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Reconciling predator conservation with public safety

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Reconciling predator conservation with public safety

Francesco Ferretti[1*], Salvador Jorgensen[2], Taylor K Chapple[1], Giulio De Leo[1], and Fiorenza Micheli[1]

Global loss of predators calls for increased conservation of these crucial ecosystem components. However, large predators can also threaten public safety and adversely affect economic activities, creating conflicts between different public interests. In the ocean, although many shark species are facing worldwide declines, recorded instances of unprovoked attacks by sharks on humans have been increasing, stirring public concern and generating radical policies such as culling. Here we show that despite increasing records of white shark (*Carcharodon carcharias*) attacks in California, the individual attack risk for ocean users has decreased by >91% over a 63-year period (1950 to 2013). The decrease in risk could be explained by an undetected long-term shark population decline and/or changes in behavior and spatial distribution of people and sharks, the latter possibly associated with the recovery of pinniped (Phocidae and Otariidae) populations. Promoting safer behaviors among human ocean users could prove orders of magnitude more effective than culling, while meeting the dual goal of improving public safety and conserving endangered marine predators.

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Reconciling the expansion of human activities with conservation of endangered predators is an increasingly important issue in both marine and terrestrial ecosystems (Ripple *et al*. 2014). Documented declines of large predators have caused major losses of ecosystem health and services – benefits that nature provides to people (Estes *et al*. 2011; McCauley *et al*. 2015). Reductions of lions (*Panthera leo*) and leopards (*Panthera pardus pardus*) in sectors of sub-Saharan Africa have led to population increases of olive baboons (*Papio anubis*), which in turn have led to higher rates of intestinal parasite infections among their populations and humans living in close proximity (Brashares *et al*. 2010). Overfishing of large predatory sharks in the coastal Northwest Atlantic was linked to the collapse of a century-old fishery for bay scallops (*Argopecten irradians*) in North Carolina as a result of an overabundance of cownose rays (*Rhinoptera bonasus*), which prey on scallops but were controlled numerically by the once-abundant predatory sharks (Myers *et al*. 2007). Yet efforts to protect and recover large predators may also result in high personal risk for people and domestic animals sharing the same environments. Recent analyses have highlighted recoveries of carnivores in human-dominated European landscapes (Chapron *et al*. 2014), but the question of how widespread this coexistence model can be remains open. Here we address this issue for the marine environment.

In coastal areas around the world, the number of unprovoked shark attacks on humans has grown at a steady pace (Burgess 2015). In western Australia, in the past 3 years there have been seven deaths from shark bites (Gross 2014). Recently, 12 attacks resulting in five fatalities occurred off Reunion Island in the Indian Ocean (Séret 2014). These events elicit intense media and public attention, and prompt local governments to take radical actions, including shark-culling campaigns, to improve beach safety (Curtis *et al*. 2012; Neff and Yang 2013).

Culling is predicated on the assumption that increasing shark attacks are driven by greater shark abundances. Nevertheless, alternative explanations exist. More people in the water, easier communication of shark encounters facilitated by the internet and social networks, and changes in shark and human distributions and behavior can increase the number of shark attacks on record (Curtis *et al*. 2012). Under these scenarios, culling may be ineffective in reducing public risk and instead may remove sharks from populations that are already depleted.

In light of the poor conservation status of many shark species globally (Dulvy *et al*. 2014), culling already threatened populations might be irreparably detrimental for their persistence, cause unforeseen ecosystem effects (Ferretti *et al*. 2010), and have negligible effects on public safety (Curtis *et al*. 2012). In Hawaii, for example, no change in attack rate was detected following the intentional eradication of 4668 sharks around the Island of Oahu in response to a surge in shark attacks during the 1960s (Wetherbee *et al*. 1994).

Analyses of long-term shark attack records and human ocean use statistics can provide quantitative assessments of changes in shark bite risk in a region, identify the possible factors contributing to encounters between sharks and people, and inform alternative measures to avert or minimize the occurrence of injurious interactions (Neff and Yang 2013). Here, we analyzed these data from coastal California, a well-monitored ocean sector where most attacks are attributed to white sharks (*Carcharodon carcharias*). After decades of unregulated exposure to off-

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shore and coastal fisheries, the Northeast Pacific (NEP) white shark population is predicted to experience a phase of growth due to (1) a reduction in fishing mortality; (2) improved protection at the state, federal, and international levels; (3) impacts of climate change; and (4) increased availability of food resources (Dewar *et al.* 2013). Using records of shark bites and statistics on human ocean use, we addressed the hypothesis that risk has increased over the past six decades and evaluated whether a coexistence model between large predatory sharks and people is feasible under expanding human ocean use.

Methods

Probability framework

The probability of a recorded shark attack can be modeled as the joint probability of multiple processes: the probability that a person and a shark encounter one another $p(E)$, that such an encounter results in a bite $p(B)$, and that the attack is communicated $p(C)$. $p(E)$ depends on the abundance of humans (H) and sharks (S) in the water, and on the spatial overlap between people and sharks (O). If we assume that for any given encounter $p(B)$ and $p(C)$ remain constant, then the probability of a recorded shark attack depends only on H, S, and O. Because shark attacks are rare and discrete events (Curtis *et al.* 2012), it is reasonable to assume that the number of attacks per unit time and location (observation unit) follow a Poisson distribution that can be a function of covariates reflecting H, S, and O. By using this probability framework, we analyzed data on shark attacks recorded in California and information on local human ocean use (commercial or recreational activities exposing people to shark encounters [eg surfing, diving, and beach visitation]) to estimate the expected number of attacks at any time and location per unit of people predicted to be in the water, and to predict changes in attack risk over time and space.

Shark attack data

Data on shark attacks were extracted from the Global Shark Attack File (WebPanel 1; GSAF 2014). We selected only shark attacks recorded in California between 1950 and 2013 that involved white sharks and resulted in injuries. Injurious white shark bites often result in the victim's hospitalization, and consequently, we expected that few cases, if any, would have failed to be recorded and communicated even in historical times (thus ensuring that $p[C]$ was constant throughout the study period).

Ocean use data

For the same period, we constructed time series of population abundance for California coastal counties adjusted for seasonal and weekly patterns of coastal beachgoing (WebPanel 1). We also constructed time series of annual indices of people engaged in the main ocean activities of the attack victims: surfing, scuba diving, abalone (*Haliotis* spp) diving, and recreational swimming (see Results section). Surfing was quantified in terms of surfing events per year, scuba diving as annual diving days by certified scuba divers, and abalone diving as annual diving days recorded in abalone fisheries; swimming intensity was predicted by estimating the annual number of coastal beach visits (WebPanel 1).

Estimating standardized attack rates

Temporal and spatial covariates associated with each attack record, and data on ocean use, were used to estimate: (1) the expected number of attacks at any given time and location per unit of human ocean use (attack rate); (2) the corresponding individual risk of experiencing a shark attack; and (3) the change in (1) and (2) over time and space.

Because data on ocean use were available at different spatial and temporal resolutions, we estimated attack rates at two different levels of spatial and temporal aggregation. Initially, we estimated a standardized attack rate for each county, year, month, and victim activity. We fitted a generalized linear model (GLM) with a Poisson distribution and a log link function (the logarithm of the distribution mean is a linear function of the model predictors) to the number of attacks recorded in each observation unit, and used the county-specific adjusted monthly index of coastal population abundance as an offset term (equivalent of dividing the number of attacks by the number of people present in coastal areas while retaining the probabilistic model framework; WebPanel 1). This aggregation level allowed us to detect seasonal, annual, and spatial patterns of attack rates and to test whether there were differences in attack rate across victim categories. We assumed that human ocean use was proportional to human density in proximity of the coasts and to the seasonal and weekly propensity of people to visit the shore for recreation (WebPanel 1). In fact, within coastal California, recreational ocean use (surfing, diving, and oceangoing) has increased at a faster rate than the growth of the state's human coastal population. To account for this pattern, we then used the more detailed indices of ocean use (available only at the state level). Accordingly, for each victim category, we aggregated the attack data at the state level, fitted a Poisson GLM to the annual number of attacks recorded in California, and used the victim-specific index of activity intensity as an offset term (WebPanel 1).

Finally, to estimate an overall change in risk of shark attack, we stacked all activity-specific time series together and estimated an average instantaneous rate of change of standardized attack rate by fitting a Poisson generalized linear mixed-effects model (GLMM) to the annual number of attacks by victim category, using the activity-specific index of ocean use as an offset term, and treating victim activity as a random effect (WebPanel 1).

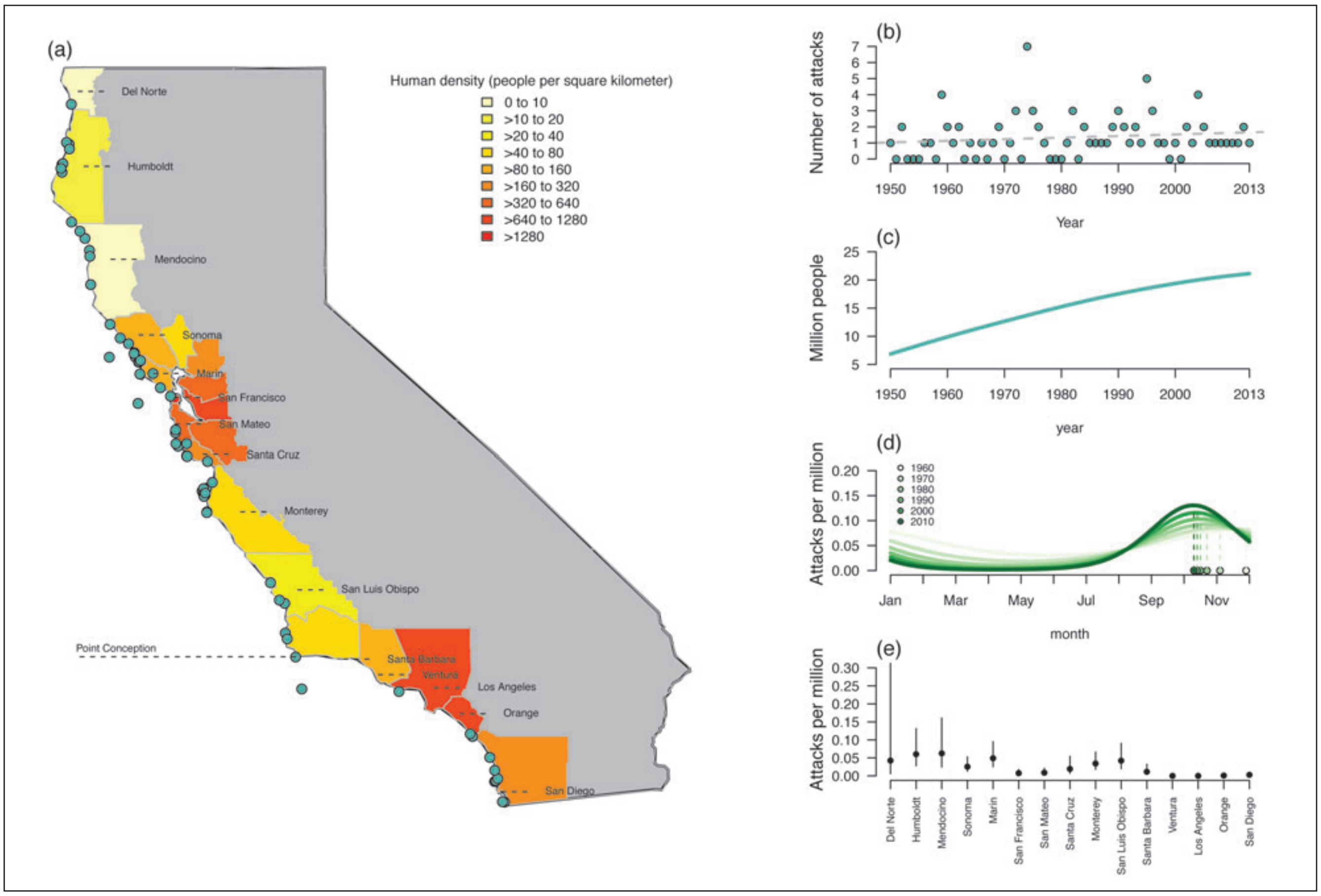

Figure 1. *Geographic and temporal patterns of shark attacks. (a) Map of shark attacks and human population density in California coastal counties; attack positions (circles) have been slightly offset to facilitate identification of single attacks in nearby locations. (b) Time series of annual number of attacks (a regression line has been superimposed on the points). (c) Growth curve of California coastal population. (d) Seasonal variation of standardized attack rate; dots indicate peaks of the attack rate across decades; note a shift from early winter to mid-fall. (e) Changes in attack rates across counties; counties have been ordered from north (left) to south (right). Error bars indicate 95% confidence intervals.*

Results

Between 1950 and 2013 there were 86 injurious attacks – 13 of which were fatal – attributed to white sharks along the California coast (Figure 1a). Throughout this period, there was an average of 1.37 attacks per year with an increasing trend, from an average of 0.9 attacks per year in the 1950s to about 1.5 attacks per year in the final 10 years (from 2004 to 2013; Figure 1b). Attacks clustered close to areas of high human population density, such as southern California between San Diego and Orange counties and in proximity to San Francisco Bay, as well as in sparsely populated areas to the north between Del Norte and Mendocino counties (Figure 1a). Incidents were recorded progressively closer to northern elephant seal (*Mirounga angustirostris*) colonies (Figure 2a), reflecting the sharks' coastal aggregation in proximity to their primary prey (Brown *et al.* 2010; Dewar *et al.* 2013).

During the same period, human ocean use for commercial and recreational purposes increased with increasing human population and easier access to the coastal ocean (WebPanel 2). Human population in coastal California tripled, from 7 million inhabitants in the 1950s to 21 million in 2013 (Figure 1c). Ocean activities increased at much faster rates. There were about 7000 surfers in 1950, and more than 872 000 in 2013 (a 125-fold increase). Likewise, the estimated number of certified scuba divers was about 2000 at the beginning of the 1960s and about 408 000 in 2013 (a 204-fold increase), while beachgoers increased from approximately 53 million in the 1950s to about 165 million in 2013 (Figure 3a; WebPanel 2).

After weighting shark attack numbers by the coastal human population, we detected a decline in attack rate by 2.4% annually, amounting to a 78% reduction between 1950 and 2013 (WebTable 1). Attack rate varied throughout the year, being highest between October and November, and lowest between March and May (Figure 1d); this pattern matches the seasonal occurrence of sharks in California waters detected with satellite and radio-transmitting tags (Jorgensen *et al.* 2010), and from records of shark attacks on seals, sea otters (*Enhydra lutris*), and cetaceans (Klimley and Ainley 1996). However, seasonality changed over time (Figure 1d). In the 1960s, attacks had a less obvious seasonal trend, peaking at the end of

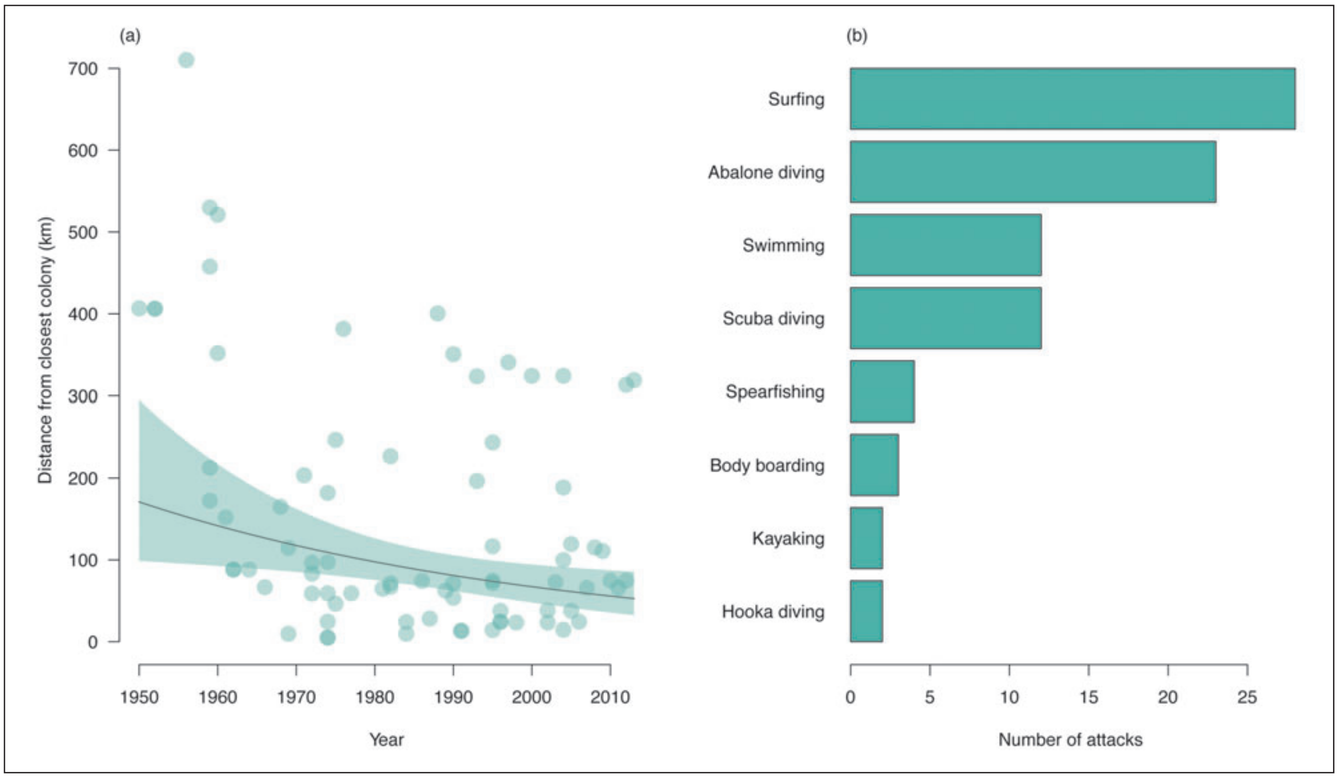

Figure 2. *(a) Temporal changes in the distance of attack from the closest elephant seal colony. The trend line represents a significant exponential model between distance from the closest colony and year (*$\log(\text{Distance}) = 41.5 - 0.019 * \text{Year}; R^2 = 0.078$*). The blue region represents the 95% confidence intervals around this model. (b) Number of attacks sorted by victim activity.*

November. In subsequent years, this seasonal variation became increasingly more pronounced, and the peak moved progressively toward the beginning of October. Finally, attack rate increased from southern to northern California and was above detectable levels only in areas where large adult sharks are known to congregate (Dewar *et al.* 2013). Peak attack rates were detected around San Luis Obispo and Mendocino counties (Figure 1e).

Surfers were attacked most frequently (33%), followed by abalone divers, scuba divers, and swimmers (27%, 14%, and 14% respectively; Figure 2b). Modeling attack rates while controlling for the numbers of people engaged in each of these activities highlighted that abalone diving was the activity most prone to shark incidents, followed by surfing, scuba diving, and swimming. In 2013, the chances of a shark attack on an abalone diver were one in 1.44 million or close to 0.69 attacks for every million diving days. For scuba divers, they were 0.007 per million (or one attack for every 136 million diving days). For surfers, the chances were one in 17 million. Swimmers had the lowest chance of shark attack, with one attack for every 738 million beach visits (0.0014 attacks per million beach visits; Figure 3).

Individual, activity-specific attacks showed significant declines for scuba and abalone divers and for swimmers, but not for surfers (Figure 3c). Standardized attack rate for scuba divers declined by more than 99.67% (confidence interval [CI]: 99.98–93.56) between 1962 and 2013. For abalone divers, attack rates declined by about 97.46% (CI: 99.58–84.68) between 1959 and 2013. For swimmers, attack rates declined by about 81.49% (CI: 95.69–20.48) between 1950 and 2013. Overall, when all individual estimates of temporal change in attack rate were combined, there was a significant decline in attack rate of about 91.24% (CI: 96.42–78.55) over the entire period (1950–2013) (Figure 3; WebTable 3).

Discussion

Analysis of shark attack trends off California supports a coexistence model of ocean users and large sharks. Similar to analyses conducted on land (Chapron *et al.* 2014), policies aimed at protecting large marine predators and predicted to promote recovery of the NEP white shark population (Dewar *et al.* 2013) are not associated with increasing risk to people. On the contrary, California oceangoers are safer today than at any other time since the 1950s due to a significant decline in the risk of injurious shark encounters. Such a pattern might be evident in other regions with records of increasing attacks, once the intensification of human ocean use is taken into account (Curtis *et al.* 2012; Burgess 2015).

If attack rate is taken as a proxy of white shark abundance, these results raise the question of whether white sharks have in fact declined in California, and warrant further investigations on the status and current trajectory of the NEP population. In particular, data are needed on the total amount of fishing-related mortality that white sharks are exposed to in international waters and

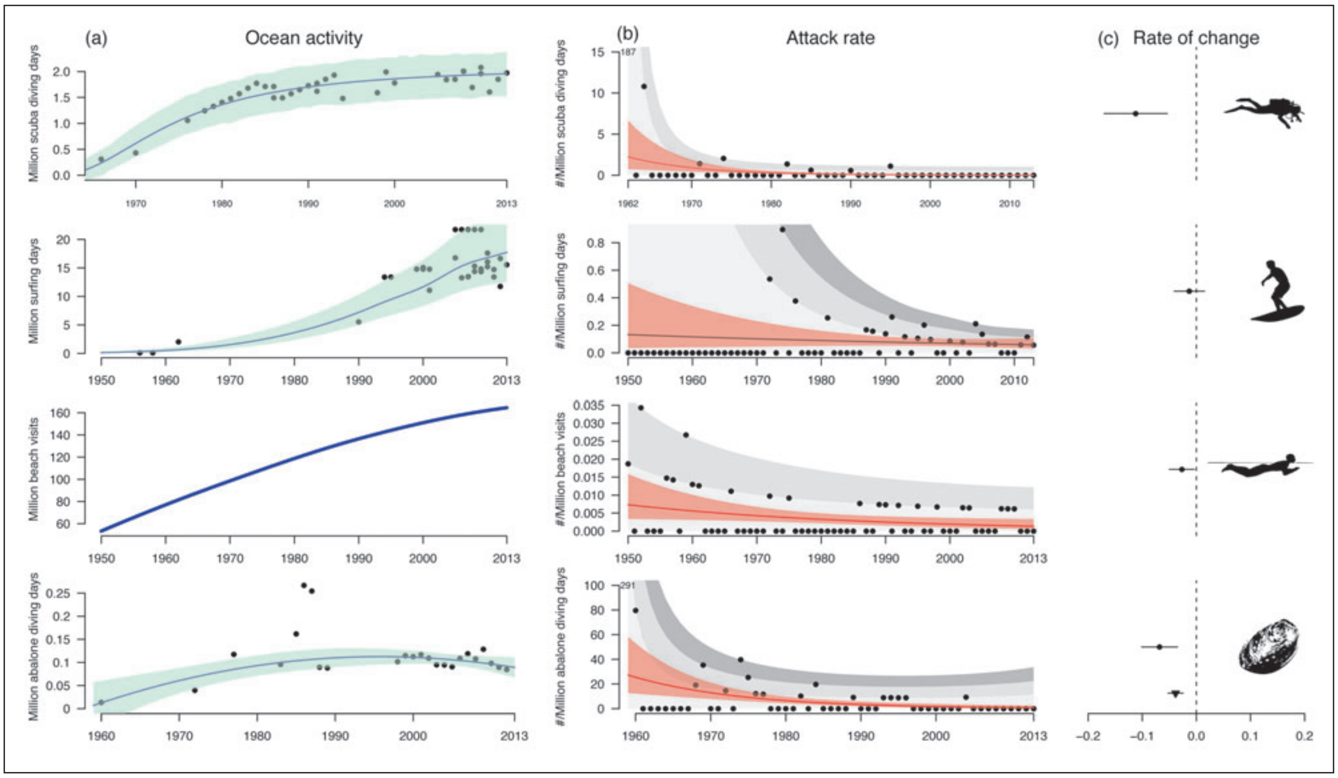

Figure 3. *Change in attack rate by victim activity. (a) Trajectories of people's engagement in ocean activities (ie offset variables) used to standardize the activity-specific attack rates (b). Red regions in (b) represent 95% confidence intervals (CIs) around the trend line. Gray regions highlight the discrete nature of the attack data (ie there were only one, two, or three attacks per year per victim category). Values 187 and 291 near the top of the highest and lowest charts indicate points beyond the y-axis limits. (c) Instantaneous rates of change (IRS) of attacks. Dots and superimposed segments are the independently estimated activity-specific IRS and 95% CI; the triangle is the IRS of the attacks combined together.*

Mexican waters, as current estimates are incomplete and highly uncertain (Dewar *et al.* 2013).

The decline in attack rate off California could also result from a change in the sharks' spatial distribution in response to parallel recovery of other large marine animals. White sharks respond to changing prey population abundance (Klimley and Ainley 1996; Brown *et al.* 2010; Skomal *et al.* 2012). Recovering pinniped populations in California (WebPanel 2) might have influenced movement and spatial distribution of white sharks in coastal areas, concentrating these predators near pinniped rookeries and away from areas frequented by ocean users. Elephant seals, in particular, influence the predatory behavior of local white sharks (Pyle *et al.* 1996; Brown *et al.* 2010). After being completely eradicated from California in the 19th century by overhunting, elephant seal colonies were gradually re-established in the past six decades due to a northward range expansion from Isla Guadalupe, Mexico (WebPanel 2). Sharks returning from their offshore phase (WebPanel 1) might now spend less time roaming in inshore areas in search of food and instead go directly toward pinniped colonies, thereby reducing the probability of encountering people. The detected decline in distance between shark attacks and elephant seal colonies (Figure 2a), and the change in attack seasonality with peaks moving toward the haul-out season of juvenile elephant seals (Le Boeuf and Laws 1994), are consistent with the hypothesis that white sharks have been tracking their major prey's population dynamics (WebPanel 2).

Finally, behavioral changes of sharks and humans might also explain a decline in interactions. Sharks may avoid highly populated areas or, because of the increased availability of preferred prey such as pinnipeds, may be less inclined to explore alternative food resources. This potential mechanism is particularly important because it would indicate that effective conservation of endangered marine populations may also result in greater public safety. People may have also learned where and when sharks are present and thus adapted their behavior when engaging in ocean activities. For example, some aspects of surfing (preference for timing activities at dawn or dusk, and selecting particular locations where conditions are ideal) are difficult to change and might partly explain why the decline in attack rate on this victim category was not significant (see WebPanel 2 for other caveats associated with surfers). These hypotheses remain untested.

Although the reasons for the declining attack rates need to be evaluated with additional data, we demonstrated that the probability of shark bites is extremely low. Comparing our data with statistics of the Centers for Disease Control and Prevention (www.cdc.gov), we calculated that, in California, a person is 1817 times more likely to die by unintentional drowning than from a shark attack and is

6897 times more likely to be hospitalized for decompression sickness when diving (Dardeau *et al.* 2012) than being a victim of a shark bite. Nonetheless, shark attacks do occur, and thus the concern and need for policy makers and natural resource managers to address the risk is justified. We suggest that an in-depth analysis of available attack data can inform alternative strategies that are more efficient than culling, and that will improve beach safety while protecting threatened shark populations. For instance, our results show that in California it is 1566 times safer to surf in March between San Diego and Los Angeles as compared with surfing between October and November in Mendocino. In Mendocino County, risk decreases by about 24 times if surfing in March. These are order-of-magnitude decreases in shark bite risk that have never been demonstrated with culling (Curtis *et al.* 2012), and can be used to promote safer behaviors for ocean users (eg avoiding riskier locations and seasons). Attack statistics for shark species (white sharks and others) and auxiliary data on ocean use from other regions could be analyzed in depth, as we have done here for California. These analyses may reveal spatial and temporal patterns of attack rate, determine whether bite risk has actually increased or decreased, investigate possible causes, and inform management strategies to address public safety and risk perception by the public (eg through ocean user associations such as scuba diving or surfers' organizations, and natural resource management agencies, such as those responsible for managing wilderness parks). This approach could be applied to other carnivores, both in marine and terrestrial environments, to inform policies and behaviors aimed at supporting the coexistence of people and potentially dangerous predators.

Large predators, including sharks, are important ecosystem components and public safety is a priority, but meeting the seemingly conflicting goals of protecting people and large predators is possible. Any initiative aimed at reducing populations of sharks and other top predators should be based on careful consideration of their abundance, conservation status, the potential ecosystem effects of these actions, and, importantly, the costs, benefits, and rationales of alternative actions. An improved understanding of the behavior, distribution, and ecological role of sharks, as well as the factors influencing the risk of shark bites, may ultimately be the most effective way for humans to stay safe while enjoying nature.

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WebPanel 1. Methods

General modeling framework

For both the analysis at the county level and the state level, we assumed that the number of attacks (x_i) falling in each observation unit i followed a Poisson distribution with mean μ,

$$P\ (x_i|\mu)\ = \mu^{x_i} e^{-\mu}/x_i! \qquad \text{for} \qquad x_i = 0, 1, 2,..., n. \qquad (1)$$

Thus, to estimate a predicted change in number of attacks in the observation domain (the study area) over time and space, we employed this generalized linear modeling structure:

$$\log(\mu) = X\beta + \log(H) \qquad (2)$$

where X is a matrix of covariates and β a vector of parameter to be estimated from the data, while log(H) is the logarithm of the index of ocean use (eg number of people in the water, number of surfers, number of divers, etc). This index, included as an offset parameter, allows the prediction of a standardized change in attack rate (eg number of attacks per unit of ocean use [ie people in the water]), while retaining the probabilistic nature of the discrete response variable.

Attack data

The Global Shark Attack File (GSAF; www.sharkattackfile.net/spreadsheets/GSAF5.xls) is an open-access global database of human–shark interactions curated by the Shark Research Institute (www.sharks.org). The database contains information on location, date, and time of the attacks; details about the victims: name, age, sex, activity, and description of the injury; species of shark involved and an estimate of its size; and details on the attack file: case number, investigator, source references (eg scientific or newspaper articles documenting the incident), and a link to the complete report of the attack file.

Data validation

We validated each record by cross-checking source references, and making additional searches to make sure all injurious white shark (*Carcharodon carcharias*)–human interactions in California were documented. We also cross-checked the GSAF with the International Shark Attack File

(ISAF), an authoritative database of shark attacks curated by the American Elasmobranch Society and the Florida Museum of Natural History (Burgess 2015). Although the ISAF data are not freely available at the single-incident level, ISAF summary statistics are available online (www.flmnh.ufl.edu/fish/sharks/isaf/graphs.htm).

For two attacks we had imprecise dates: “Prior to June 19 1959” in case GSAF ND.0060, and “August 95” in case GSAF 1995.08.00. These dates were transformed to 19 June 1959 and 1 August 1995.

Geolocation of attacks

Coordinates of the attacks were usually available from the case pdf files downloaded http://sharkattackfile.net/spreadsheets/pdf_directory. When coordinates were not available, we geocoded the attacks using the Google Maps Geocoding API, and searching for locations reported as text strings (eg “Point Lobos, Monterey, California”).

Victim activities

The GSAF data on white shark attacks in California reported about 46 textual variations of victim activities. For exploring differences in attack rate across victim activities, we binned them into 8 categories – swimming (SW), surfing (SU), scuba diving (SD), kayaking (KY), body boarding (BB), spearfishing (SF), abalone (*Haliotis* spp) diving (AD), and hookah diving (HD) – and explored their frequency of occurrence (Figure 2).

Eventually, for the attack rate standardizations, we consolidated these classes into four categories representing the most frequent activities of shark attack victims: surfing, scuba diving, abalone diving, and swimming (Figure 2). Spearfishing and hookah diving were included in the “abalone diving” category. We reasoned they had a similar exposure to shark attacks. All involve spending a substantial amount of underwater time per activity episode, occupied in a fishing activity that potentially attracts sharks, while being less alert to the surroundings. Body boarding, kayaking, and kayak fishing were included in the “swimming” category. All of them represent ocean activities expected to be proportional to the level of beachgoing in an area.

Human ocean-use data

Human ocean-use is expected to be related to human density in proximity to the coasts, and the propensity of people in using the ocean for recreation (surfing, diving, etc) or work (fishing).

California coastal population

Time series of human population by counties were obtained from the California Department of Finance (www.dof.ca.gov), which publishes census data at intervals of decades. Data for years between censuses were interpolated by fitting a locally weighted polynomial regression (LOWESS) to the time series, and using the LOWESS' parameter estimates to predict the populations of missing years.

Census data used to produce population densities in Figure 1 and WebFigure 2 were obtained through the R packages `USCensus2010` and `USCensus2010County`.

Statistics of ocean activities

Surfing

We compiled a time series of surfer estimates from different published and online sources (WebTable 4; WebPanel 2). Using the published estimates of number of surfers in California, we fit a generalized additive mixed-effects model to the time series. To avoid numerical instability, we transformed the data into thousands of surfers and rounded the numbers to the nearest integer. We assumed that the expected number of surfers per year followed a Poisson distribution:

$$S \sim \text{Poisson}(\mu) \tag{3}$$

$$\log(\mu_i) = a + s(y) + a_j \qquad a_j \sim N\,(0, \sigma_a^2) \tag{4}$$

where S is the number of surfers in thousands, a is an intercept, $s(y)$ is a penalized tin plate regression spline of year, and a_j is the random contribution given by data source j. Since surfer estimates were taken from different sources, we assumed that these sources were overestimating or underestimating the number of surfers consistently by a random quantity $a_j \sim N\,(0, \sigma_a^2)$. Such a random structure accounted for the correlation of residuals within data source. Model fitting was performed through the use of R version 3.1.2 with the `gamm( )` function in the `mgcv` package.

We then used the parameter estimates of the model to predict a complete continuous time series over the whole period. Finally, to find the number of surfing events per year, we multiplied this value by 20.32, which is the average annual number of surfing days California surfers spent in 2001 (WebPanel 2; Leeworthy and Wiley 2001).

Swimming

For general swimming and other oceangoing activities, we used an estimate of beachgoing. There is a direct relationship between beachgoing and the actual number of people entering the water (WebFigure 1). To estimate beachgoing, we summed the county-specific time series of human population over all the coastal counties to find a cumulative time series of people living in coastal California. Then we used available estimates of beach days spent by Californians in 2001

(Leeworthy and Wiley 2001; Pendleton *et al*. 2006) and took the ratio between the mean of this estimate (152 million beach days) and the population estimate in the corresponding year. We then multiplied this ratio by the coastal population estimates of all the other years having no information on beachgoing.

Scuba diving

For scuba diving we estimated a time series of annual diving days generated by scuba divers in California. First we collated estimates of the US scuba diving population extracted from different published sources (WebTable 5). We then fit a two-parameter sigmoid mixed-effect model to these data to predict a complete time series of diving populations,

$$d_{ij} = \frac{(\alpha + a_i) * y_j^2}{((\beta + b_i)^2 + y_j^2)} + \epsilon_{ij}, \tag{5}$$

where y is year, α and β are the mean values of two equation parameters, and a_i and b_i are the random-effect deviations from the population-level parameter estimates, given by the different sources of data. These parameters were assumed to follow a normal distribution with mean 0 and variance–covariance matrix Ψ; the residuals ϵ_{ij} were normally distributed with mean 0 and variance σ^2, or $\epsilon_{ij} \sim N(0, \sigma^2)$. In this way we accounted for the correlation between observations coming from the same data source.

The US diving population estimates were converted to California estimates by multiplying these values by the proportion between recreational divers in California (371 000) estimated in 2001 (Leeworthy and Wiley 2001) and the same year’s estimate for the entire US. Finally, we multiplied the number of divers in California by the average number of per-diver diving days (1.383) estimated for this category in 2001 (Leeworthy and Wiley 2001) to obtain an estimated number of dives per year (Figure 3a).

Abalone diving

Intensity of abalone diving was expressed in terms of diving days per year. These estimates were produced by the California Department of Fish and Wildlife by using telephone survey data, number of abalone fishing permits, aerial and creel survey data, and interview surveys (J Kashiwada unpublished data; WebTable 6).

Estimates of diving days were obtained by multiplying abalone permits by the percentage of divers obtained from telephone surveys, and then by the average number of diving days per diver. Telephone survey data from 2002–2009 were used to estimate the proportion of divers fishing for abalone from a cumulative figure of sales that do not distinguish between divers and rock pickers (rock pickers are also called shore pickers because they take abalones without diving).

These surveys were also used to estimate the number of diver days for the years not having telephone survey data (1998–2001 and 2010–2012). In these years, percentage of divers, and dive-days per diver, were set as the average of the values from 2002–2009. Data mainly pertained to northern California, from Pismo Beach to the Oregon border. We assumed that they were adequate to represent the intensity of abalone diving necessary to standardize the attacks on this victim category we had on record.

The resulting time series of diving days followed a parabolic trajectory (see WebPanel 2 for explanations) and thus it was modeled with a quadratic linear model:

$$DD_{ij} = \alpha + \beta Y_{ij} + \beta_2 Y_{ij}^2 + \varepsilon_{ij} \qquad (6)$$

where α, β, and β_2 are parameters to be estimated by generalized least squares (GLS), DD_{ij} are diving days per year *i* and recording method *j*, *Y* is the year, and ε_{ij} are residuals. Here

$\varepsilon_{ij} \sim N(0, \sigma_j^2)$, allowing them to have a different variance structure for each level of the recording method *j*. We used this variance structure because estimates of diving days varied in accuracy, usually dependent on the methods used for collecting data. Data from random telephone surveys to households had very low sample sizes and were highly variable due to variable contact success for the telephone surveys (J Kashiwada pers comm). The most accurate data were those for the years since 1998, when abalone permits began to be sold. Finally, to avoid autocorrelation of residuals coming from similar survey methods, we included a correlation structure. We chose an autoregressive model of order 1 (AR1, selected over a compound symmetry correlation structure due to a lower-model Akaike information criterion [AIC] value; Zuur *et al*. 2009).

Attack standardization

County-level analysis

We counted the number of attacks falling in every combination of county (*C*), month (*M*), year (*Y*), and victim activity (*A*) characterizing the spatial and temporal domain of our system. We considered all California coastal counties excluding those having marine access only in the San Francisco Bay (ie Alameda, Contra Costa, Napa, Santa Clara, and Solano; no attacks were recorded in these counties). Counts for combinations with no attacks were set to zero. We fitted a generalized linear model with Poisson distribution and log link to the count data and used county, year, month, and activity as explanatory variables. Month was expressed as an ordinal variable going from 1 (January) to 12 (December), and included in the model as part of a two-term sinusoidal function ($f(M) = \beta_{s1} S_1 + \beta_{s2} S_2 = \beta_{s1} \cdot \sin\left(2\pi\frac{M}{12}\right) + \beta_{s2} \cdot \cos\left(2\pi\frac{M}{12}\right)$). This function allowed us to capture a seasonal effect on the attacks (Ferretti *et al*. 2013).

The general model structure is given in Equation 2. In this case, μ is the expected number of attack per combination of year, month, county, and activity. *H* is the index of human ocean use of each statistical unit (combination of county, year, and month).

Index of ocean use **H**

We assumed that ocean use was proportional to coastal population abundance. To make coastal population abundances as close as possible to indices of ocean use, we took into account seasonal patterns of beach visitation observed in California (Dwight *et al*. 2007). We rescaled the county-specific population abundances by a monthly coefficient representing an index of beach visitation going from 0 to 1, where 1 is the month with the peak in beach visitation, and all the other months are proportional to this maximum value. Hence we generated a county-specific monthly index of coastal population abundance $H_{y,m,c}$.

Model selection

From an initial list of covariates deemed to explain the variability of the attacks (C, Y, S1, S2, and A), we fitted a model including main effects and two-way interactions between year, county, and the sinusoidal terms S1 and S2. We wanted to test temporal changes in geographic and seasonal occurrence of attacks. Then we proceeded with model selection by initially using a multi-model inferential approach (Burnham and Anderson 2002). We fitted all combinations of the selected variables by taking into account marginality (ie fitting models containing interactions only if their main effects were included; Calcagno and de Mazancourt 2010). Multimodel selection was performed with the R package glmulti (Calcagno and de Mazancourt 2010). After obtaining a first set of plausible models according to their corrected AIC (AICc) and Akaike weights (Burnham and Anderson 2002), we selected the model in WebTable 1 as our best model because of its minimal AIC and the statistical significance of the individual variables. For example, even though covariate S2 was not statistically significant ($P > 0.05$), we retained it to complete the sinusoidal function of month. Finally we tested for autocorrelation of residuals over time by fitting a generalized estimating equation (GEE) with the same linear predictor and an AR1 correlation structure on residual clusters identified by counties and activities, and we found no significant deviation from independence.

Complex trajectories of change

It is currently hypothesized that the northeast Pacific (NEP) white shark population is in a recent increasing phase (Dewar *et al*. 2013). Hence, we tested whether there were more complex temporal trajectories of attack rate. We refitted a model structure equivalent to the best one selected in the previous stage by using a generalized additive model (GAM) where month was included as a cyclic cubic regression spline interacting with year. Results suggested that attack rate had a constant decline throughout the period.

State-level analysis

For each main group of victims (surfers, abalone divers, scuba divers, and beachgoers), we modeled the annual number of attacks recorded along the whole coast of California as a function of year and the pertinent annual index of activity intensity:

$$\log(\mu) = \alpha + \beta_y Y + \log(H_a) \qquad (7)$$

where $H_a = f(Y)$ is an annual index of engagement for activity a (ie surfing, abalone diving, scuba diving, and beachgoing, estimated as detailed above), α is the intercept, and β_y is the instantaneous rate of change of attack rate. We controlled for temporal autocorrelation of residuals by fitting a GEE with the same linear predictor and an AR1 correlation structure. We detected no significant correlation.

Combining activity-specific time series

We combined all activity-specific time series together and estimated an average instantaneous rate of change of standardized attacks in a unique generalized linear mixed-effects model (GLMM), where the offset variable changed by victim category (A):

$$\log(\mu_a) = \alpha + \beta_y Y + \log(H_a) + \gamma_a A + \epsilon \qquad (8)$$

where $\gamma_a \sim N(0, \theta)$ and $\epsilon \sim N(0, \sigma^2)$. β_{ya} is the instantaneous rate of change of the annual expected number of attacks for activity a. The offset H_a is the activity index normalized by rescaling each value H_{ai} to $\max(H_a)$.

Activity effort uncertainty

Concerned with the effect of the offset estimate uncertainty on the activity-specific changes in attack rate (β_y), we generated a distribution of 10 000 time series of H_a from the parameter estimates and standard errors of the offset models (Equations 3–6). These series were then plugged into the attack model (Equation 8) to obtain 10 000 estimates of β_y from which we estimated the mean and 2.5% and 97.5% quantiles (for confidence intervals [CIs]).

From this sensitivity analysis, the resulting year effect estimate was –0.038 (CI: –0.041, –0.034), which is essentially identical to the year effect obtained in model of Equation 8, but with a narrower CI (about 25% smaller). This means that the offset uncertainty accounts for a minimal portion of the year effect estimate’s uncertainty.

WebPanel 2. Additional information

White sharks in California

White sharks in California are part of the NEP population, a discrete demographic unit that extends from Mexico to the Bering Sea and seasonally offshore as far as the Hawaiian Archipelago. The core of this population is in the California Current, where white sharks show distinct adult aggregation sites: one wintering at Guadalupe Island and another off the coast of Central California (Jorgensen *et al*. 2010).

In California, white sharks have a well-defined, seasonal pattern of distribution and population structure. Juveniles are mainly distributed in southern California and northern Mexico year-round, feeding primarily on fish and invertebrates. Sub-adults and adults are mainly distributed north of Point Conception, aggregated around pinniped rookeries (Klimley 1985; Lowe *et al*. 2012). Sharks greater than 2.4 m in length remain in coastal aggregation sites from mid-summer to early winter. Then, a fraction thereof move offshore to discrete open-ocean aggregation sites between California and Hawaii (Domeier and Nasby-Lucas 2008; Jorgensen *et al*. 2010). While males return from offshore migrations every year, females tend to return to coastal aggregation areas less frequently, possibly due to gestation and parturition (Nasby-Lucas and Domeier 2012).

White shark population status

There is great uncertainty about the status of the NEP white shark population. Combined estimates based on photographic mark–recapture analyses and demographic models suggest that the NEP population might number between 500 to 5000 individuals (Chapple *et al*. 2011; Sosa-Nishizaki *et al*. 2012; Dewar *et al*. 2013; Burgess *et al*. 2014). Historical benchmarks are absent. In the past century, white sharks have been exposed to multiple sources of anthropogenic mortality, from offshore drift gillnet fisheries for flying squid, salmon tuna, and billfishes, to coastal inshore fisheries of California and Baja California (Lowe *et al*. 2012). However, the effect of these fisheries on the white shark population has been difficult to demonstrate. It is known that inshore set-net fisheries produced important levels of fishing mortality on juvenile white sharks (Klimley 1985; Lowe *et al*. 2012), but bycatch data from offshore long-line and driftnet fisheries are often scattered, incomplete, or taxonomically uncertain. As a result, the total level of fishing mortality that NEP white sharks have been exposed to over recent decades is unknown.

In the past 20 years, however, there has been an increasing protection of white sharks at the state (California), federal, and global level. After 1990, fishing mortality of juveniles due to coastal fisheries was reduced in California by the closure of the gillnet fisheries operating within three miles of the coast and one mile from islands (Lowe *et al*. 2012). In 1992, large-scale offshore driftnet fisheries were banned by an international resolution, and since 1994, California prohibited fishing for all white sharks (Dewar *et al*. 2013). White sharks were listed in 2002 in the appendices of the Convention on Migratory Species (CMS), and in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2013.

Finally, during the past century, there has been a substantial increase in pinniped populations along the California shore, especially after the passage of the Marine Mammal Protection Act in 1972 (Le Boeuf and Laws 1994). These animals are white sharks' most important prey and so it is expected that they have influenced the abundance and spatial distribution of sharks.

Northern elephant seal recovery in California

Northern elephant seals (NES; *Mirounga angustirostris*) were considered extinct by the late 1870s. However, in 1880, a small herd was discovered on the Baja California mainland, south of Isla Cedros, at Bahia San Cristobal. From the late 1890s through the 1920s, NES bred only at Isla de Guadalupe. In 1890, the total population numbered fewer than 100 animals (possibly as few as 20 individuals). During the 1900s, seasonal immigrants began to be detected along the North American west coast, from San Diego to Alaska, and the NES population started to recover (Le Boeuf and Laws 1994). It was estimated that in 1957, the total population numbered approximately 13 000 individuals, and approximately 15 000 individuals in 1960. About 91% of the population resided at Isla de Guadalupe, 8% at Isla San Benito, and 1% on the Channel Islands (WebFigure 2). From 1965 to 1991, the total elephant seal population increased by 6.3% annually (Le Boeuf and Laws 1994). By 1991, there were 127 000 elephant seals (Stewart *et al*. 1994), and by 2010 there were between 210 000 and 237 000 individuals (Lowry *et al*. 2014). The rapid increase in births at San Miguel Island (Channel Islands), the largest colony in the species' range, accounted for most of the population growth in California. Today, California has at least eight colonies (WebFigure 2).

Surfing history

Surfing was brought to California in 1907 and grew slowly in the years before World War II (WWII). In the late 1920s, there were about 30 regular surfers in southern California and about 80 by 1934 (Crawford 1999). Small surfing communities developed in southern California and Santa Cruz (Nelsen *et al*. 2007). The rapid increase of surfing culture started after WWII with the introduction of new material for making boards (Crawford 1999). Eventually, the number of surfers grew from about 5000 in 1956 to 100 000 in 1962 (Strathern 2006). The invention of the wetsuit was a notable improvement that allowed surfers to play in the cold season and to expand in northern California. This spatial expansion of surfing could not be captured in the activity-specific attack model, and might have contributed to the lack of statistical significance of the year effect. A northward expansion of surfing exposed an increasing number of surfers to areas where adult white sharks occur and therefore increased their risk of injurious interactions. Sources of data are in disagreement about the temporal trend in surfing popularity. Warshaw (2011) reported that between 1954 and 1958 there were just over 5000 surfers in California, and between 1959 and 1967, the number grew by 25% per year (totaling about 30 000 surfers in 1967). Surges of surf popularity also occurred in response to episodic events like the release of the book and movie "Gidget" in 1957 and 1959, respectively, and the success of the band The Beach Boys (Strathern 2006). No quantitative information was available between the end of the 1960s and 2000. Then a national survey on recreation activities and the environment (Leeworthy and Wiley 2001, NSRE) provided the first scientifically produced estimate of surfers in California. It indicated that at least 742 000

Californians surfed at least once in 2000 in the US. Assuming that these people spent most of their surf time in California, we used this figure as a good estimate of numbers of people surfing in California for that year. Eventually, by using socioeconomic demographic parameters such as age, class, gender, income, and race, Leeworthy *et al*. (2005) estimated a national figure for 2005 and 2010. From these national estimates, we estimated the Californian portions by multiplying the ratio of Californian to American surfers recorded in 2000 by the national 2005 and 2010 projections.

More recently, private investigations (mainly for market assessment purposes) used socioeconomic parameters similar to those used by Leeworthy and Wiley (2001, NSRE) to project a trajectory of the surfing population between 2007 and 2011. This trajectory suggests a decelerating increase in numbers of surfers in the US and a final decline between 2010 and 2011. They calculated that in 2011 the number of surfers in the Pacific states (California, Oregon, and Washington) was 747 000 (Anonymous 2012). Using the proportions of surfers between California, Oregon, and Washington reported in Leeworthy and Wiley (2001), we estimated that there were 732 000 surfers in California that year. The average number of surfing days California surfers spent in 2001 is 20.32 (Leeworthy and Wiley 2001). This may be an underestimate of the average annual surfing days per Californian surfer because it is an average of the surfing days US surfers spent surfing in California, and not just locals.

Results from online surveys show that surfers in California (Wagner *et al*. 2011) and Trestles' Beach (the border between Orange and San Diego counties; Nelsen *et al*. 2007) record on average 120 and 109 visits per year, respectively. Yet, these values may inflate the actual number of surf days per surfer in California because respondents of these surveys were likely more avid surfers (Nelsen *et al*. 2007; Wagner *et al*. 2011). We decided to use the most conservative factor.

Patterns of beachgoing in California

In southern California, between 2000 and 2004 there were about 129 million beach visits annually (60% of all beach visits in the US; Dwight *et al*. 2012). About 88% of summer visitors are California residents (Dwight *et al*. 2007). Each year, it is estimated that 56 million bathing events occur in the waters of southern California (Dwight *et al*. 2007). Beach visitation has a well-defined weekly and seasonal pattern. It is greatest on the weekends and in summer (WebFigure 3). It is expected that this pattern could influence the seasonal variation of shark attacks detected from the models.

For the whole of California it has been estimated that there are between 151 and 153 million beach visits per year (estimates are for 2000 and 2001; Leeworthy and Wiley 2001; Pendleton *et al*. 2006). An estimated 80% of these occur in Orange, Los Angeles, and San Diego counties (Pendleton *et al*. 2006).

In relative terms, the estimated trend in beach visitation (Figure 3a) tracks the trend in coastal population abundance, and likely is an underestimate of the actual increase in beachgoing (Hall 2001; Cordell 2008).

Patterns of abalone diving effort

The increase in diving effort occurring between the 1960s and the end of the 1980s (Figure 3a) has been explained by increased access to federal, state, and county parks (Miller *et al*. 1974). Greater use of party boats and skiffs, new advances in diving equipment, and larger and more stable paddleboards facilitated access to rugged cliff areas several miles to either side of access points. Eventually there was a decrease in abalone fishing intensity due to increased fishing regulations and fisheries closures: the black abalone fishery was closed in 1993; the pink and white abalone fisheries were closed in 1996; fishing for all species has been prohibited from San Francisco to the Mexican border since 1997; an annual limit of 100 abalones per person was instituted in 2000; and in 2002, this limit was reduced to 24 abalones per person. Currently, commercial abalone fishing is allowed from Point Lobos to the Oregon border.

Change in distance between attacks and NES colonies

We extracted NES colony positions from Lowry *et al*. (2014). Then we calculated the distance between the shark attack positions and their closest NES colony, also taking into account the colony's establishment year. For example, if a shark attack was close to Piedras Blancas (San Luis Obispo), and it occurred before 1992 (when the colony of Piedras Blancas was established), we calculated the distance between the attack and the closest existing colony at that time (ie San Miguel Island). Then we fit a linear regression between the logarithm of distances and attack years (Figure 2).

WebTable 1. Best model standardizing the attacks at the county level

Covariate	Estimate	Standard error	*z* value	Pr(>|*z*|)
Intercept	28.311	16.065	1.762	0.078
Y	–0.024	0.008	–2.985	0.003
Monterey	2.393	0.476	5.029	<0.001
San Luis Obispo	2.602	0.518	5.028	<0.001
San Francisco	0.894	0.537	1.664	0.096
Sonoma	2.101	0.504	4.169	<0.001
Marin	2.752	0.476	5.778	<0.001
Santa Cruz	1.821	0.627	2.906	0.004
San Mateo	1.035	0.557	1.859	0.063
Santa Barbara	1.300	0.627	2.074	0.038
Mendocino	2.995	0.586	5.111	<0.001
Del Norte	2.613	1.069	2.444	0.015
Los Angeles	–3.358	1.069	–3.140	0.002
Humboldt	2.957	0.519	5.700	<0.001
Orange	–1.202	0.802	–1.499	0.134
Ventura	–13.741	430.517	–0.032	0.975
S2	–32.121	18.107	–1.774	0.076
S1	65.328	20.911	3.124	0.002
Y:S1	–0.033	0.011	–3.153	0.002
Y:S2	0.017	0.009	1.823	0.068

WebTable 2. GLMM evaluating changes in attack rates considering all series of ocean activities

	Estimate (standard error)
(Intercept)	–0.68 (1.38)
year	–0.04 (<0.001)
AIC	395.62
BIC	406.00
Log Likelihood	–194.81
Num obs	235
Num groups: activity	4
Variance: activity.(Intercept)	7.28
Variance: Residual	1.00

Notes: BIC = Bayesian information criterion.

WebTable 3. Year effect estimate of each victim-specific time series of shark attacks

Estimate	Standard error	Pr(>|*z*|)	Deviance explained	Victims
–0.112	0.030	<0.001	0.266	Scuba divers
–0.013	0.014	0.363	0.017	Surfers
–0.027	0.012	0.023	0.089	Beachgoers
–0.068	0.017	<0.001	0.256	Abalone divers

WebTable 4. Sources of surfing estimates found in the literature and on the internet

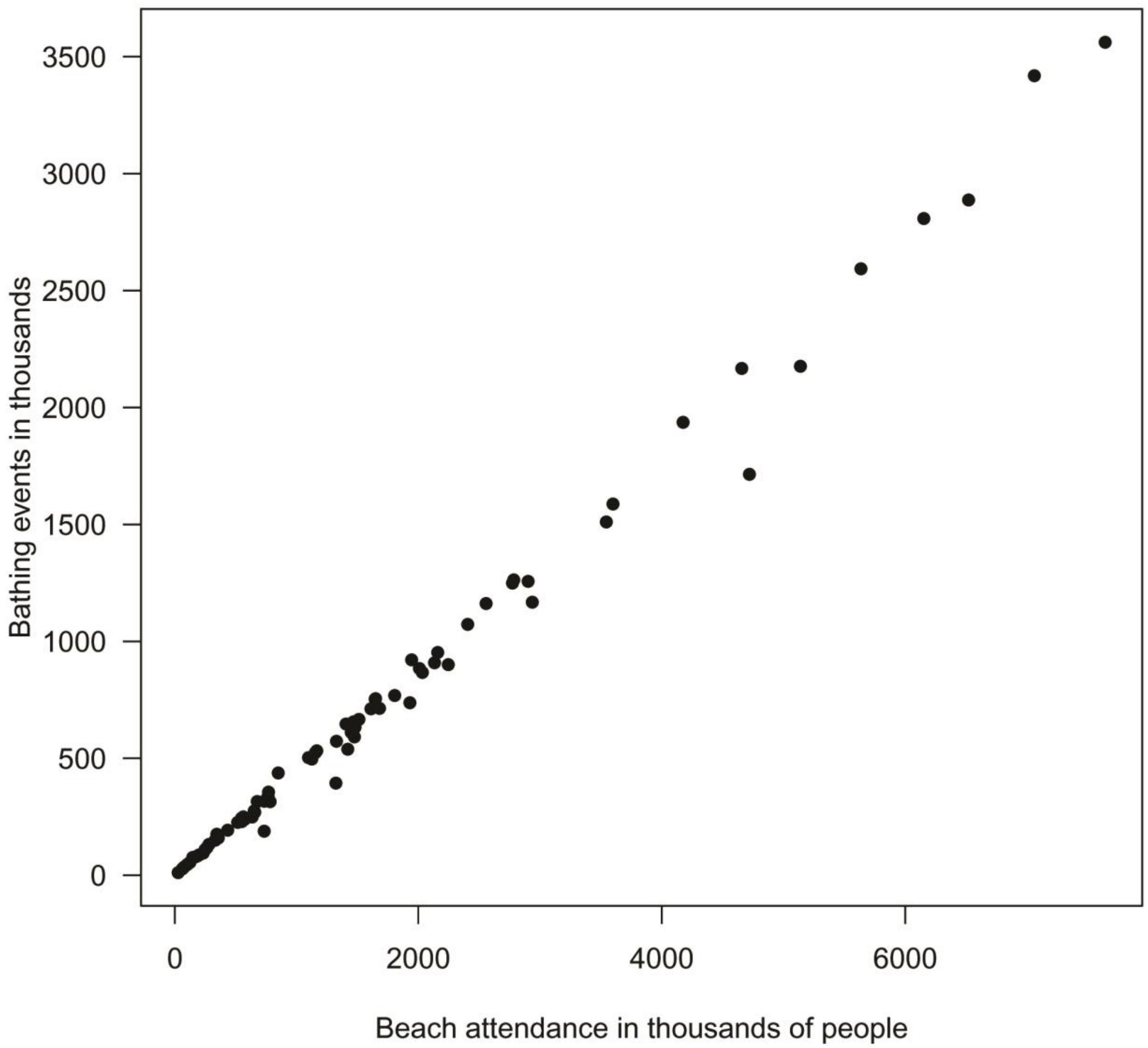
People	Year	Reference(s)
30	1929	Crawford (1999)
80	1934	Crawford (1999)
5000	1956	Strathern (2006)
5000	1958	Warshaw (2011)
100 000	1962	Strathern (2006); Dugan (2012)
273 129	1990	The Associated Press (2002)
660 061	1994	Cordell (2012)
660 061	1995	Cordell (2012)
728 344	1999	Cordell (2012)
742 000	2000	Leeworthy and Wiley (2001)
728 344	2000	Cordell (2012)
546 258	2001	The Associated Press (2002)
728 344	2001	Cordell (2012)
826 215	2005	Leeworthy *et al.* (2005)
1 069 755	2005	Cordell (2012)
1 069 755	2006	Cordell (2012)
654 144	2006	Anonymous (2014)
662 337	2007	Anonymous (2012)
1 069 755	2007	Cordell (2012)
663 248	2007	Anonymous (2014)
708 087	2008	Anonymous (2012)
1 069 755	2008	Cordell (2012)
754 291	2008	Anonymous (2014)
730 392	2009	Anonymous (2012)
1 069 755	2009	Cordell (2012)
706 493	2009	Anonymous (2014)
867 184	2010	Leeworthy *et al.* (2005)
748 601	2010	Anonymous (2012)
790 708	2010	Anonymous (2014)
724 929	2011	Anonymous (2012)
660 972	2011	Anonymous (2014)
579 261	2012	Anonymous (2013)
820 297	2012	Anonymous (2014)
765 671	2013	Anonymous (2014)

WebTable 5. Sources of diving population estimates

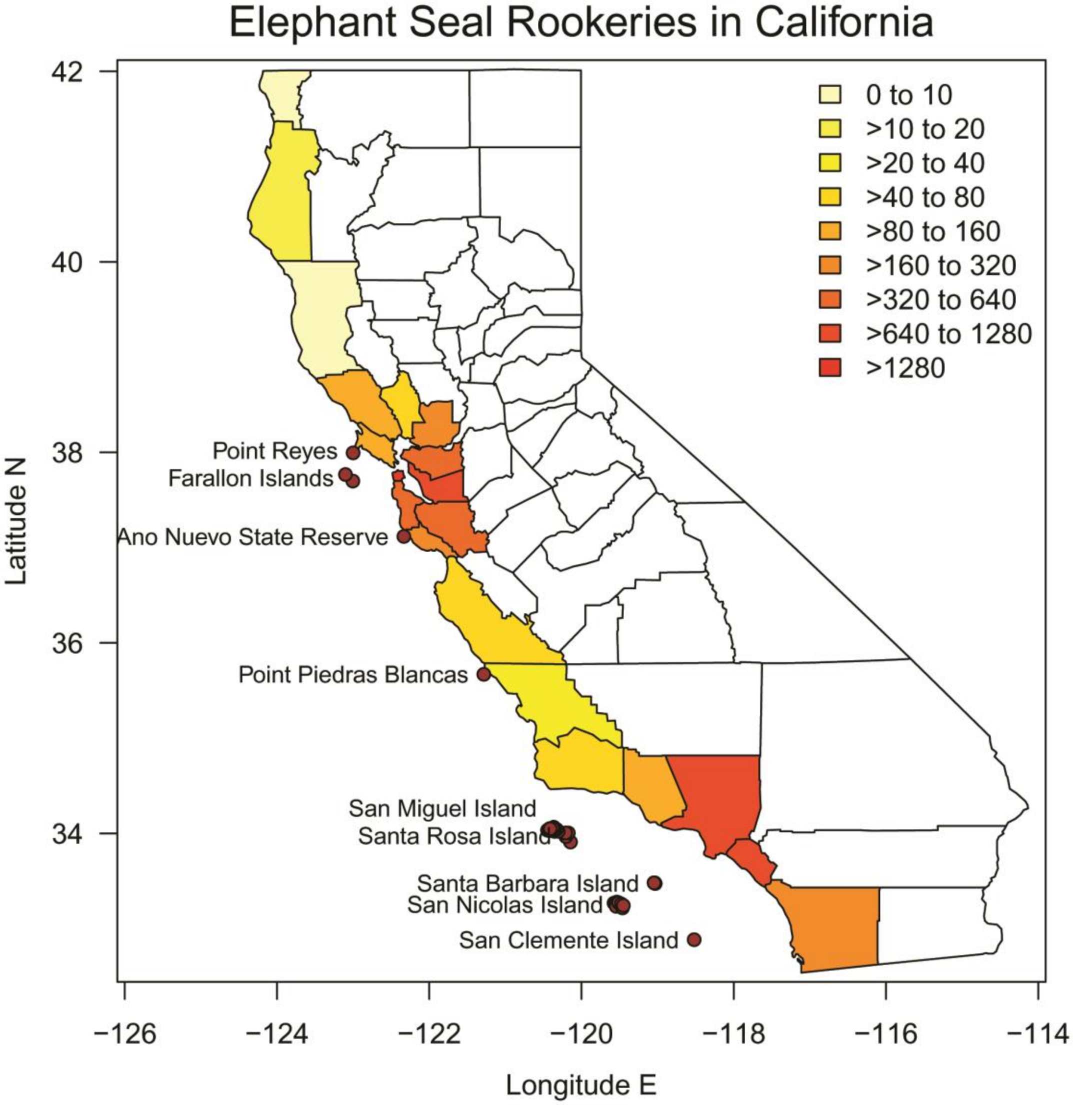
People	Year	Reference
64 860	1966	McAniff (1995)
90 026	1970	McAniff (1995)
220 524	1976	McAniff (1995)
259 441	1978	McAniff (1995)
276 953	1979	McAniff (1995)
293 168	1980	McAniff (1995)
308 734	1981	McAniff (1995)
327 544	1982	McAniff (1995)
350 245	1983	McAniff (1995)
369 703	1984	McAniff (1995)
356 731	1985	McAniff (1995)
356 731	1986	McAniff (1995)
311 329	1986	McAniff (1995)
311 329	1987	McAniff (1995)
327 544	1988	McAniff (1995)
343 759	1989	McAniff (1995)
359 974	1990	McAniff (1995)
369 703	1991	McAniff (1995)
337 273	1991	Hornsby (2011)
385 918	1992	McAniff (1995)
402 133	1993	McAniff (1995)
308 475	1994	Hornsby (2011)
331 824	1998	Hornsby (2011)
415 105	1999	Hornsby (2011)
371 000	2000	Leeworthy and Wiley (2001)
404 727	2005	Leeworthy *et al.* (2005)
383 972	2006	Hornsby (2011)
385 269	2007	Anonymous (2014)
417 180	2008	Hornsby (2011)
417 699	2008	Anonymous (2014)
352 839	2009	Anonymous (2014)
433 266	2010	Leeworthy *et al.* (2005)
408 619	2010	Anonymous (2014)
334 678	2011	Anonymous (2014)
385 269	2012	Anonymous (2014)
411 213	2013	Anonymous (2014)

WebTable 6. Sources of estimates of abalone diving days

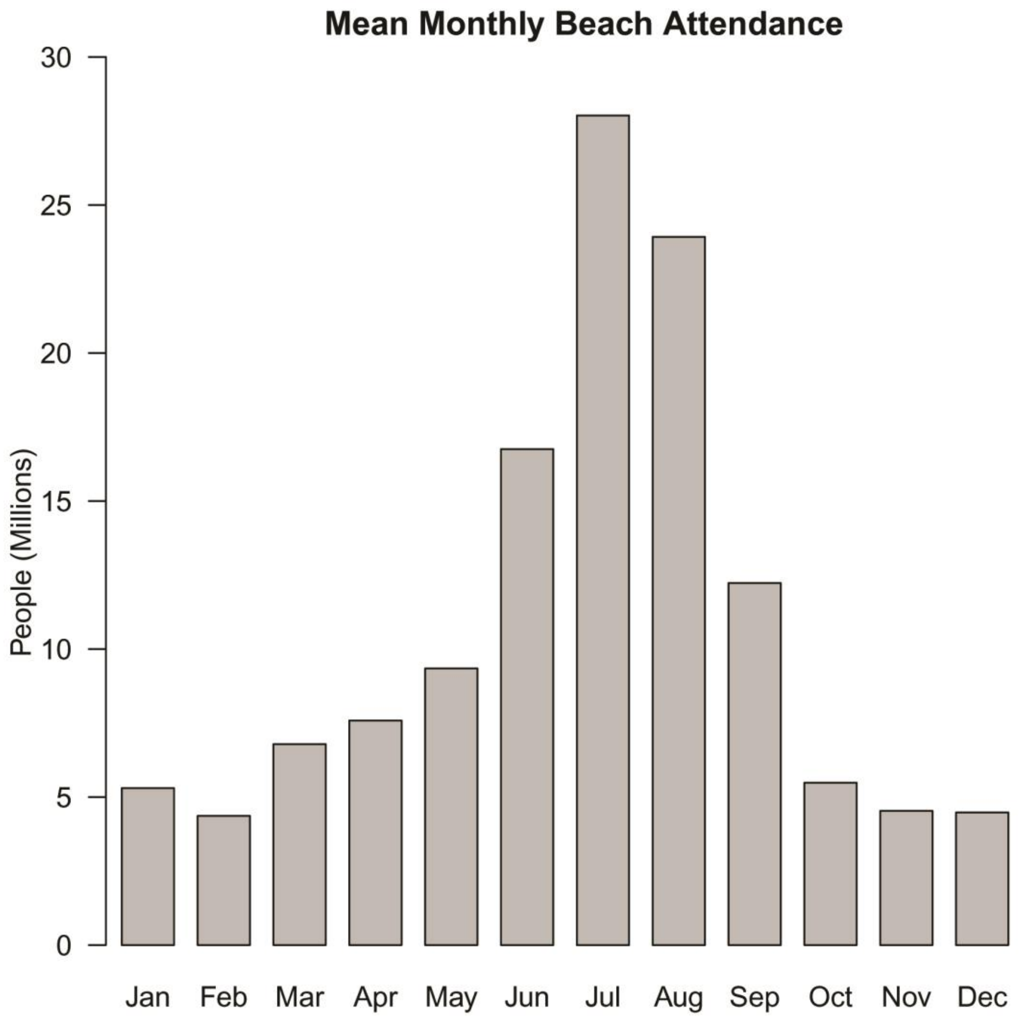
Diver days	Year	Method	Reference
13 615	1960	Interview survey	Miller *et al.* (1974)
39 863	1972	Interview survey	Miller *et al.* (1974)
117 632	1977	Aerial and creel survey data	J Kashiwada unpublished data
96 000	1983	Aerial and creel survey data	J Kashiwada unpublished data
161 760	1985	Random telephone surveys	J Kashiwada unpublished data
266 884	1986	Random telephone surveys	J Kashiwada unpublished data
254 618	1987	Random telephone surveys	J Kashiwada unpublished data
89 696	1988	Random telephone surveys	J Kashiwada unpublished data
88 320	1989	Random telephone surveys	J Kashiwada unpublished data
101 908	1998	Abalone permits	J Kashiwada unpublished data
114 702	1999	Abalone permits	J Kashiwada unpublished data
112 728	2000	Abalone permits	J Kashiwada unpublished data
117 263	2001	Abalone permits	J Kashiwada unpublished data
109 427	2002	Abalone permits	J Kashiwada unpublished data
94 978	2003	Abalone permits	J Kashiwada unpublished data
94 597	2004	Abalone permits	J Kashiwada unpublished data
90 615	2005	Abalone permits	J Kashiwada unpublished data
108 910	2006	Abalone permits	J Kashiwada unpublished data
119 078	2007	Abalone permits	J Kashiwada unpublished data
107 947	2008	Abalone permits	J Kashiwada unpublished data
128 623	2009	Abalone permits	J Kashiwada unpublished data
98 188	2010	Abalone permits	J Kashiwada unpublished data
89 497	2011	Abalone permits	J Kashiwada unpublished data
84 874	2012	Abalone permits	J Kashiwada unpublished data



WebFigure 1. Relationship between bathing events and beach attendance. Data refer to 75 beaches in the southern California counties Los Angeles, Orange, and San Diego, and are taken from Dwight *et al.* (2007).



WebFigure 2. Northern elephant seal rookeries (circles) in California. Color shading of polygons shows the human population density for coastal counties (people per square kilometer).



WebFigure 3. Seasonal pattern of beachgoing. Data taken from Dwight *et al.* (2007).

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