} * \text{Month}$  was included in daily models of both  $K h^{-1}$  and  $(K+AP) h^{-1}$  models as a negative coefficient. In the monthly GLMs,  $\text{Month}$  was the largest magnitude coefficient for both  $K h^{-1}$  and  $(K+AP) h^{-1}$  (Table 1 c,d). For both monthly  $K h^{-1}$  and  $(K+AP) h^{-1}$ ,  $T_w * \text{Year}$  and  $\text{Wind} * \text{Vis}$  were included as negative coefficients. Annual GLMs had the best fit, as expected for the smaller number of observations fitted to a similar quantity of explanatory variables (adjusted  $r^2$  for the model and p-value for the  $F$ -statistic = 0.950 and 0.0112 and 0.805 and 0.00965 for  $K h^{-1}$  and  $(K+AP) h^{-1}$ , respectively). The annual GLM of  $K h^{-1}$  included interaction terms with both La Niña and El Niño occurrence, while the annual GLM of  $(K+AP) h^{-1}$  included interactions with only El Niño occurrence (Table 1 e,f). The highest-magnitude positive term in both annual GLMs was  $\text{EN} * \text{Wind}$ , while  $\text{EN} * \text{Vis}$  was a high-magnitude negative coefficient. No  $T_w$  terms were included in the annual model. All GLMs exhibited a normal distribution.

## DISCUSSION

Within a given year, the distribution of  $K h^{-1}$  and  $(K+AP) h^{-1}$  appears to correspond with temporal trends in water temperature. However, although  $T_w$  at Seal Island was a coefficient in the daily and monthly models of kill and total predation rates, the absence of  $T_w$  from the annual model indicates that temperature variability at Seal Island may play an intra-annual rather than inter-annual role with respect to white shark *Carcharodon carcharias* predation. The interaction terms of El Niño and La Niña with wind speed and water visibility were suggestive of inter-annual variability in these environmental parameters with possible ties to ENSO cycling, which may have played a greater role than water temperature in influencing inter-annual predation trends.

Clark et al. (1996) found that fish assemblages in the surf zone of False Bay were influenced by water temperature and wind speed, among other factors. In this study, wind speed was implicated as an explanatory variable in monthly and annual GLMs, including as an interaction with El Niño and La Niña occurrence in the annual models. Taken together with the results of Clark et al. (1996), teleost distribution may be vacillating with wind speed and water temperature, with possible bottom-up impacts at the level of white shark predation patterns, or white sharks may be responding to similar environmental drivers as the fish monitored by Clark et al. (1996). In another study, Weltz et al. (2013) monitored visual sightings of white sharks at beaches in False Bay (Fish Hoek and Muizenberg), finding that probability of shark sighting increased as SST rose from 14 to 18°C. Although we did not directly measure sightings, frequency distribution of daily  $T_w$  recorded for days when shark predation on seals were observed show that attacks peaked at 14–14.5°C and that very few occurred above 18°C ( $T_w > 18^\circ\text{C}$ : 6.4 % of days for  $(K+AP) h^{-1} > 0$ , 6.2 % of days for  $K h^{-1} > 0$ , and 5.1 % of all observation days). El Niño events are characterized by changes in wind strength on global and local scales (Rasmusson & Wallace 1983); here, there may be a contemporaneous effect from El Niño from anomalies in the Pacific changing global circulation patterns driving global atmospheric circulation and thereby wind speed. However, it is

Table 1. For daily, monthly, and annual generalized linear models of kills + attempted predations per hour,  $(K+AP) h^{-1}$ , and kills per hour,  $K h^{-1}$ : coefficient estimates, SE,  $t$ -statistic, and  $p$ -value of each variable included in the final model, adjusted  $r^2$ , number of observations (obs.),  $F$ -statistic versus the initial model, and  $p$ -value of the  $F$ -statistic. Abbreviated variables are water temperature ( $T_w$ ), visibility (Vis), day of year (DOY), El Niño (EN), and La Niña (LN).

	Coefficient	SE	$t$	$p$
<b>(a) Daily <math>K h^{-1} \sim 1 + T_w \cdot \text{Vis} + T_w \cdot \text{Month} + \text{Vis} \cdot \text{Month} + \text{DOY} \cdot \text{Month}</math></b>				
Adj. $r^2 = 0.173$ , obs. = 538, $F = 15$ , $p = 6.97E^{-20}$				
(Intercept)	-2.48	5.88	-0.422	0.673
$T_w \cdot \text{Vis}$	-0.0288	0.0164	-1.76	0.0798
$T_w \cdot \text{Month}$	0.216	0.0514	4.20	3.10E-05
Vis $\cdot$ Month	-0.0400	0.0195	-2.05	0.0406
DOY $\cdot$ Month	-0.00964	0.00158	-6.08	2.24E-09
<b>(b) Daily <math>(K+AP) h^{-1} \sim 1 + T_w \cdot \text{Vis} + T_w \cdot \text{DOY} + \text{Vis} \cdot \text{Month} + \text{DOY} \cdot \text{Month}</math></b>				
Adj. $r^2 = 0.245$ , obs. = 538, $F = 20.2$ , $p = 1.14E^{-26}$				
(Intercept)	-26.1	9.60	-2.71	0.00687
$T_w \cdot \text{Vis}$	-0.0572	0.0283	-2.02	0.0439
$T_w \cdot \text{DOY}$	0.00916	0.00293	3.12	0.00188
Vis $\cdot$ Month	-0.0637	0.0333	-1.91	0.0571
DOY $\cdot$ Month	-0.0256	0.00272	-9.56	4.49E-20
<b>(c) Monthly <math>K h^{-1} \sim 1 + \text{Month} + T_w \cdot \text{Vis} + T_w \cdot \text{Year} + \text{Wind} \cdot \text{Vis}</math></b>				
Adj. $r^2 = 0.245$ , obs. = 64, $F = 3.55$ , $p = 0.00221$				
Month	0.308	0.0963	3.20	0.00228
$T_w \cdot \text{Vis}$	-0.143	0.0705	-2.023	0.0475
$T_w \cdot \text{Year}$	-0.125	0.0502	-2.49	0.0157
Wind $\cdot$ Vis	-0.0339	0.0139	-2.44	0.0180
<b>(d) Monthly <math>(K+AP) h^{-1} \sim 1 + \text{Month} + T_w \cdot \text{Year} + \text{Wind} \cdot \text{Vis}</math></b>				
Adj. $r^2 = 0.139$ , obs. = 64, $F = 2.45$ , $p = 0.0291$				
(Intercept)	-4235	2286.4	-1.85	0.0693
Month	0.428	0.181	2.37	0.0214
$T_w \cdot \text{Year}$	-0.149	0.0801	-1.87	0.0674
Wind $\cdot$ Vis	-0.0729	0.0255	-2.86	0.00597
<b>(e) Annual <math>K h^{-1} \sim 1 + \text{Wind} \cdot \text{Vis} + \text{Wind} \cdot \text{EN} + \text{Wind} \cdot \text{LN} + \text{Vis} \cdot \text{EN} + \text{Vis} \cdot \text{Year} + \text{EN} \cdot \text{Year}</math></b>				
Adj. $r^2 = 0.950$ , obs. = 15, $F = 25.1$ , $p = 0.0112$				
(Intercept)	1361	196	6.94	0.00614
Wind $\cdot$ Vis	-0.723	0.0916	-7.91	0.00423
Wind $\cdot$ EN	1.60	0.248	6.46	0.00753
Wind $\cdot$ LN	0.499	0.109	4.56	0.0198
Vis $\cdot$ EN	-3.39	0.996	-3.41	0.0423
Vis $\cdot$ Year	0.115	0.0162	7.07	0.00582
EN $\cdot$ Year	-0.725	0.286	-2.54	0.0849
<b>(f) Annual <math>(K+AP) h^{-1} \sim 1 + \text{Wind} \cdot \text{Vis} + \text{Wind} \cdot \text{EN} + \text{Vis} \cdot \text{EN} + \text{Vis} \cdot \text{Year}</math></b>				
Adj. $r^2 = 0.805$ , obs. = 15, $F = 8.22$ , $p = 0.00965$				
(Intercept)	1276	555	2.30	0.0613
Wind $\cdot$ Vis	-1.25	0.179	-6.96	0.000438
Wind $\cdot$ EN	2.41	0.446	5.40	0.00166
Vis $\cdot$ EN	-2.14	0.494	-4.32	0.00496
Vis $\cdot$ Year	0.100	0.0439	2.29	0.0624

speculative to presume that our measurements captured this ENSO-modulated variability in wind speed, particularly given that meteorological teleconnections differ between ENSO events (Gershunov & Barnett 1998). Although the annual GLMs indicated that El Niño and La Niña occurrence had explanatory power for inter-annual variability in predation rates, the ab-

sence of  $T_w$  from these annual models suggests that, at a local scale, ENSO-influenced water temperatures had minimal effects on white shark predation. However, it is possible that ENSO-mediated changes in water temperature are impacting predation-related factors external to the study area surrounding Seal Island; for instance, large-scale changes in biological

productivity under El Niño conditions (Barber & Chavez 1983).

Greater visibility appeared to have a negative effect on both kill and total predation rates across temporal scales; Robbins (2007) found that increased visibility was inversely related to white shark presence at Neptune Island (Australia). In the present study, low visibility may lead to greater abundance, and thus greater chance of observing an attack, or the lower visibility may provide a higher chance of success for the attacking shark as an individual may be less visually apparent to the targeted seal (Martin & Hammerschlag 2012). Given the high energetic requirements of a predation attempt, white sharks are observed to launch attacks on seals only when environmental conditions are optimal for success, increasing efficiency of energy expenditure (Hammerschlag et al. 2006). These conditions include targeting seals during a specific range of low-light levels as well as staging attacks from identifiable deep-water locations around the Island that provide sharks with a visual and tactical advantage over seals (Hammerschlag et al. 2006, Martin et al. 2009).

Considering the 2 metrics of predation patterns, both  $(K+AP) h^{-1}$  and  $K h^{-1}$  showed similar temporal trends (Fig. 2d) and frequency distribution with respect to water temperature (Fig. 3), as well as similar final GLMs. However, kill rates tended to have higher model fit (adjusted  $r^2$ ), which may have been due to this metric showing slightly greater correspondence to variability in the explanatory variables considered, while total predation rates may be more reflective of shark presence as a whole. However, without direct evidence of physiological response to changes in environmental condition (e.g. telemetry of internal temperature as per Goldman (1997) or swimming speed as per Semmens et al. (2013)) it is not possible to draw inferences from our measurements of kill rates to conclusions regarding metabolism or feeding.

Change in ambient  $T_w$  can influence metabolic demand (e.g. metabolic  $Q_{10}$ ), with an estimated  $Q_{10}$  of between 2 and 3 presumed for the white shark as per Carlson et al. (2004). Change in metabolic rate with temperature increase has not been directly measured for this species, although studies have measured body temperature as an indicator (Carey et al. 1982, McCosker 1987, Goldman 1997) or body mass and swimming speed (Semmens et al. 2013) as field-based approaches to estimating metabolic rate. White shark oxygen consumption has previously been measured in transit to an aquarium (Ezcurra et al. 2012); however as temperature was not manipu-

lated, its direct impact on metabolic demand could not be ascertained. Complicating estimates of change in metabolic rate with respect to temperature in the white shark, (1) the large body size of this species allows for thermal inertia with movement through heterogeneous water temperatures, and (2) heat shedding is facilitated through manipulation of the hepatic sinus which bypasses the suprahepatic rete (Carey et al. 1981). As white sharks are among the largest elasmobranchs (Compagno 1984, Schmidt-Nielsen 1984) and have a lower surface area to volume ratio for gaining or losing heat, they may be less sensitive to temperature variability than smaller species given greater capacity for thermal inertia. Similarly, metabolic  $Q_{10}$  has been found to be higher with lower body mass, suggesting higher sensitivity to temperature with smaller-bodied species and the inverse for larger species (Du Preez et al. 1988); given that the white shark's ability to regulate body temperature, the  $Q_{10}$  value may have less significance for metabolic rate in response to ambient temperature change. In our study, daily and monthly GLMs suggested that increasing  $T_w$  corresponded with increasing  $(K+AP) h^{-1}$  and  $K h^{-1}$ , but the influence of water temperature was not supported on an inter-annual scale. Taken together with the heat regulation capacity of white sharks, it is not directly evident that the predation patterns observed here were a result of rising metabolic demand with temperature.

Both a strength and limitation of this study is that our results are based on comparing long-term observational data sets and not controlled laboratory experiments. Although it appears that predation trends across daily, monthly, and annual timescales are related to environmental and seasonal (temporal) variability, there are several other factors that could have contributed, at least partly, to the documented changes in predation rates and likely contributed to the variability unexplained by the GLM. These factors could include, for example, variability in seal, shark and teleost abundance. Although seal population size has been shown to be relatively consistent over the study period (Kirkman et al. 2007), there may be unaccounted marginal changes impacting predation. White shark population declines have been speculated for the region based on mark-recapture and genetic analysis (Andreotti et al. 2016), although interpreted with some level of skepticism (Irion et al. 2017). Further, white shark sightings have declined at Seal Island in False Bay over a 9 yr monitoring period (Hewitt et al. 2018). If predation rates were reflective of white shark population trends alone, such as those suggested in the aforementioned stud-



ies, it would likely manifest as prolonged long-term declines in predation rates, rather than the alternating increases and decreases observed here. Changes in teleost prey cannot be ruled out, however were not monitored in this investigation. Future studies including measurement of prey abundance may be revealing of ecosystem-level interactions among predators and other constituents of the regions they occupy. One of the major challenges in projecting the climate response of a predatory species is unknowns surrounding respective spatial shifts in predator–prey distribution (Winder & Schindler 2004); namely, will there be changes in overlap (Hunsicker et al. 2013), or will predators remain synchronized with their prey species (Sergeant et al. 2014). Given the role of wind and visibility in the GLMs, we recommend further study exploring how local meteorology may impact spatiotemporal patterns of predator and prey abundance, and predation behavior. Further, the strong signal of temporal variability in intra-annual predation patterns may be tied to broader seasonal shifts in diet of white sharks, which may be explored via methods such as stable isotope analysis and opportunistic stomach content analysis.

Laboratory experiments with Port Jackson sharks *Heterodontus portusjacksoni* exposed to water temperature increases to projected 2100 levels increased their feeding but not growth (compared to a control treatment), as feeding simply supplemented the rise in metabolic demand associated with higher temperatures (Pistevos et al. 2015). However, oceanographic consequences of climate change are not limited to a temperature increase. Indeed, with increasing CO<sub>2</sub> emissions comes increased ocean acidification (IPCC 2013), which has been shown to negatively impact olfactory ability and hunting behavior of some sharks in controlled settings (Dixon et al. 2015, Pistevos et al. 2015). If the hunting ability of white sharks is impaired by ocean acidification, but their predation patterns are not directly impacted by water temperatures (i.e. through metabolic demand), they may be well placed to balance their energy budget in warmer and more acidic waters. It may be that climate change will lead to changes in the availability of preferred or alternative prey for white sharks, indirectly impacting predation rates, rather than directly impacting shark metabolism and hunting. For instance, spatiotemporal changes in water temperature may lead to shifts in prey availability due to such factors as temperature-regulated phenological events (e.g. timing of migrations or reproductive events), or different thermal sensitivities between predator and prey species leading to changes in relative attack

and escape speeds (Grigaltchik et al. 2012, Creel et al. 2016), contributing to asynchronous trophic relationships. These questions highlight areas for directed future experimentation when considering climate-driven effects on predator–prey dynamics.

In summary, our analysis of white shark predation rates on seals paired with environmental monitoring over 15 years suggests that water temperatures on an intra-annual scale might contribute to predation patterns in white sharks either directly or indirectly, but do not implicate water temperature as a primary driver of predation rates in this scenario, or on an interannual scale. In contrast, inter-annual variability in predation rate appeared linked to other environmental factors (wind, water visibility, and the occurrence of El Niño and La Niña events) which may drive both prey abundance and predation efficacy. Quantifying ecosystem-scale change in the wild to a reliable and useful extent is not a feasible goal in many natural systems due to known and unknown complexities, and the limits of scientific measurement in capturing these complexities. However, prolonged monitoring of species with known predator–prey relationships, such as the white shark and Cape fur seal *Arctocephalus pusillus pusillus* in False Bay, may provide an opportunity for ongoing investigations of how climate variability might impact the ecology of an ecosystem and for generating hypotheses to be tested in controlled experimental studies.

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