

Trends in White Shark Predation at the South Farallon Islands, 1968–1993

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Introduction

During 1968–1986, observations of white shark *Carcharodon carcharias* activity at the South Farallon Islands (SFI), 48 km west of San Francisco, California, were conducted consistently, but at a low to moderate effort level (Ainley *et al.*, 1981, 1985). An increase in shark predation on pinnipeds from 1970 to 1982 was correlated with an increase in the number of their preferred prey, immature (1- to 3-year-old) northern elephant seals *Mirounga angustirostris*. On October 2, 1982, a fisherman removed four adult white sharks from SFI waters, an event that negatively affected the frequency of white shark sightings from the islands in 1983–1984, despite continued prey abundance (Ainley *et al.*, 1985). In 1983, the population of elephant seals at SFI stabilized at 350–400 breeding animals (Stewart *et al.*, 1994), and in 1987, we standardized our heretofore opportunistic observation effort by maintaining a directed continuous watch for shark activity during all daylight hours in autumn (Klimley *et al.*, 1992). In this chapter, we assess population trends of adult white sharks at SFI on the basis of observations both prior to and subsequent to (1) the removal of four adults in 1982, (2) the stabilization of the seal population, and (3) the standardization of our observation program.

Methods

Because of the changed protocol as of 1987, we separately examined trends during the periods 1968–1986 and 1987–1992. We standardized observational data as much as possible by confining analyses to attacks observed during September 1–November 30, when >95% of shark activity at SFI occurs (Ainley *et al.*, 1985). We assessed attacks rather than nonpredatory sightings because the former were far more obvious events (see Chapter 26, by Pyle *et al.*); hence, frequency of detection was not strongly influenced by observer biases.

To assess trends in attack frequency, we used simple and multiple linear regression (Stata Corporation, 1993, pp. 110–125) on log-transformed values (see Chapter 26, by Pyle *et al.*). For 1968–1986, we simply used the number of attacks observed during each autumn. The dependent variable for 1987–1992 was attacks recorded per 100 hours of observation from the lighthouse, arcsine square root transformed to equalize the variances (Sokal and Rohlf, 1981, pp. 380–387). No observation from the lighthouse was performed in September 1987, affecting certain analyses. For all analyses, we reexamined trends in attack frequency after statistically adjusting for the mean number of elephant seals present each autumn, as determined from weekly counts [Huber *et al.*, 1985; Point Reyes Bird Observatory (PRBO), unpublished data].

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Results

Abundance of immature elephant seals increased dramatically during the period 1968–1983 ($t = 23.64$, $p < 0.001$) (Fig. 1), but leveled off after 1982 ($t = 0.48$, $p = 0.630$; 1983–1993). The number of observed shark attacks also increased from 1968 to 1982 ($t = 4.57$, $p = 0.001$) (Fig. 1), but after adjustment for the number of seals, no correlation was evident ($t = 1.20$, $p = 0.254$). Conversely, a significant correlation between attacks and number of seals ($t = 3.81$, $p = 0.002$) became insignificant after adjusting for year ($t = -0.45$, $p = 0.664$), indicating colinearity and making it difficult to ascertain which effect (seals or year) caused the increase in shark observations. The removal of four large sharks in 1982 resulted in a decline in attacks observed in the years 1983–1985, significantly below what would be expected given the increasing trend in 1968–1982 (Fig. 2). Attacks observed rebounded between 1983 and 1986 (Fig. 1) ($t = 14.86$, $p = 0.005$ unadjusted; $t = 13.51$, $p = 0.047$ adjusted for seal abundance).

The mean number of attacks per 100 hours of observation increased between 1987 and 1992 (Fig. 3), both before ($t = 2.30$, $p = 0.020$) and after ($t = 2.28$, $p = 0.023$) adjustment for the number of seals. When

the unadjusted indices were separated by month for analyses (Fig. 4), no trends were found in September ($t = -0.476$, $p = 0.635$; 1988–1993) or October ($t = 0.47$, $p = 0.639$), but an increase in attack frequency was evident in November ($t = 2.25$, $p = 0.026$). Levels of significance were the same for trends in all three months, after adjustment for the mean number of seals present.

Discussion

Our results support the observations of Ainley *et al.* (1985) that the increase in white shark attack frequency at SFI through the mid-1980s was correlated with the abundance of immature elephant seals, and that the removal of four adult sharks in 1982 impacted the shark population in island waters. Observed increases in attack frequency became insignificant when adjusted for seal abundance; however, colinearity between attack frequency and prey abundance made it difficult to infer whether or not the shark population was increasing. The trends for this period can be explained by (1) a static shark population with an increasing individual predation rate (due to an increase in prey), (2) an increase in sharks with a

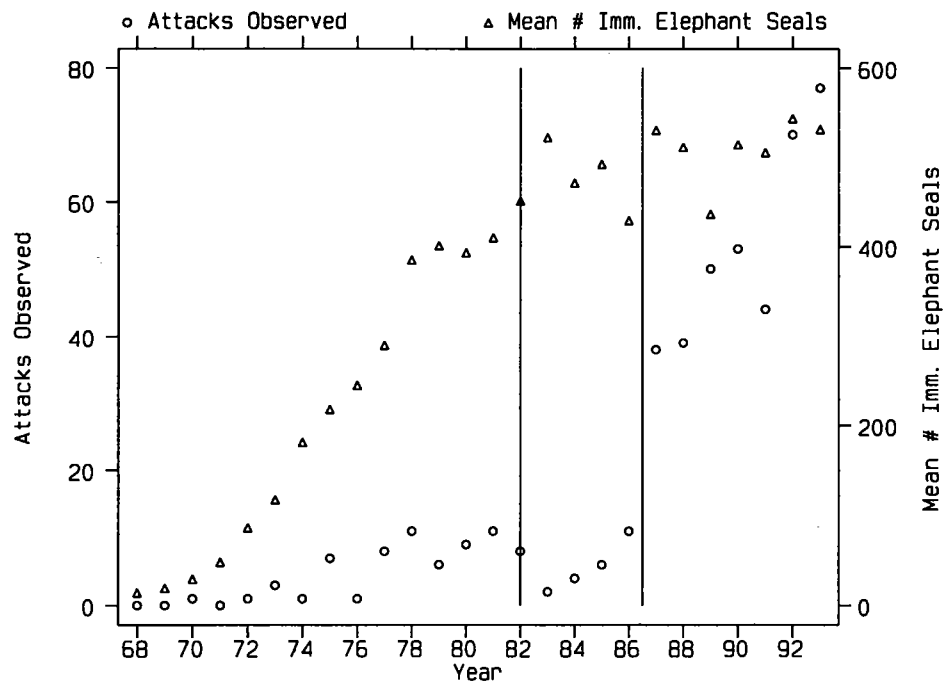


FIGURE 1 The number of white shark attacks observed and the mean number of immature northern elephant seals at the South Farallon Islands during September 1–November 30, 1968–1993. Vertical lines indicate 1982, when four adult white sharks were removed from the population, as well as the break between 1986 and 1987, when our observation effort was intensified.

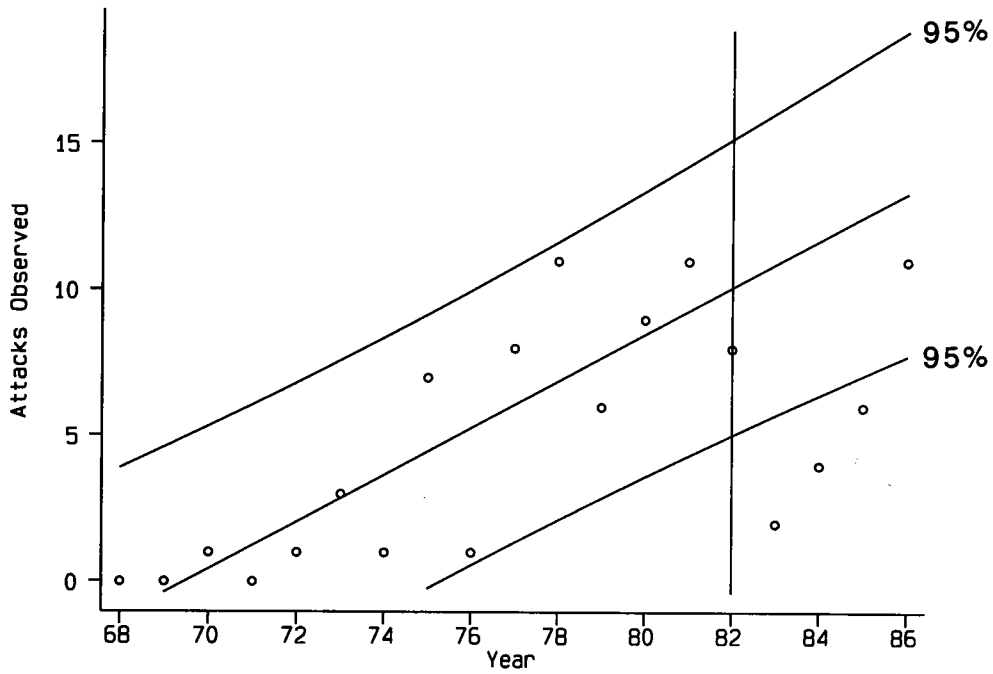


FIGURE 2 The trend in the number of white shark attacks observed at the South Farallon Islands from 1968 to 1986 (central regression line) and 95% confidence intervals calculated from the sum of the standard error in the prediction (slope) plus the residual error (Stata Corporation, 1993, pp. 79–80).

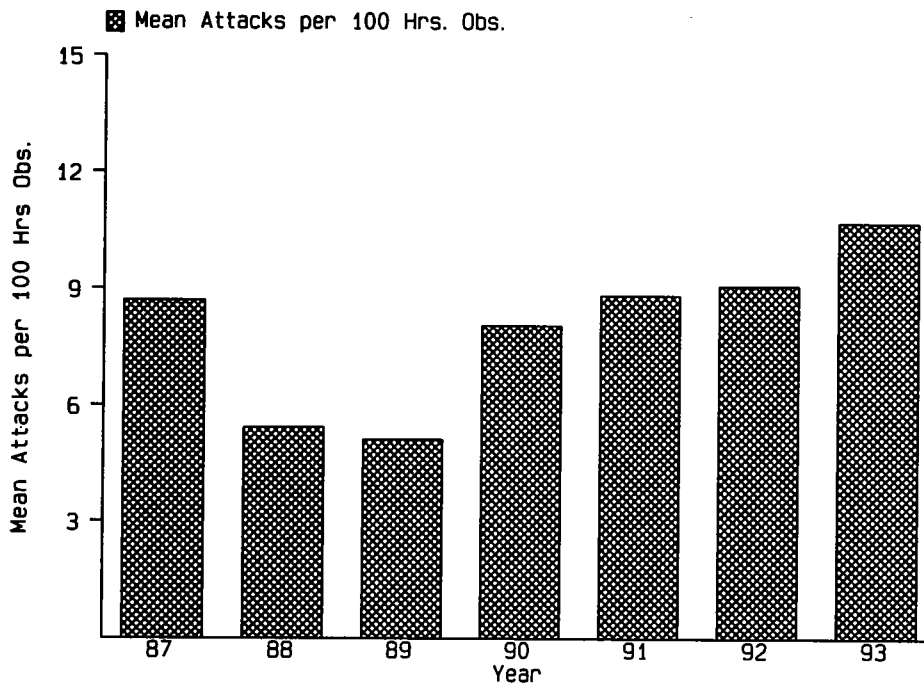


FIGURE 3 The frequency of white shark predation observed during a standardized effort at the South Farallon Islands from 1987 to 1993. The higher attack frequency in 1987 may partially reflect the lack of observation during September of that year, when frequency is typically lower (see Fig. 4).

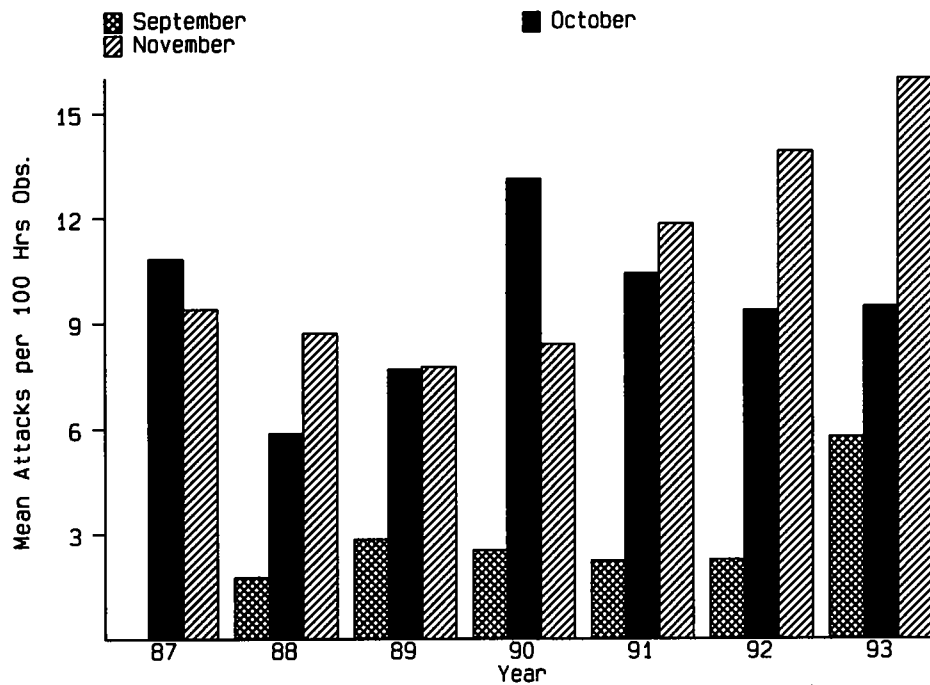


FIGURE 4 The frequency of white shark predation observed during September, October, and November 1987–1993.

constant individual predation rate, or, perhaps most likely, (3) increases in both of these factors. The increase in attacks during 1983–1986, after the removal of four adults and the stabilization of the seal population, indicates an increase in shark abundance during this period (see Chapter 33, by Klimley and Anderson).

Attack frequency also increased significantly during the period 1987–1993, both before and after adjustment for seal abundance and despite a constant population size of seals. These results, along with increases in both the incidence and percentage of shark-bitten elephant seals at SFI (see Chapter 24, by Long *et al.*), suggest that the shark population had increased during this period. It is unlikely that changes in sea-surface temperature (SST) explain this trend. Although SST at SFI averaged warmer in 1991–1993 than in 1987–1988 (PRBO, unpublished data), Pyle *et al.* (Chapter 26) found no relationship between SST and attack frequency. Continued observation of attack frequency from SFI will help to clarify the relationship between observed trends and environmental effects.

An increase in attack frequency during November 1987–1993, but not September or October, indicates either that shark occurrence patterns had shifted later each autumn or that shark abundance increased dur-

ing November for other reasons. Pyle *et al.* (Chapter 26) showed that attacks are more frequent later in the fall during years of warmer mean SST. This seasonal effect may have contributed to the trend, although we may then have expected attack frequency to decrease in September, an effect not observed (see Fig. 4).

We suggest that the inferred increase in the SFI shark population from 1983 to 1993 may be related to increased recruitment of younger white sharks, 10–15 years of age. This might be expected given (1) the rapid increase and stabilization in the prey resource during the 1970s and early 1980s (Fig. 1), (2) the slow growth rate of white sharks, which take an estimated 9–12 years to reach maturity (Cailliet *et al.*, 1985), and (3) predator–prey population dynamics (Begon and Mortimer, 1981, pp. 89–138). An increase in prey abundance should result in an increase in predator abundance, with a lag period roughly equivalent to the maturation rate of the predator. On November 15, 1993, Pyle and Anderson documented an unprecedented number (12–15) of different sharks at one attack, most of them smaller animals, 3–4.5 m in length (corresponding to subadults) (Cailliet *et al.*, 1985). These subadults may be more abundant around SFI in November, after the larger adult sharks have fed and/or departed. Again, continued observation of activity and predation frequency of white sharks at SFI

is needed to elucidate the population dynamics of this apex predator.

Summary

Trends in predation frequency by white sharks *C. carcharias* at SFI were assessed. The increased frequency of observed attacks from 1968 to 1983 could be attributed to increases in preferred prey, immature northern elephant seals *M. angustirostris* and/or an increase in sharks, whereas an increase subsequently, from 1987 to 1993, likely reflected an increase in the shark population at SFI. Significantly fewer attacks than expected were observed in 1983, 1984, and 1985, after the removal of four adults from SFI waters in

1982. This indicates the possible vulnerability of the shark population at SFI. Recent increases in shark predation in November may reflect recruitment into the population of younger white sharks, an expected occurrence given (1) increases in pinniped prey during the 1970s, (2) the slow growth rate of white sharks, and (3) predator-prey dynamics.

Acknowledgments

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