

Environmental Factors Affecting the Occurrence and Behavior of White Sharks at the Farallon Islands, California

PETER PYLE

*Point Reyes Bird Observatory
Stinson Beach, California*

SCOT D. ANDERSON

Inverness, California

A. PETER KLIMLEY

*Bodega Marine Laboratory
University of California, Davis
Bodega Bay, California*

R. PHILIP HENDERSON

*Point Reyes Bird Observatory
Stinson Beach, California*

Introduction

White shark *Carcharodon carcharias* behavior has been linked to environmental variables such as ocean temperature, water clarity, and current patterns (Limbaugh, 1963; Bass *et al.*, 1975; Bass, 1978; Miller and Collier, 1981; Ainley *et al.*, 1981, 1985; Carey *et al.*, 1982; Casey and Pratt, 1985; Cliff *et al.*, 1989; Strong *et al.*, 1992); however, comprehensive analyses of these and other environmental effects have not been performed. The occurrence of large white sharks off the central California coast has been correlated with season (Klimley, 1985b) and prey availability (Ainley *et al.*, 1985), and this information has been used by surfers, divers, and others to assess the risk of encountering this species while involved in commercial or recreational marine activities. A greater understanding of the effects of weather, lunar cycle, current patterns, tidal cycle, and physical oceanographic parameters on white shark behavior could further help to reduce white shark attacks on humans.

Biologists of the Point Reyes Bird Observatory (PRBO) have been monitoring white shark activity and predation on pinnipeds from the South Farallon Islands (SFI; 37°42' N, 123°00' W), off San Francisco, California, since 1968 (Ainley *et al.*, 1981, 1985; Pyle *et al.*, Chapter 34). Large white sharks forage in waters around the islands each autumn, coincident with the seasonal occurrence peak of their preferred prey, the northern elephant seal *Mirounga angustirostris*. From 1987 to 1992, we stationed an observer at Southeast Farallon's highest peak in autumn to watch specifically for white shark activity (see Klimley *et al.*, 1992). Here, we use frequency of predatory events and sightings, standardized by observational effort, to assess the effects of environmental variables on the behavior of white sharks at SFI. Multivariate models were developed to assess each environmental effect, after statistical adjustment for other examined effects. Variation in observed activity could relate to (1) behavior of the white sharks, (2) behavior of the prey species, and/or (3) variable observation conditions.

By synthesizing all results and comparing those based on attacks with those based on sightings, we infer which of these three causes most likely account for significant environmental effects.

Study Site, Materials, and Methods

Observations of white shark activity around SFI in 1968–1986 indicated a strong peak of occurrence during autumn (Ainley *et al.*, 1981, 1985). Therefore, we conducted standardized watches from the lighthouse (elevation, 102 m) atop Southeast Farallon Island (Fig. 1) during autumn 1987–1992 (see Klimley *et al.*, 1992). Trained observers rotated 2-hour shifts from dawn to dusk each day, weather and visibility permitting. Observations were terminated if ocean surface visibility in any direction was <1 km, or if wind speeds were >12.4 m/sec (25 knots). Observers continuously scanned the ocean within 1 km of SFI for shark activity. Most predatory events involving pinnipeds (here-

after referred to as "attacks") lasted >5 minutes and were accompanied by blood or a slick on the water, a circling flock of gulls, and/or vigorous thrashing of a shark on the surface (Ainley *et al.*, 1981, 1985; Klimley *et al.*, 1992). Because of the obvious nature of attacks, we believe that we missed few within 1 km of SFI. Nonpredatory events (hereafter called "sightings") often lasted <15 seconds; thus, it is likely that we missed many of these events. We assume, however, that our sightings data represent a randomized sampling of these activities. Observation occurred during the following periods: October 11–November 13, 1987; September 9–November 18, 1988; August 9–December 14, 1989; and September 1–November 30 during each of 1990, 1991, and 1992. A total of 434 observation periods (here defined as those lasting >90 minutes) on 404 days, totaling 3626.5 hours, were logged.

We define an attack ($N = 248$) as an event including the presence of blood, a victimized pinniped in the water, and/or an actively feeding shark. The prey

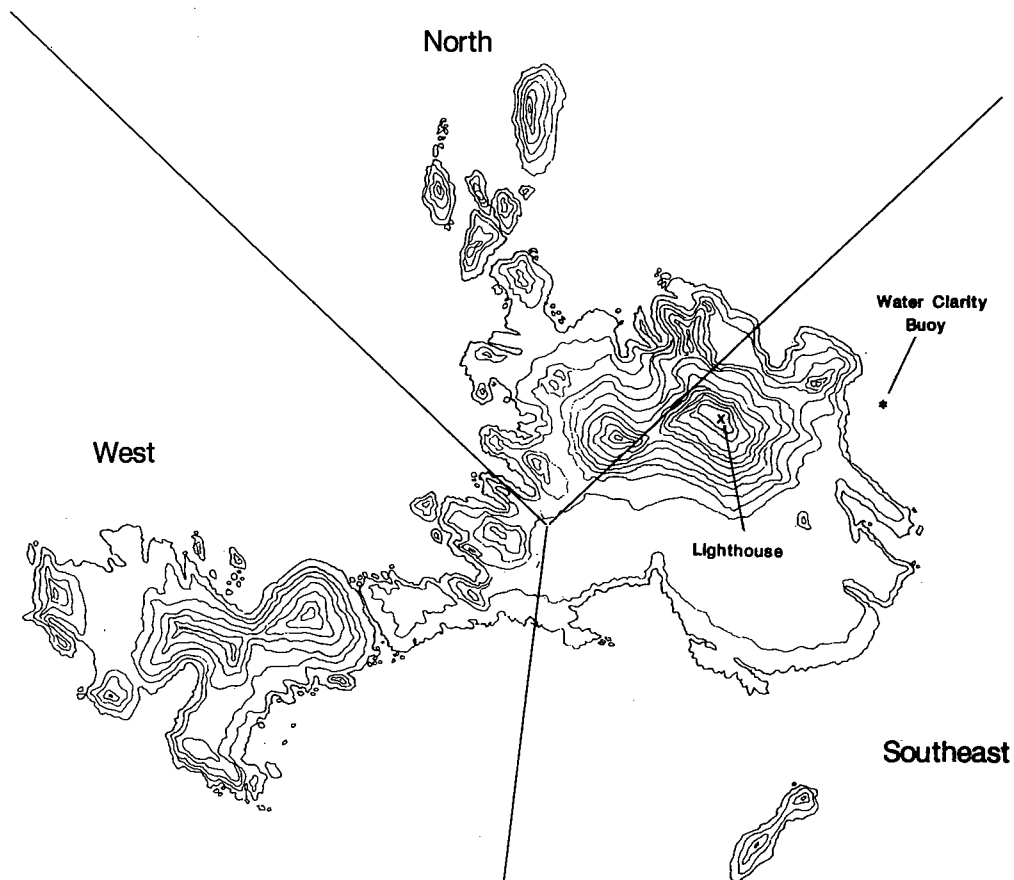


FIGURE 1 The South Farallon Islands, including positions of the lighthouse (from which observations were made), the water clarity buoy and areas of concentrated white shark activity, separated for various analyses.

species was identified during 37.9% of attacks. We separately examined environmental factors associated with attacks on northern elephant seals ($N = 87$), those on California sea lions *Zalophus californianus* ($N = 13$), and those on other species of pinnipeds ($N = 4$). Three attacks on brown pelicans *Pelecanus occidentalis* and one on a human are here considered sightings, rather than attacks. Other sightings were categorized for separate analyses into horizontal surfacings ($N = 29$) and breaches ($N = 32$), the latter often including vertical leaps that cleared the water surface (P. Pyle and S. D. Anderson, unpublished observation).

We determined the spatial components of environmental effects by dividing the waters around SFI into three distinct areas—southeast, west, and north (Fig. 1)—on the basis of wind patterns (see below) and concentrations of observed activity (see the map in Klimley *et al.*, 1992); positions of all events, except 15 sightings (which were not sufficiently described as to location), were assigned directional areas. To investigate for lagged effects, we examined correlations of environmental variables recorded on the day of observation and during each of the 3 previous days.

Environmental variables examined included wind direction (see below), surface wind speed (m/sec) and visibility (km), air temperature ($^{\circ}\text{C}$), barometric pressure (mb), cloud cover (tenths of the sky obscured), swell direction (true; range, $180\text{--}320^{\circ}$), swell height (nearest 0.305 m), sea-surface temperature ($^{\circ}\text{C}$), sea-surface salinity (‰), water clarity (see below), daily upwelling index (see below), and moonlight (see below). The first seven of these variables were recorded daily at SFI at 0600, 0900, 1200, 1500, and 2000 hours PST (see Pyle *et al.*, 1993). To obtain daily values for wind speed, visibility, air pressure, cloud cover, swell direction, and swell height, we averaged data recorded during and within 1 hour of start and end times of observation periods to obtain daily values. We used wind direction recorded at the time closest to the midpoint of the observation period, and categorically scored it for analysis as east ($30\text{--}140^{\circ}$ true), south ($150\text{--}260^{\circ}$), or northwest ($270\text{--}20^{\circ}$), reflecting the three prevailing wind directions recorded at SFI (Pyle *et al.*, 1993). We used the highest air temperature recorded during the observation period.

We collected a water sample from the southeast end of SFI to determine sea-surface temperature and salinity at 1200–1300 PST each day (see Walker *et al.*, 1992). Water clarity was scored during the 1990–1992 seasons by examining white disks, suspended 1.2 m apart, beneath a buoy anchored in a sheltered area, approximately 50 m east of SFI (Fig. 1). The clarity score represented the number of disks visible

through a $25\times$ scope from the lighthouse between 1200 and 1400 PST. Comparison of observations indicated that underwater visibility (facing downward) was about 1.75 times the number of disks visible (N); thus, underwater visibility $\sim N^{*2.1}$ m, although this relationship may not be linear. From a model that included the terms Julian date, wind direction, wind speed, swell height, sea-surface temperature, and upwelling index as independent variables [both linear and quadratic terms; $F_{(13,215)} = 8.74$, $p < 0.000$, adjusted $r^2 = 0.3305$], we calculated daily clarity scores for 1987–1989 to use in multivariate analyses.

Upwelling indices were provided by the National Oceanographic and Atmospheric Administration (see Bakun, 1973) for both 36° and 39° N, bracketing SFI. We found similar effects of upwelling using indices from both latitudes; our analyses included indices from 39° N. Moonlight was scored 0–100 relative to the proportion of the moon that was complete at midnight prior to the observation day.

White shark activity at SFI is known to be affected by season, number of immature elephant seals present (Ainley *et al.*, 1985), and tidal cycle (see Chapter 25, by Anderson *et al.*); we therefore adjusted for these effects in analyses. Date and date², represented as the Julian date within each season, were included as factors in all daily analyses. This “date adjustment” procedure controlled for linear and curvilinear seasonal cycles in both weather and oceanography and in behavioral phenology and occurrence patterns of pinnipeds and sharks. Daily totals and seasonal means of immature elephant seals were estimated from linear interpolation of weekly counts (Huber *et al.*, 1985; PRBO, unpublished data). Tidal heights and currents (incoming or outgoing) were determined using the Tides program (Wallner, 1990), adapted for SFI. We examined several tidal calculations and found that the proportion of observation time (arcsine square root transformed) when tidal height was >1.3725 m (4.5 ft) explained the greatest amount of variation in shark behavior; hereafter, the variable “tide” refers to this calculation. We excluded portions of observation periods before sunrise and after sunset. Otherwise, we did not adjust for relative times of observation periods, because white shark activity at SFI varies little with time of day during daylight hours (Klimley *et al.*, 1992).

We examined both daily and interannual effects of environmental variables on white shark attacks and sightings. Because collinearity is a problem in analyses involving daily weather and oceanographic data, the results of both single-variable (including date adjustment) and multivariate analyses are pre-

sented to differentiate actual from confounded effects (see Richardson, 1978). To estimate the effects of environmental variables, we used linear multiple regression (Seber, 1977) in both single-variable and multivariate analyses, with the STATA computer statistical package (Computing Resource Center, 1992). To reduce skew and to adjust for time duration of daily observation periods, we used $\log[(\text{events} + 0.001) \text{ per } 100 \text{ hours of observation}]$ as the dependent variable. Analyses of covariance were used to compare trends.

The purpose of the interannual analyses was to determine whether season-long environmental conditions (e.g., El Niño events) (Philander, 1989) affected white shark abundance or behavior in a given year. For these analyses, we used as the dependent variable events per 100 hours of observation over the period September 1–November 30. For 1987 and 1988, we used actual data within the shortened periods of those years (see above), extended before and after using predicted values from event models based on all years (see below). For interannual analyses, environmental variables were represented by mean values of daily observations during the period September 1–November 30 each year.

We had two objectives in our use of multiple regression analyses: (1) to explore the effects of each environmental variable controlling for other effects and (2) to develop single predictive models of white shark activity based on date and those environmental variables with significant effects. Linear and quadratic terms, the latter estimating curvilinear effects, were fitted in a forward stepwise manner by (1) examining the date-adjusted effects of all terms independently and simultaneously, (2) refitting the models after eliminating terms that had insignificant effects in both single-variable and multivariate analyses, and (3) reexamining the effects of each previously dropped variable, independently, within final models. Except for date terms, final models included only those environmental variables having significant linear or quadratic effects. In the sightings model, terms were included if they had significant effects on shark surfacings, breaches, or both. Linear effects of variables with significant quadratic terms were determined by refitting the models without their quadratic terms. Significance was assumed when $p < 0.05$, although it should be noted that many unreported tests were performed; therefore, probability statements should be interpreted with caution.

Results

A peak in attack frequency with date and increased frequency with higher tide and number of immature

elephant seals present (Table I) were confirmed as reported elsewhere (Ainley *et al.*, 1985; Anderson *et al.*, Chapter 25), and adjustments for these variables were made in the attack model (Table II). Neither the tide nor the number of seals present significantly affected nonpredatory sightings of white sharks after adjustment for date (Tables I and III). Wind direction, air temperature, barometric pressure, swell direction, and sea-surface salinity had no significant effects on either attacks or sightings.

Attack frequency increased significantly with swell height (Fig. 2) and decreased with water clarity (Fig. 3), in both single-variable (Table I) and multivariate (Table II) analyses. The significant linear and curvilinear pattern of attacks with clarity was similar in analyses using both original clarity scores only (1990–1992) and predicted (1987–1989) plus original (1990–1992) scores (Fig. 3). This finding justified our use of the latter in the overall attack model. Neither swell height nor clarity significantly affected sightings (Table I).

Attack frequency was not significantly affected by upwelling that day (Table I); however, the frequency of both attacks (Table II) and sightings (Table III) increased with higher upwelling the previous day. This correlation was similar in single-variable analyses of both attacks ($t = 2.23$, $p = 0.026$) and sightings ($t = 2.42$, $p = 0.015$). In contrast, sightings of white sharks increased significantly with decreased upwelling on the same day (Tables I and III). Sightings also increased significantly with decreased wind speed, increased cloud cover, and increased sea-surface temperature as well as during periods of decreased moonlight (Tables I and III). The moonlight effect was not completely confounded by a tidal effect, as it was still significant ($t = -2.31$, $p = 0.021$) when tide was added to the model. The negative single-variable effect of visibility on sightings (Table I) was likely the result of confounding with other variables (probably cloud cover and wind speed), as the effect of visibility was insignificant when it was added to the sightings model ($t = -0.99$, $p = 0.322$). Besides upwelling, no other significant lagged effects were found.

Most environmental effects on daily attack frequency were similar when examined using attacks on elephant seals only (Table II); however, only clarity affected attacks on California sea lions (Table II). The fewer significant effects with sea lions could be an artifact of smaller sample size. For sightings, the effects of wind speed and moonlight were significant with surfacings but not breaches, whereas significant effects of sea-surface temperature and upwelling were present with breaches but not surfacings (Table III). Surfacing increased linearly with cloud cover, whereas insignificant linear but negative curvilinear

TABLE I Environmental Effects on the Frequency of Observed Attacks and Sightings

Variable ^a	Mean	SD	Attacks		Sightings	
			<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Elephant seals ^b	505.700	158.00	1.92	0.056	0.96	0.340
Tide	0.344	0.23	3.73	0.000	0.92	0.356
Wind direction ^c			1.18	0.316	1.50	0.215
Wind speed	5.050	2.17	0.99	0.325	-2.94	0.003
Visibility	21.960	11.40	1.63	0.104	-2.21	0.028
Air temperature	15.640	1.60	-0.24	0.810	0.80	0.425
Barometric pressure	1014.300	3.92	-0.80	0.424	0.32	0.748
Cloud cover	5.217	3.90	0.57	0.571	2.91	0.004
Swell direction	284.500	3.22	0.08	0.936	0.01	0.988
Swell height	1.584	0.55	3.36	0.001	1.14	0.255
Sea temperature	13.710	1.12	1.83	0.069	2.45	0.015
Sea salinity	33.510	0.17	-0.44	0.663	-0.82	0.412
Water clarity ^d	2.655	0.89	-6.28	0.000	0.00	0.998
Water clarity ^e	2.721	0.76	-5.77	0.000	0.16	0.872
Upwelling	40.520	63.80	1.61	0.108	-2.57	0.010
Moonlight	49.780	29.10	-1.65	0.099	-2.56	0.011

^aDate-adjusted single variable; see text for units of measurement.

^bThe effects of immature elephant seals present, without date adjustment, were $t = 6.77$, $p < 0.0001$ for attacks and $t = 2.97$, $p = 0.003$ for sightings.

^c*p* values for wind direction are based on *F* statistics rather than *t* values.

^dScores recorded in 1990–1992 ($N = 229$). For all other variables, $N = 434$.

^eActual plus predicted values in 1987–1992 ($N = 434$).

TABLE II Environmental Effects on the Attack Frequency on Northern Elephant Seals and California Sea Lions

Variable	Overall attacks ^a		Elephant seals ^b		California sea lions ^c	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Date	-0.55	0.585	1.42	0.155	-0.32	0.753
Date ²	-2.65	0.008	-2.14	0.033	-1.49	0.138
Elephant seals	2.46	0.014	2.33	0.020	-0.52	0.601
Elephant seals ²	3.92	0.000	2.03	0.043	1.58	0.115
Tide	3.28	0.001	2.81	0.005	1.48	0.141
Swell height	3.47	0.001	2.52	0.012	1.20	0.231
Water clarity	-5.27	0.000	-2.40	0.017	-2.04	0.042 ^d
Water clarity ²	-2.14	0.033	0.36	0.719	-2.06	0.040 ^d
Upwelling the day before	2.42	0.012	2.58	0.010	-0.09	0.927

^a $F_{(9,424)} = 15.19$, $p < 0.000$, adjusted $r^2 = 0.2289$, $N = 248$ attacks.

^b $F_{(9,424)} = 7.80$, $p < 0.000$, adjusted $r^2 = 0.1245$, $N = 87$ attacks.

^c $F_{(9,424)} = 1.22$, $p < 0.125$, adjusted $r^2 = 0.0046$, $N = 13$ attacks.

^dActual plus predicted values (see Table I).

TABLE III Environmental Effects on the Frequency of White Shark Sightings, Surfacing, and Breaches

Variable	Overall sightings ^a		Surfacings ^b		Breaches ^c	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Date	2.96	0.003	1.74	0.082	2.62	0.009
Date ²	-1.47	0.142	-0.54	0.590	-1.83	0.067
Wind speed	-2.22	0.027	-2.68	0.008	-0.00	0.998
Wind speed ²	1.88	0.061	3.00	0.003	-0.23	0.821
Cloud cover	1.53	0.128	2.71	0.007	0.65	0.514
Cloud cover ²	-2.40	0.017	-0.75	0.452	-2.46	0.014
Sea temperature	2.28	0.023	1.14	0.255	2.45	0.015
Upwelling	-2.23	0.027	-1.30	0.195	-1.68	0.093
Upwelling ²	2.17	0.006	0.24	0.807	2.38	0.018
Upwelling the day before	2.79	0.005	1.17	0.244	1.84	0.066
Moonlight	-2.33	0.020	-2.44	0.015	-1.43	0.154

^a $F_{(11,422)} = 4.97, p < 0.000, \text{adjusted } r^2 = 0.0927, N = 68 \text{ events.}$

^b $F_{(11,422)} = 3.88, p < 0.000, \text{adjusted } r^2 = 0.0691, N = 29 \text{ events.}$

^c $F_{(11,422)} = 3.22, p < 0.000, \text{adjusted } r^2 = 0.0541, N = 32 \text{ events.}$

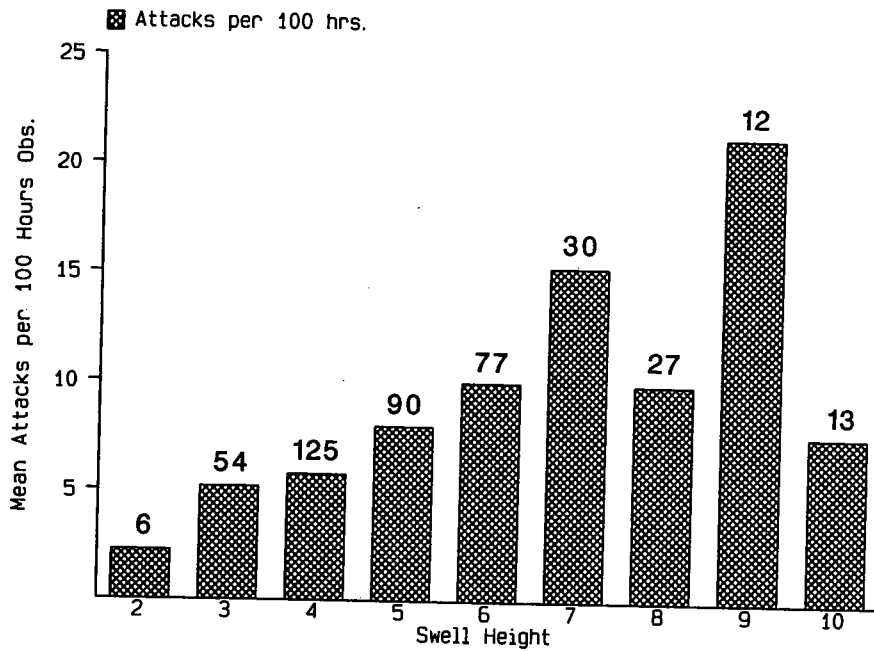


FIGURE 2 The mean number of white shark attacks observed per 100 hours relative to swell height, separated into increments of 0.305 m (1 ft); the sample sizes of the observation periods are shown above each bar.

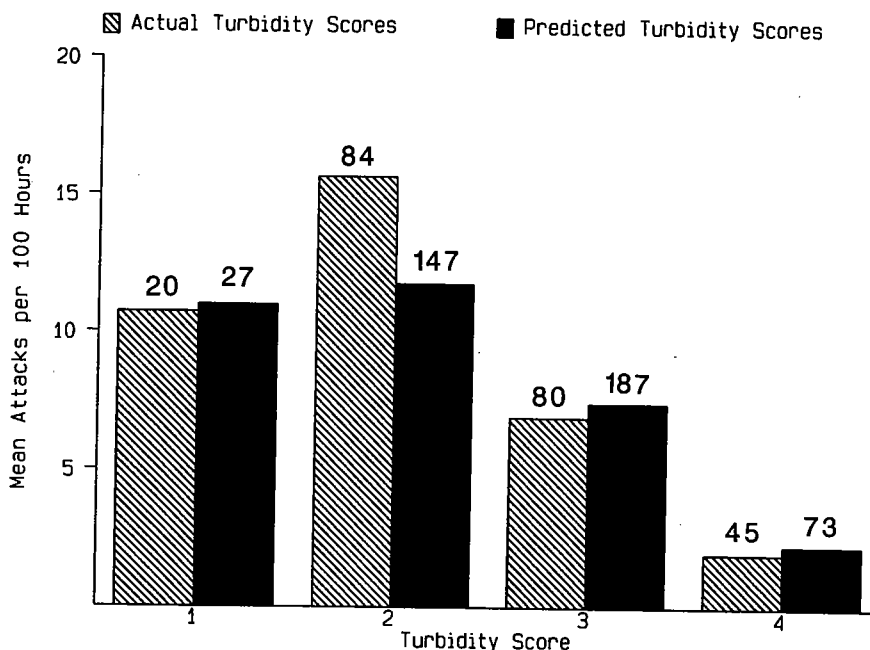


FIGURE 3 The mean number of white shark attacks observed per 100 hours relative to water clarity. Actual clarity scores ($N = 229$) were recorded during 1990–1992; “predicted scores” ($N = 434$) represent actual scores plus predicted values for 1987–1989, based on a model (see text). The sample sizes of the observation periods for each turbidity score category are shown above each bar.

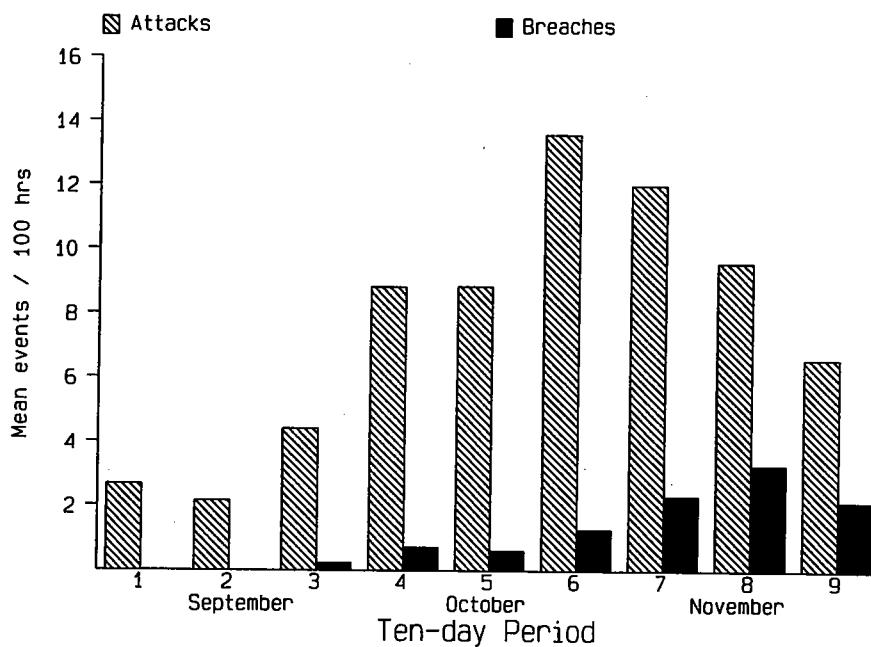


FIGURE 4 The mean number of white shark attacks and breaches observed per 100 hours by season, separated into 10-day periods, September 1–November 30 (period 5 contains 11 days). The curvilinear seasonal pattern of attacks (see Table II) differs from the linear seasonal pattern of breaches (Table III) [by 10-day period: analysis of covariance, $F_{(3,14)} = 5.17$, $p = 0.031$].

results indicated that more breaches occurred during partly cloudy skies than during either clear skies or complete cloud cover (Table III). Breaches showed a linear relationship with date (Table III); that is, more occurred later in seasonal periods (Fig. 4). This relationship was significantly different from the parabolic relationship of date with attack frequency (Table II and Fig. 4).

No significant correlations existed between mean environmental variables and attack frequency in interannual analyses; however, the timing of attacks varied significantly between years, as indicated by the effects of an interaction term, either year*date [$F_{(19,414)} = 4.47, p = 0.035$] or year*date² [$F_{(19,414)} = 6.64, p = 0.010$], when these and a year term were added to the attack model (Table II). This difference in timing was positively correlated with mean sea-surface temperature (Fig. 5); the warmer the mean seasonal temperature, the later the mean date of attacks. Differences in both analyses were similarly significant when 1987, the year of least original data, was excluded.

The location of attacks also varied significantly with date (Fig. 6). Early in the season, a higher proportion of attacks occurred to the southeast, whereas a higher proportion occurred later in the season to the

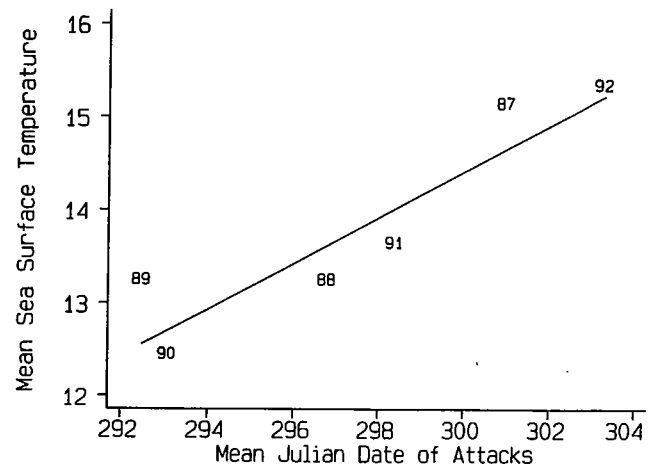


FIGURE 5 The mean seasonal sea-surface temperature by weighted mean date of observed white shark attacks per 100 hours, September 1–November 30, 1987–1992. Weighted mean date calculations for 1987 and 1988 included predicted observations for periods that occurred before and after actual observation periods (see text; with or without 1987, $t > 4.13, p < 0.026$).

north. Suspecting that this might be related to current patterns around SFI, we compared the locations of shark attacks and sightings with tidal current (in going versus outgoing) and found a similar signifi-

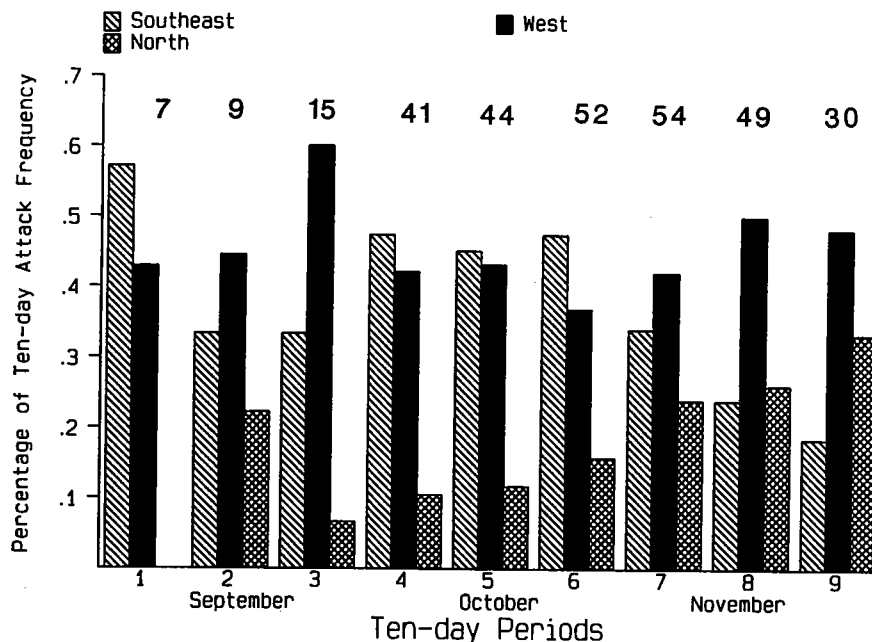


FIGURE 6 The proportion of mean white shark events recorded per 100 hours southeast, west, and north of SFI (see Fig. 1) during 10-day periods, September 1–November 30 (period 5 contains 11 days). Sample sizes during each 10-day period are indicated. The pattern of events by date between directional areas is significant (analysis of covariance): overall, $F_{(5,21)} = 8.68, p = 0.002$; between southeast and north, $F_{(3,14)} = 15.61, p = 0.001$; between west and north, $F_{(3,14)} = 6.16, p = 0.026$; but not between southeast and west, $F_{(3,14)} = 3.59, p = 0.079$.

TABLE IV Frequencies of White Shark Attacks and Sightings Relative to Location and Tidal Current

Direction	Tidal current	
	Rising	Falling
Southeast	58	54
West	62	73
North	14	40

cant difference (Table IV): more activity occurred southeast of the islands during incoming tides, whereas more activity occurred to the west and north during outgoing tides (G test, $G = 10.47$, $df = 2$, $p = 0.005$). A marginally significant interaction was also found between the locations of the attacks and the tide [analysis of covariance after adjustment with the attack model, $F_{(13,1279)} = 3.00$, $p = 0.050$]. More attacks occurred to the west compared to the southeast of SFI during higher tides. No significant interactions between other environmental effects and location of activity were found.

Discussion

SFI is located in one of five eastern boundary current systems known for their abundant marine biota (Ainley and Boekelheide, 1990) and in the midst of the largest upwelling center in the California Current system (Parrish *et al.*, 1982; Minerals Management Service, 1987). Three major oceanographic processes affect waters surrounding SFI in the fall: the southbound California Current, which is weakened at that time; the northbound Davidson Current, which strengthens and reaches the surface in early November; and coastal upwelling of nutrient-rich water, which is also weakened in fall (Bolin and Abbott, 1963; Hickey, 1979; Chelton, 1984). Weather patterns at SFI (Pyle *et al.*, 1993) are strongly influenced by these marine processes (Namais, 1969; Ainley and Boekelheide, 1990), and both the marine systems and, in turn, weather patterns in the area show substantial interannual variation (Norton *et al.*, 1985). Shark occurrence and behavior at SFI appear to be influenced by all of these climatological processes.

White shark attack frequency at SFI was not significantly affected by any nonoceanic weather variables, indicating that these variables influenced neither the behavior of prey nor our ability to detect attacks. The effect of wind speed on sightings (Table III), espe-

cially surfacings, however, probably does reflect our reduced ability to detect these events during rougher sea conditions. Our ability to detect sightings may have improved during greater cloud cover, which reduced solar glare. Alternatively, darker or less contrasting light conditions may have caused white sharks to occur closer to the water surface, explaining the increased number of surfacings during cloudier skies (Table III).

Both increased swell height and decreased water clarity were correlated with greater attack frequency, but neither of these variables influenced white shark sightings (Tables I–III). These findings suggest that both of these effects result, at least in part, from behavior of the prey. Increased swell height, like increased tidal height, reduces the haul-out area for elephant seals (see Chapter 25, by Anderson *et al.*), forcing them into the water and, in effect, increasing prey availability for white sharks (Fig. 2). We infer that decreased water clarity limited the ability of pinnipeds to detect stalking white sharks, thus increasing the chance of successful predation. The negative curvilinear correlation with clarity (Table II and Fig. 3) may result from a decreased ability by sharks to detect prey in the most turbid conditions. Although it is also possible that white shark activity generally increases with decreased clarity (see Myrberg, 1969; Cliff *et al.*, 1989), we might then expect to see a concomitant increase in the frequency of sightings, which we did not find (Table I). On the other hand, more white sharks may have moved into SFI waters during turbid periods, remaining at stalking depths during these improved conditions for predation.

The only correlation significant in analyses of both attacks and sightings was that of increased activity with increased upwelling the day before observation (Tables II and III). We infer from this that more white sharks are present around SFI during periods about 24 hours after bouts of coastal upwelling. This pattern was not directly related to water clarity, as clarity and upwelling the day before were not significantly related (date-adjusted analysis, 1990–1992; $t = -0.60$, $p = 0.549$). Although numerous studies have correlated fish movement in the California Current with upwelling on seasonal and interannual bases (e.g., Bakun and Parrish, 1980; Parrish *et al.*, 1981), few have reported on daily response patterns. Briggs *et al.* (1988; see also Minerals Management Service, 1987) found that Cassin's auklets *Ptychoramphus aleuticus* and their prey—euphausiids and juvenile fish—concentrated along frontal boundaries that appeared near SFI after intensified upwelling. Carey *et al.* (1982) found that a telemetered white shark preferred moving along a thermocline, perhaps for orientation or to enable

sampling of two water masses. It is possible that white sharks concentrate along frontal boundaries created by upwelling near SFI for these reasons. Alternatively, the white shark may be a member of a pelagic fish assemblage showing movement patterns responding to upwelling-related changes in water mass, as has been documented in the Gulf of California with hammerhead sharks *Sphyrna lewini* (Klimley and Butler, 1988). Telemetry studies on tagged white sharks in the area would greatly elucidate the responses of sharks to local upwelling.

Although significant only with sightings and surfacings, an increase in shark presence at SFI during dark-moon periods was indicated in all analyses (Tables I and III; $t = -1.36$, $p = 0.175$, when moonlight was added to the attack model: Table II). It is possible that this weak effect might be caused by more nocturnal movement by (and predation on) pinnipeds around SFI during full-moon periods (see Trillmich and Mohren, 1981; Watts, 1993). Although an illumination threshold has yet to be quantified, evidence from retinal examinations (Gruber and Cohen, 1985), attack patterns versus time of day around SFI (Klimley *et al.*, 1992), and underwater movement patterns (Strong *et al.*, 1992) indicate that the white shark is mainly a diurnal predator. Thus, it is also possible that white sharks have an endogenous or direct response to ocean variables influenced by lunar cycles, as has been documented in other fish (reviewed by Gibson, 1978). Effects on white shark occurrence and predatory activity of periodic variables such as lunar phase, swell height, water clarity, and upwelling might explain the periodicity and occasional 7- to 10-day hiatuses of observed attacks at SFI (Klimley *et al.*, 1992).

The effects of environmental factors and date on white shark breaches (Table III and Fig. 4) indicate that this activity may be social rather than predatory in nature. Most breaches occurred late in fall, in a pattern significantly different from that of attack frequency, and when white sharks could be shifting from a fall predatory to a spring reproductive mode. Up to three repeated breaches were recorded on two occasions from SFI. The frequency of breaches was not significantly affected by prey abundance, tide, water clarity, or swell height, which might be expected if they represented failed predatory attempts. Higher sea-surface temperatures, the lack of immediate upwelling, and partly cloudy skies may possibly simulate environmental conditions on breeding grounds (probably in subtropical neritic waters south of Point Conception) (Klimley, 1985b), resulting in more breaches by white sharks at SFI during these conditions. We infer that the splash caused by breaches may repre-

sent social signaling (see Chapter 22, by Klimley *et al.*), perhaps by male white sharks defending a territory, attempting to attract a female, or both. Similar communication through breaching has been inferred for whales (Herman and Tavolga, 1980).

Strong *et al.* (1992) found that white sharks often circled downstream of islands and bait sources, apparently as part of a searching pattern. Our spatial results also reflect this phenomenon. The shift in attack frequency from southeast to north of the island as the season progressed (Fig. 6) is temporally consistent with the replacement at the surface of the southbound California Current by the northbound Davidson Current (Hickey, 1979; Chelton, 1984). Spatial results of tidal current and height further support this conclusion, although interactions between ocean and tidal currents (Noble and Gelfenbaum, 1990) likely complicate movement patterns by white sharks around SFI.

Although seasonal patterns of white shark occurrence differ between SFI and the adjacent coast (Ainley *et al.*, 1985), where many attacks on humans occur (Miller and Collier, 1981; Lea and Miller, 1985), some of our results might apply to the coast, and thus may be useful to humans interested in avoiding large white sharks. Those effects that we attribute primarily to pinniped behavior (i.e., increased tide and swell height and decreased water clarity) could be unrelated to attacks on humans; indeed, more attacks on humans seem to occur in clearer water along the coast (Miller and Collier, 1981; see also Limbaugh, 1963). We suggest, however, that effects of upwelling, moonlight, current patterns, and interannual patterns of water temperature be considered in relation to human attack frequency. Analyses of these and other environmental effects on white shark-human interactions, similar to those presented here, could elucidate these potential influences.

Summary

We examined the daily and seasonal effects of 13 weather, oceanographic, and lunar variables on the predatory and nonpredatory behavior of white sharks *C. carcharias* at SFI, California, during autumn 1987–1992. Effects were assessed using both single-variable and multivariate analyses. Daily frequency of observed white shark attacks on pinnipeds increased with swell height and upwelling the day before observation, and decreased with water clarity. Daily frequency of nonpredatory sightings (including surfacing and breaches) increased with cloud cover, sea-surface temperature, and upwelling the day before

observation, and decreased with wind speed, upwelling the day of observation, and lunar stage. Spatial patterns of activity indicate that white sharks stalk prey "downstream" in oceanic and tidal currents. No significant interannual patterns were apparent relative to environmental factors; however, the temporal pattern of attacks shifted later in the season during years of warmer sea-surface temperature. White shark breaches showed a different temporal pattern than attacks, suggesting that they may represent social signaling rather than failed predatory attempts. On the basis of all results, we infer that sea-surface temperature, upwelling, and lunar illumination likely affected shark behavior; swell height and water clarity likely affected prey behavior relative to predation; and wind speed and possibly cloud cover likely affected our ability to detect shark activity. Some of our findings can possibly be used to help reduce the incidence of white shark attacks on humans.

Acknowledgments

The research program at the South Farallon Islands, part of the Farallon National Wildlife Refuge, is conducted through the cooperation and support of the U.S. Fish and Wildlife Service, the U.S. Coast Guard, and the Farallon Patrol. The white shark program was funded in part by the National Geographic Society, the Gulf of the Farallones Marine Sanctuary, and PRBO, and it depended heavily on the PRBO interns acknowledged in the work of Klimley *et al.* (1992) and Anderson *et al.* (Chapter 25). We especially thank L. Gilbert for preparing the computer files used in all analyses presented here. M. Silkey assisted with the preparation of the lunar data. P. Adams (National Marine Fisheries Service, Tiburón) and P. Walker (Scripps Institution of Oceanography, La Jolla) provided the recent oceanographic information; M. Elliot (U.S. Geologic Survey, Menlo Park), and E. Ueber and J. Roletto [Gulf of the Farallones National Marine Sanctuary (GFNMS), San Francisco] provided us the theodolites for determination of attack locations. GFNMS also permitted employment of our water turbidity buoy. D. G. Ainley, D. Evans, and W. J. Sydeman provided helpful comments on the manuscript. We especially thank D. G. Ainley for frequent feedback and unconditional support throughout the course of our white shark research program. This is PRBO contribution 583.