



Dramatic increase in sea otter mortality from white sharks in California

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ABSTRACT

Although southern sea otters (*Enhydra lutris nereis*) are not considered prey for white sharks (*Carcharodon carcharias*), sharks do nonetheless bite sea otters. We analyzed spatial and temporal trends in shark bites on sea otters in California, assessing the frequency of shark bite wounds in 1,870 carcasses collected since 1985. The proportion of stranded sea otters having shark bites has increased sharply since 2003, and white shark bites now account for >50% of recovered carcasses. The trend was most pronounced in the southern part of the range, from Estero Bay to Point Conception, where shark bite frequency has increased eightfold. Seasonal trends were also evident: most shark-bitten carcasses are recovered in late summer and fall; however, the period of elevated shark bite frequency has lengthened. The causes of these trends are unclear, but possible contributing factors include increased white shark abundance and/or changes in white shark behavior and distribution. In particular, the spatiotemporal patterns of shark-bitten sea otters match increases in pinniped populations, and the increased availability of marine mammal prey for white sharks may have led to more sharks spending more time in nearshore waters utilized by both sea otters and pinnipeds.

Key words: *Enhydra lutris nereis*, sea otter, *Carcharodon carcharias*, white shark, mortality, investigatory bite, stranding, carcass.

White sharks (*Carcharodon carcharias*) are known to be significant predators for a number of marine mammal populations, including Cape fur seals (*Arctocephalus pusillus*; Stewardson 1999, Martin *et al.* 2005), northern elephant seals (*Mirounga angustirostris*; Ainley *et al.* 1980, Le Boeuf *et al.* 1982), California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*; Long *et al.* 1996, Lucas and Stobo 2000), and small cetaceans (Long and Jones 1996, Heithaus 2001). In some cases, shark predation can have substantial population-level impacts on these marine mammal species (Lucas and Stobo 2000). White sharks have also been reported to prey upon sea birds (Johnson *et al.* 2006), although some such incidents have been shown to be nonconsumptive investigatory bites (Hammerschlag *et al.* 2012). Similarly,

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historic examination of shark-bitten sea otter carcasses (Ames and Morejohn 1980) suggested that most (if not all) bites were nonconsumptive, presumably investigatory bites (Fig. 1). Nonconsumptive bites have been noted in other systems as an interesting behavior (Hammerschlag *et al.* 2012), and may have implications for recreational use of coastal waters by people (West 2011), but have not previously been reported to have a significant impact on any “nonprey” species. Here we report on an unprecedented increase in nonconsumptive bites by white sharks on southern sea otters (*Enhydra lutris nereis*) over the past 10–15 yr, a trend which may have consequences for the recovery of this protected marine mammal population.

Southern sea otters are found in nearshore waters of coastal California, from approximately Half Moon Bay in the north to Point Conception in the south (Fig. 2).

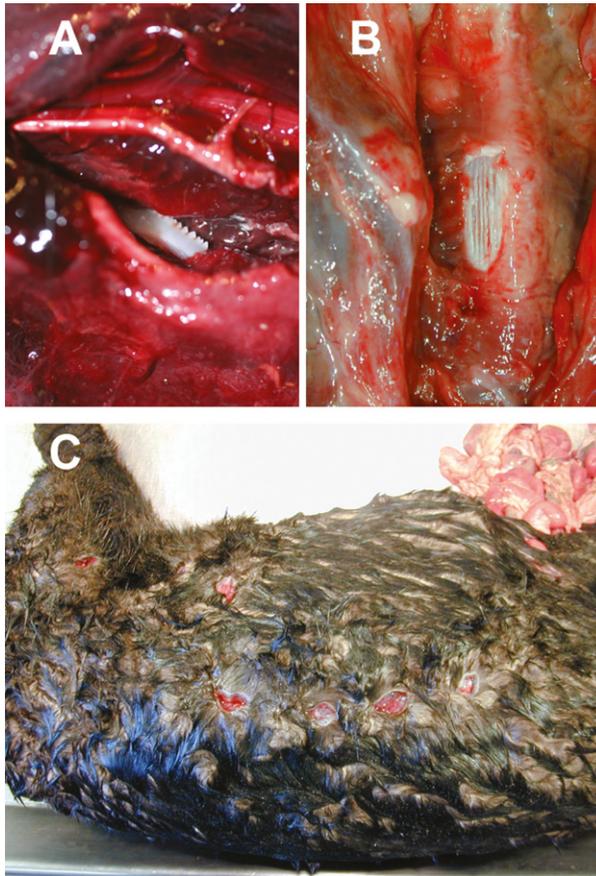


Figure 1. Photographs taken during sea otter necropsies illustrating evidence considered diagnostic of shark bites. (A) A white shark tooth fragment found in tissue associated with puncture wound (note the serrated tooth edge, a diagnostic characteristic of white shark teeth). (B) Parallel scratches found on a sea otter bone, assumed to be the result of contact with the serrated edge of a white shark tooth. (C) Abdominal region of a sea otter, showing a series of stab-like puncture wounds arranged in an arc on either side of the body, assumed to be the result of a shark bite.

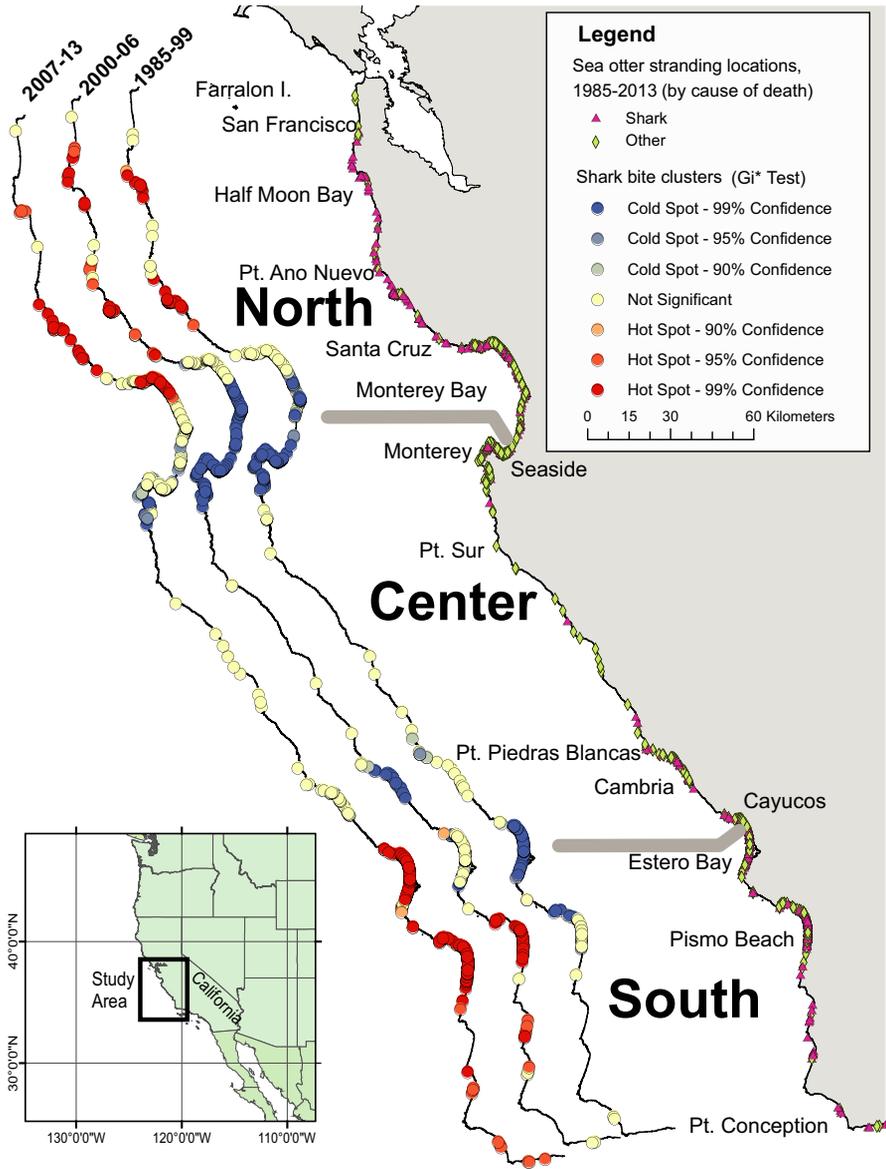


Figure 2. Map of the study area, spanning coastal regions of central California from San Francisco in the north to Point Conception in the south. Beach-cast carcass recovery locations are plotted on the coast and coded by general cause of death (shark bite related mortality or “other”). On the left side of the figure, the results of a spatial hot-spot analysis are shown for three time periods (1985–1999, 2000–2006 and 2007–2013), with significant hot spots of shark bite mortality (orange-red = higher than expected by chance) and cold spots (blue = lower than expected by chance) plotted along coastline vectors. Note that time was actually treated as a continuous variable for the hot spot analysis, but results are plotted in three discreet time periods for simplicity of interpretation.

Because this coastline includes many beaches that are used extensively for recreation by people, a relatively large proportion (40%–50%) of animals that die in the wild are recovered as beach-cast carcasses (Gerber *et al.* 2004). The systematic salvage of stranded sea otters in California was implemented in 1968 by the California Department of Fish and Wildlife (CDFW, formerly California Department of Fish and Game) and continues through the present as a collaborative effort primarily between CDFW, U.S. Geological Survey (USGS), Monterey Bay Aquarium (MBA), and The Marine Mammal Center (TMMC). The resulting data set has provided an unparalleled opportunity to keep track of the relative frequency of various causes of death, including lethal shark bite (Estes *et al.* 2003, Kreuder *et al.* 2003). Although some carcasses are too decomposed or fragmented to determine the specific cause of death, the presence or absence of major trauma (including shark bite) can be determined in almost all cases, either by field examination, minimal exam in a laboratory or comprehensive necropsy by a veterinary pathologist. White sharks have been recognized as a source of mortality ever since a fragment of a white shark tooth was found in a wound on a sea otter carcass in 1959 (Orr 1959). In an analysis of shark-bitten sea otter cases from 1968 through 1992, Ames *et al.* (1996) found that (1) frequency of bites varied by region, (2) bites were clustered in time, (3) shark bites contributed to cause of death in approximately 11% of the stranding assemblage overall, and (4) there was no apparent trend in the number of shark-bitten sea otters over this period, even though the population of sea otters was growing.

Over the past 10–15 yr the number of shark-bitten sea otters in California has increased, with shark related injuries becoming the most frequently identified primary cause of death in the assemblage of beach-cast carcasses (Miller *et al.* 2014). Here we examine this phenomenon more closely, testing for spatial, temporal, seasonal, and demographic patterns in the frequency of shark bites in stranded southern sea otters.

METHODS

Data Collection

Sea otter strandings were collected by members of the sea otter stranding network (USGS, CDFW, MBA, and TMMC) during routine beach walks and (more often) following reports by the general public and representatives of management agencies (*e.g.*, California State Parks, Municipal Harbor Patrols, County Parks, *etc.*). Stranding recovery locations cover the entire sea otter range, and although large sandy embayments (including Monterey Bay, Estero Bay, and Pismo Beach) accounted for a disproportionately large number of recovered cases, this spatial bias was essentially constant through the study period. The intensity of monitoring of some beaches has increased over time because of the establishment of programs such as snowy plover (*Charadrius alexandrinus nivosus*) monitoring (USFWS 2007) and the National Marine Sanctuary “Beach Comber” program (<http://www.sanctuarysimon.org/monterey/sections/beachCombers>). While these projects have increased the overall likelihood of carcass retrieval they have not substantially changed the spatial allocation of effort, nor is there reason to believe they would have affected the proportion of carcasses with shark bite. All beach-cast sea otters (almost all of which were dead, but also a few live animals that later died or would have died without intervention) from 1985 to 2013 are included in our analyses: we excluded data from earlier years due to smaller

sample sizes, inconsistent data records and lack of any obvious trend in shark bite frequency prior to that time (Ames *et al.* 1996).

The date, geographic location, and degree of decomposition of each recovered carcass was recorded, as well as the sex and age class. Field ages of carcasses were determined primarily by size, tooth eruption/replacement and wear, and degree of loss of pigment in the fur—mainly about the head and chest (“grizzle”), and all carcasses were classified as immature (6 mo–1.5 yr), subadults (1.5–3 yr), adults (3–10 yr) and aged-adults (>10 yr). All cases were examined or necropsied by experienced biologists or veterinarians: the level of examination was dictated by the carcass condition, with fresh cases receiving more detailed necropsies and cases in advanced stages of decomposition receiving field-level, gross necropsies. For all cases we recorded the relative amount of subcutaneous fat (absent, low, moderate, or abundant) as an index of relative body condition at time of death. Finally, all cases were examined for indication of trauma, including evidence of shark bite wounds, using the criteria established by Ames and Morejohn (1980). Sea otters that were certainly bitten by a white shark include those in which a white shark tooth fragment was found (Fig. 1a) or where scratch patterns matching the serrated edges of a white shark tooth were found on bone near a puncture wound (Fig. 1b). Sea otters that had little doubt of being bitten by a shark include those with deep stab-like wounds or lacerations associated with multiple smaller penetrating wounds indicative of a bite pattern (Fig. 1c). While we do not present detailed pathology results in this report, we note that thorough necropsies of a random subset of carcasses were conducted by veterinary pathologists, and these indicated that (1) in the vast majority of shark bite cases examined (when-ever it could be reliably determined) the bite wounds were antemortem, and thus represent encounters with living animals and not postmortem scavenging of carcasses; and (2) the shark bite wounds were a primary (or “primary-contributing”) cause of death in virtually all shark bite cases examined (Kreuder *et al.* 2003, Miller *et al.* 2014). Sea otter carcasses that were too decomposed or fragmented to reliably determine cause of death or those that were documented but not recovered (*i.e.*, all carcasses for which cause of death was assigned “unknown”) were excluded from further analysis. Small dependent pups were also excluded because recovery of pup carcasses is less reliable (they are more subject to scavenging) and because shark bitten pups were usually associated with a shark-bitten adult female (their mother) and thus did not represent independent shark bite events. Note that exclusion of these two classes was done to reduce potential biases, but it means that the resulting estimates of proportions will not be directly comparable to previous analyses where this was not done (*e.g.*, Ames *et al.* 1996). After excluding these cases, our sample size was 1,868 carcasses.

Data Analysis

We used a generalized linear model (GLM) to analyze variation in the relative frequency of shark bite occurrence in stranded sea otters. For this analysis strandings were coded as a binary response variable (1 = shark bite, 0 = no shark bite), which was related to a linear model using a logit link function (Nelder and Baker 2004). We examined a number of potential sources of variation in shark bite frequency, including temporal effects (across-year variation), geographic differences, age/sex effects and seasonal effects (within-year variation). In the case of temporal effects, previous analyses (Ames *et al.* 1996) suggested that changes might not follow a simple linear trend. Accordingly, we evaluated four different functional forms for describing

variation in shark bite frequency across years:

$$f(t) = \beta_0 + \beta_1 \cdot t(\text{linear}) \quad (1)$$

$$f(t) = \beta_0 + \beta_1 \cdot t + \beta_2 \cdot t^2(\text{quadratic}) \quad (2)$$

$$f(t) = \beta_0 + \beta_1 \cdot t + \begin{cases} 0 & \langle \text{if } t < \beta_3 \rangle \\ \beta_2 \cdot (t - \beta_3) & \langle \text{if } t \geq \beta_3 \rangle \end{cases} (\text{piecewise linear}) \quad (3)$$

$$f(t) = \beta_0 + \beta_1 \cdot t + \begin{cases} 0 & \langle \text{if } t < \beta_3 \rangle \\ \beta_2 \cdot (t - \beta_3)^2 & \langle \text{if } t \geq \beta_3 \rangle \end{cases} (\text{piecewise quadratic}) \quad (4)$$

Note that the piecewise models (Eq. 3, 4) allow for temporal trends that change abruptly at some point in time, with the temporal breakpoint itself (β_3) treated as a parameter to be fit by maximum likelihood (we evaluated all integer values between 1990 and 2008). Prior to evaluating any other effects we identified the best-supported functional form for describing temporal effects by fitting Equations 1–4 to the data (*i.e.*, using a simplified GLM) and comparing these models against each other, and against a constant model (*i.e.*, no temporal trend), using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We next accounted for geographic differences using the categorical variable "region," as previous research (Tinker *et al.* 2006) suggested that spatial variation in demography and mortality patterns in southern sea otters can be well-described by dividing the range into three regions: (1) the northern part of the sea otter's range, from Seaside north ($n = 686$); (2) the center part of the range, from Seaside to Cayucos ($n = 397$); and (3) the southern part of the range, south of Cayucos ($n = 785$; Fig. 2). Sex and age differences were also treated as categorical variables, and in the case of age class we collapsed the data to just two levels, juvenile (immature and subadult) or adult (adult and aged-adult). We also treated seasonal effects as a categorical variable, assigning each case to one of four seasons: December–February = winter, March–May = spring, June–August = summer and September–November = fall. We used bidirectional stepwise techniques (Nelder and Baker 2004) to identify the suite of factors that best described variation in shark bite frequency, evaluating sequentially alternative combinations of main effects and interactions between main effects (up to third-order interactions were considered), and the best-supported model form was selected using AIC. We initiated stepwise procedures from a variety of different candidate model forms (including fully saturated and constant-only models) to ensure consistency of results. To account for potential overdispersion of the data (recognizing that shark bite cases could potentially be clumped in space or time), we estimated and included a dispersion inflation parameter in GLM fitting procedures, thereby resulting in more conservative *P*-values and AIC statistics (Aitkin 1996).

To further examine spatiotemporal patterns of carcass recovery, we conducted a spatial cluster analysis to determine whether there were spatial "hot spots" in shark-bite strandings. Each carcass in our data set had an associated stranding location, specified as a latitude/longitude coordinate for the coastline position where the carcass was first observed (accurate to the nearest 500 m). We computed the Getis-Ord G_i^* statistic (Getis and Ord 1992) for each stranding location to determine if and where nonrandom concentrations of shark bite strandings (relative to nonshark strandings) occurred along the coast. We used inverse distance weighting for calculating

neighborhood statistics, and employed a 20 km spatial window and a 3 yr time window such that any detected hot spots (more shark-bitten carcasses relative to nonshark carcasses than expected by chance) were temporally explicit. Hot spots were identified as points in space and time with an associated $G_i^* > 2$, while cool spots (fewer shark bite strandings relative to nonshark strandings than expected by chance) were identified as points with an associated $G_i^* < -2$. We then graphically examined how the spatial distribution of hot or cool spots changed over time.

Finally, we conducted analyses aimed at evaluating two possible artifactual explanations for the apparent increase in shark bite frequency. First, over the course of the study period there have been changes in sea otter population size (USGS-WERC 2014) and also in the likelihood that stranded otters are found and picked up, due to increased utilization of California beaches by people (Crossett *et al.* 2004). One or both of these changes could theoretically lead to an apparent increase in the relative frequency of shark bite cases, even if *per capita* shark bite risk remained unchanged. For example, this could occur if other types of strandings decreased relative to population size. To evaluate this possibility, we estimated and compared indices of *per capita* stranding rates by dividing the annual number of shark bite cases and nonshark cases by the running 3 yr average number of otters counted during annual range-wide surveys of the California population (Estes *et al.* 2003, USGS-WERC 2014). Note that these values represent indices, rather than true *per capita* mortality rates, because (1) the range-wide sea otter census produces uncorrected total counts, rather than true estimates of abundance; and (2) it has been estimated that less than 50% of animals that die in the wild are recovered as beach-cast carcasses (Gerber *et al.* 2004). We used two-way ANOVA to test whether trends in *per capita* indices differed for shark-bite *vs.* nonshark-bite strandings: specifically, we grouped the data into three time periods, 1985–2003, 2004–2008, 2009–2013 (these divisions were selected for consistency with the best-fit temporal trend identified by GLM analysis, as described above), and tested for an interaction between stranding type and time period. Because the response variable represented a proportion (annual number of strandings/annual counted otters), we used an arc-sine square root transformation to improve normality, and we confirmed that transformed data met assumptions of normality and homogeneity of variance by graphical examination of residuals.

Secondly, we examined the possibility that an apparent increase in shark-bite cases might actually reflect an increase in the number of sick or moribund otters in the population at large, as moribund animals could be at greater risk for shark bite. If this explanation was true, we would expect shark-bite cases to be in relatively poor body condition at time of death. Conversely, if shark-bitten sea otters represent a representative sample of the living population, we would expect them to generally be in better body condition than otters dying of other causes (as most “other” cases involve disease and/or emaciation; Kreuder *et al.* 2003). We created a two-way cross-tabulation of stranding type (shark bite or nonshark) *vs.* body condition at time of death (“poor” = low or no subcutaneous fat, “good” = moderate to high subcutaneous fat) and used Fisher’s exact test to determine whether these two factors were independent, or whether shark-bite cases were more or less likely to be in poor condition.

All analyses were conducted and statistics computed using the MATLAB programming language (Mathworks Inc., Natick, MA) and MATLAB statistics toolbox, with the exception of the spatial cluster analysis which was conducted using ArcGIS Spatial Statistics toolbox (Esri Inc., Redlands, CA). For the GLM we report *t*-statistics and *P*-values for individual effects included in the final model, as well as odds ratios (and associated 95% confidence intervals, OR₉₅) where appropriate. In the case of the

ANOVA test we report F -statistics and P -values, while for the Fisher's exact test we report the P -value and the interaction odds ratio in the case of a significant result. All tests were considered significant at $\alpha = 0.05$, and any estimated ranges reported within parentheses represent 95% confidence intervals, unless indicated otherwise. Detailed results from the GLM analysis are presented in Table S1, and tabulations of the raw data are provided in Table S2.

RESULTS

There has been a significant increase in the number of shark-bitten sea otters in California over the past 29 yr (Fig. 3), with temporal trends best described by a piecewise quadratic model (Eq. 4; Fig. S1). The results of the GLM indicate an accelerating increase in the relative frequency of shark bite cases beginning after 2003 ($t = 3.42$, $P < 0.001$), as well as regional differences and interactions between temporal and regional effects (see Table S1 for more extensive GLM statistics). While an increase in shark-bite frequency has occurred in all three regions, the effect has been greatest in the southern region ($t = 4.71$, $P < 0.001$; Fig. 4, 5). The estimated range-wide probability that a stranded otter is shark bitten has tripled from 19% in 1990 (10.6%–30.6%) to 61% in 2013 (44.7%–75.5%), but in the southern region there has been an eightfold increase from 8% in 1990 (3.6%–16.9%) to 68% in 2013 (54.1%–79.9%). A graphical examination of the geographical distribution of hot-spots in shark bite frequency (Fig. 2) further illustrates how spatial trends varied over time: prior to 2000 there was a consistent hot spot for shark bite carcasses between Santa Cruz and Half Moon Bay in the north, but no other significant clusters, and in fact “cold spots” occurred along the south side of Monterey Bay and in the vicinity of Estero Bay. However, between 2000 and 2006 a second hot spot emerged near Pismo Beach in the south, and by 2007–2013 this southern hot spot had spread as far up-coast as Cayucos and as far down-coast as Point Conception, while the northern hot spot had expanded down-coast to include the northern portion of Monterey Bay (Fig. 2).

The best-fit GLM also indicated that there were differences in shark bite probability associated with age/sex class (Fig. 4) and season (Fig. 5), as well as interactions between age-region, sex-region, season-region, and season-time (Table S1). Stranded adult males were 1.9 times more likely to be shark-bitten than other age/sex classes ($OR_{95} = 1.2$ – 3.2 , $t = 2.64$, $P = 0.008$), and in the central portion of the range stranded adults were 2.3 times more likely to be shark-bitten than juveniles ($OR_{95} = 1.0$ – 4.5 , $t = 2.05$, $P = 0.040$) and stranded males were 4.4 times more likely to be shark-bitten than females ($OR_{95} = 2.1$ – 9.2 , $t = 3.97$, $P < 0.001$; Fig. 4). The highest frequency of shark-bite strandings occurred in the fall (Fig. 5), approximately 4.2 times higher than the spring when the frequency was lowest ($OR_{95} = 2.4$ – 7.4 , $t = 5.05$, $P < 0.001$), while in summer and winter seasons the frequency of shark bite cases was intermediate. In the central region these seasonal differences were less evident (Fig. 5b), while in the southern region the elevated fall-time risk was especially dramatic (Fig. 5c). Since 2003 there has been a sharp increase in shark-bite frequency in all seasons, but a more rapid increase in summer and winter has resulted in less pronounced seasonality over the most recent 5 yr, with the winter-time frequency becoming equivalent to fall-time frequency in the northern and southern regions (Fig. 5a, 5c).

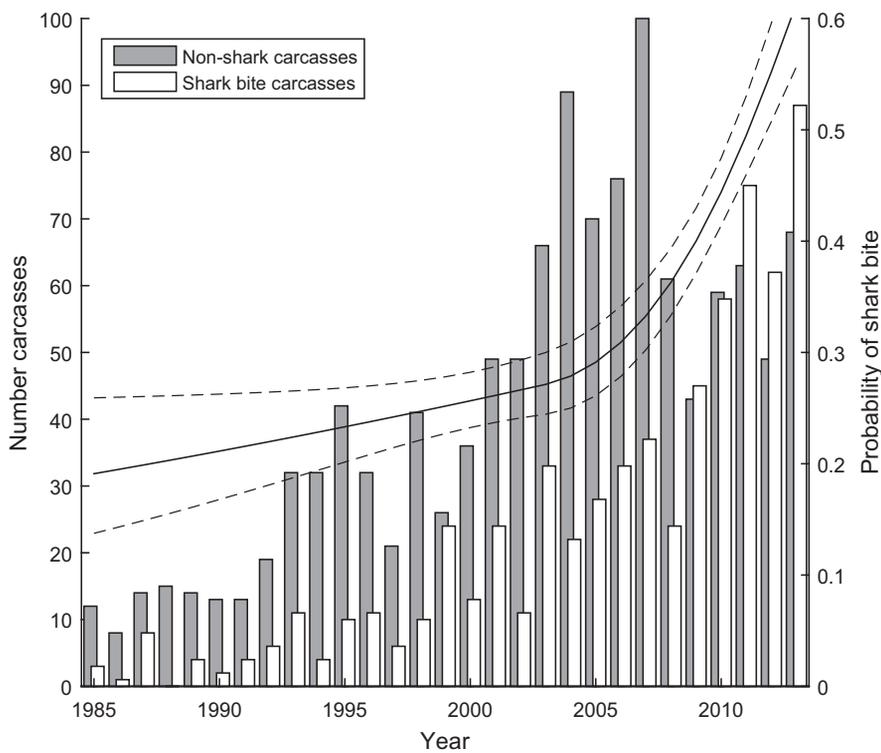


Figure 3. The number of sea otter carcasses with shark bite wounds (white bars) and without shark bite wounds (shaded bars) recovered annually between 1985 and 2013 (left-hand vertical axis). Also shown is the estimated annual probability that a recovered carcass has shark bite wounds (solid line, right-hand vertical axis), as predicted by a generalized linear model (GLM) having a piecewise polynomial time function (see text for details). The 95% confidence bounds around estimated annual values are plotted as dashed lines.

The *per capita* stranding rate index has increased over time for both shark-bite and nonshark-bite cases ($F = 32.18$, $P < 0.001$); however, there was an interaction between stranding type and time period ($F = 7.9$, $P = 0.001$) such that the proportional increase was 3.3 times greater for shark-bite strandings (Fig. 6). We also found that sea otter body condition at time of death was not independent from the occurrence of shark bite (Fisher's exact test $P < 0.001$), but rather shark bite cases were approximately 5 times more likely to be in good condition ($OR_{95} = 3.8-5.9$) than were nonshark-bite cases.

DISCUSSION

Our analysis of 29 yr of sea otter stranding data indicates a striking increase in the frequency of white shark bites on sea otters, a trend that has accelerated over the past 10 yr (Fig. 3-5). While the area at the northern end of the sea otter's range has long been an area with high sea otter mortality from shark bites (a pattern that has been assumed to be caused by proximity to the white shark aggregation area at Point Año

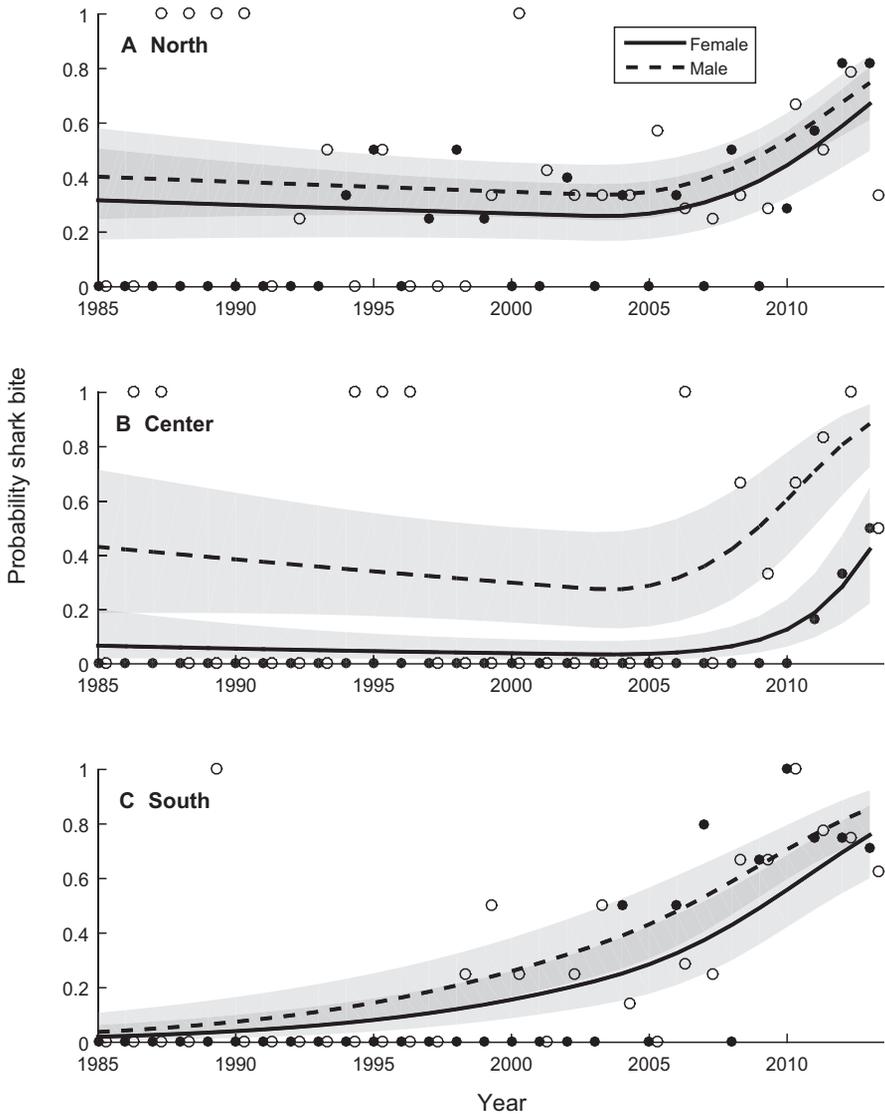


Figure 4. Trends in the sex-specific probabilities that stranded sea otters are shark bitten. Mean estimated values are plotted by region for adult females (solid lines) and adult males (dashed lines), as predicted by a generalized linear model (GLM), and the associated 95% confidence bounds are shown as gray-shaded polygons around each trend line. Raw data summaries for each year are also plotted as filled circles (females) and open circles (males) representing the actual proportion of collected carcasses having shark bite for the indicated region and age/sex class.

Nuevo; Ames *et al.* 1996), the most dramatic increase has occurred in the southern part of the sea otter's range in California (especially in the Estero Bay and Pismo Beach areas). The northern Monterey Bay area has also seen a sharp uptick (Fig. 2).

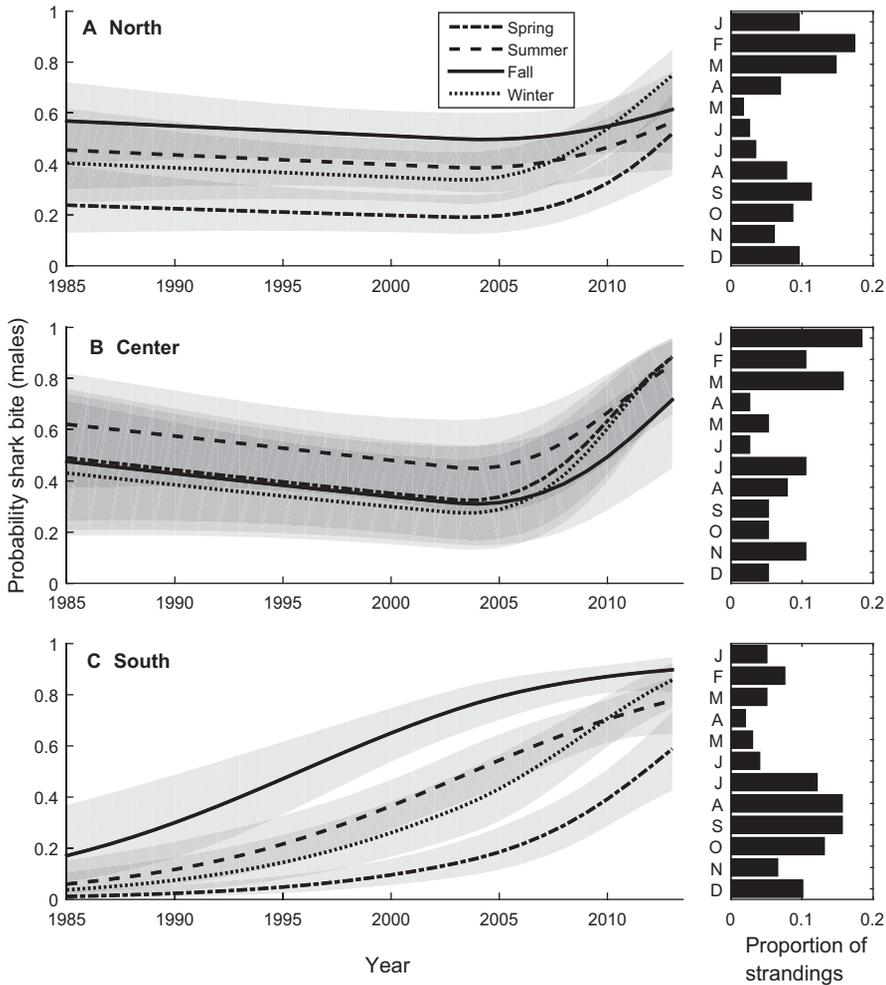


Figure 5. Trends in the seasonal probabilities that stranded sea otters are shark bitten. Mean estimated values are plotted by region and by season, as predicted by a generalized linear model (GLM), and the associated 95% confidence bounds are shown as gray-shaded polygons around each trend line (note that for simplicity we just show predicted values for adult males, however similar regional/seasonal trends were predicted for other age/sex classes; see Table S1 for details). To further illustrate recent seasonal variation in shark bite frequency, horizontal bars plotted to the right of each panel show the total proportion of shark-bite carcasses recovered during each month of the year for that region over the last 5 yr (2009–2013).

The seasonal peak in the frequency of bites in the fall has broadened such that the increase in shark bite strandings starts earlier in late summer and extends through the winter. All of these findings would be consistent with an increase in the occurrence of white sharks in the nearshore waters used by sea otters, particularly at the south end of the sea otter's range.

Based on indirect evidence (movements of adult female sharks and incidental catch of very young sharks), the nearshore waters of southern California and northern Baja

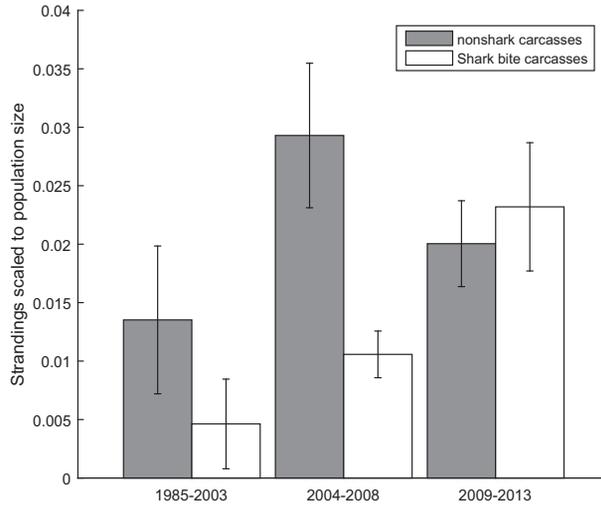


Figure 6. Variation over time in stranding rates for sea otters with and without shark bite, rescaled relative to population abundance. *Per capita* indices for each type of stranding were calculated by dividing the number of strandings by the 3 yr average range-wide population count (see text for details). Analysis of Variance (ANOVA) indicated that the *per capita* index for non-shark cases increased between the first and second time periods, but did not change significantly between the second and third periods, whereas the index for shark bite cases increased significantly across all three time periods.

California are assumed to be a nursery area for white sharks (Domeier and Nasby-Lucas 2012, Lowe *et al.* 2012, Lyons *et al.* 2013). There are indications that the northeast Pacific population of white sharks may be increasing, possibly due to restrictions placed on fisheries that incidentally catch white sharks and legislation that directly protects the species (Lowe *et al.* 2012, Lyons *et al.* 2013). Juvenile and subadult white sharks begin to range north from nursery areas into colder waters at about 3–7 yr of age (Klimley 1985, Domeier 2012), although recent evidence suggests that growth may be very slow in white sharks and sexual maturity may occur much later (Natanson and Skomal 2015). Concurrent with this shift in distribution, subadult sharks are believed to shift their primary diet from fish to marine mammals (Klimley 1985, Kim *et al.* 2012). If juvenile white shark mortality has declined due to changes in fisheries management, and more subadult white sharks are surviving and moving north into the sea otter's range, more “investigatory” encounters with sea otters would be expected. Consistent with this interpretation, a recent reevaluation of white shark population status also suggests white sharks are increasing within the sea otter's range (Burgess *et al.* 2014).

Another potential explanation of the recent increase in shark-bitten sea otters (not mutually exclusive of a population increase in white sharks) is that sharks are spending more time feeding in the nearshore waters used by sea otters. An inshore shift in shark habitat use might be expected if their preferred marine mammal prey (pinnipeds) were becoming more abundant in these same waters (Skomal *et al.* 2012). And indeed, northern elephant seals, California sea lions, and Pacific harbor seals have all experienced population increases over the period covered in this report (Carretta *et al.* 2011, Lowry *et al.* 2014). The most significant of these trends (in terms of pre-

ferred white shark prey biomass within or near the range of southern sea otters) has been the northern elephant seal, whose increase is associated with the establishment of a new breeding colony at Point Piedras Blancas (Fig. 2). This rookery became established in the early 1990s and is now approximately twice the size of the elephant seal colony at Año Nuevo Island and mainland combined (Lowry *et al.* 2014). The exponential increase in elephant seals at Point Piedras Blancas parallels closely the increase in shark-bitten sea otters in areas just to the south of this rookery (Fig. 3); however, it is also worth noting that few shark-bitten sea otters are found stranded in the immediate vicinity of the rookery (Fig. 2). Opportunistic observations of the proportion of elephant seals with fresh shark bite wounds have also failed to show an increase in white shark feeding behavior near the Piedras Blancas colony (BBH, personal observation). There is considerably more surface kelp canopy around Pt. Piedras Blancas than exists near Pt. Año Nuevo, and it is possible that kelp forest habitats near the colony reduce the effectiveness of white shark hunting behavior (Wcisel *et al.* 2014). Regardless, the increased number of elephant seals in the region overall (as well as greater numbers of sea lions and harbor seals) represents a substantial augmentation of white shark prey, perhaps sufficient to drive a shift in shark feeding behavior, distribution, and habitat use.

A close examination of the spatial distribution of shark-bitten sea otter strandings (Fig. 2) reveals three new emerging hot spots for shark bite: northern Monterey Bay, Estero Bay, and Pismo Beach. All three of these areas represent large, sand-bottom embayments having shallow bathymetric profiles and little or no surface canopy-forming kelp, and support relatively dense concentrations of sea otters that tend to rest and feed as much as several kilometers off shore (USGS-WERC 2014). White sharks use visual cues to ambush their prey and are believed to see the silhouette of their prey from below (Martin and Hammerschlag 2011), which would presumably make it more difficult for them to distinguish prey in the kelp canopy. There is strong evidence that kelp canopy does provide a refuge from white sharks for Cape fur seals in South Africa (Wcisel *et al.* 2014), and bite statistics on humans appear to corroborate this (Miller and Collier 1980, Lea and Miller 1984, Collier 1992). Thus, it might be expected that sea otters in these open water habitats are more vulnerable to shark bites, while areas with dense surface kelp canopies may represent a partial refuge from white shark encounters. Such a pattern could explain the lower rates of shark-bitten otters (particularly females) in the central portions of the otter's range (Fig. 2), a region which is dominated by rocky habitats and where sea otters tend to utilize thick kelp canopies for both resting and feeding behavior (Riedman and Estes 1990).

In addition to the shifts in spatial distribution of shark bite strandings, there has also been a change in the seasonality of shark bites. Prior to 2000, most shark bites on sea otters occurred in late summer and fall months (Fig. 5), which corresponds well to the time when adult white sharks are thought to be returning to the mainland coast from their offshore pelagic migrations to an area approximately half way between Baja California and the Hawaiian Islands (Boustany *et al.* 2002, Weng *et al.* 2007, Domeier and Nasby-Lucas 2008, Nasby-Lucas *et al.* 2009, Jorgensen *et al.* 2010, Domeier and Nasby-Lucas 2012). However in recent years the period of elevated sea otter shark bite mortality has broadened to include winter and even early spring (Fig. 5). This seasonal trend is not entirely consistent with the timing of the adult white shark offshore migration, but would be consistent with an increase in the number of juvenile and subadult sharks—and possibly nonaggregating and transient sharks—remaining within coastal waters during this time period (Burgess *et al.* 2014).

Current evidence remains most consistent with shark-bites on sea otters being caused by white sharks alone, and not by other shark species (Ames and Morejohn 1980). While we cannot rule out the possibility of multiple shark species contributing to this phenomenon, we believe that we would occasionally find tooth fragments from sharks other than white sharks in the wounds of stranded sea otters if this were the case. Perhaps the most perplexing aspect of this phenomenon is that there remains no evidence that white sharks ever actually consume the sea otters they have bitten. It is possible that occasional consumption of an otter by a shark would go undetected (since a completely consumed sea otter would leave no physical record); however, we believe such events are rare based on the lack of even partial consumption of any of the 656 shark-bitten otters examined. Considering the severity of the bite(s) on many of the recovered otters, it is difficult to imagine how these animals could have escaped predation, if consumption was indeed the intent of the predator. Possible explanations for nonconsumptive biting of sea otters by sharks include mistaken identity or investigatory bites, as well as lack of palatability of sea otters (*i.e.*, bad taste, too much/dense fur, or the lack of a substantial blubber layer). Nonconsumptive biting of nonprey species by white sharks has been documented elsewhere, including biting of sea birds (Hammerschlag *et al.* 2012), however, this is the first case we are aware of where the magnitude of such encounters represents a major source of mortality for a nonprey species.

The rate at which shark-bitten sea otters are stranding has increased sharply relative to population abundance, far more so than have strandings due to all other causes (Fig. 6). This fact argues against the possibility that a change in the relative frequency of shark-bitten otters is an artifactual outcome of increased carcass recovery efforts, or of decreased *per capita* mortality due to other factors. Indeed, mortality due to other causes appears to have increased over this period as well (Fig. 6), particularly mortality associated with density-dependent nutritional stress in the range center (Thometz *et al.* 2014). This pattern likely explains our unexpected findings of lower shark-bite risk for females and younger animals in the central region (Fig. 4): this may not be a case of females and younger animals being less likely to be bitten by a shark, but rather a case of them being more likely to die of other factors, including disease and emaciation (Kreuder *et al.* 2003). Although there is no doubt that some shark-bite cases represent animals whose cause of death included factors other than shark bite (in which case the shark bite might simply have accelerated a mortality process already underway; Miller *et al.* 2014), our results suggest this is not the case for the majority of shark bite strandings. In particular, the fact that shark-bitten animals were substantially more likely to be in good body condition than were stranded animals without shark bite indicates that most shark bite cases are not sick or moribund animals, but rather are representative samples of the population at large.

A number of lines of evidence indicate that sea otters are at carrying capacity throughout the center portion of their range (Laidre *et al.* 2001, Tinker *et al.* 2008, Thometz *et al.* 2014), and thus range expansion and growth at the northern and southern peripheries of the range will be critical for further recovery (USFWS 2012). Unfortunately, the range peripheries are the very areas where the recent increase in shark mortality has been greatest. This pattern could potentially have negative repercussions for sea otter conservation, but there may also be positive implications: because the sea otter stranding data set represents a long time series with large sample size and broad geographic distribution, it may provide a valuable index for assessing changes in the frequency of white shark activity and potential risk for humans (West 2011). Further work is needed to more rigorously assess the implications of this trend

for southern sea otter population viability, and to better understand white shark population dynamics, habitat use patterns, and predation behavior.

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Figure S1. Results of model comparisons of generalized linear models (GLM) having four different function-forms for temporal variation in shark bite frequency.

Table S1. Generalized linear regression model.

Table S2. Stranding data for sea otters, 1985–2013.