NRC Research Press

ARTICLE

Model selection and multimodel inference for standardizing catch rates of bycatch species: a case study of oceanic whitetip shark in the Hawaii-based longline fishery

Jon Brodziak and William A. Walsh

Abstract: One key issue for standardizing catch per unit effort (CPUE) of bycatch species is how to model observations of zero catch per fishing operation. Typically, the fraction of zero catches is high, and catch counts may be overdispersed. In this study, we develop a model selection and multimodel inference approach to standardize CPUE in a case study of oceanic whitetip shark (*Carcharhinus longimanus*) bycatch in the Hawaii-based pelagic longline fishery. Alternative hypotheses for shark catch per longline set were characterized by the variance to mean ratio of the count distribution. Zero-inflated and non-inflated Poisson, negative binomial, and delta-gamma models were fit to fishery observer data using stepwise variable selection. Alternative hypotheses were compared using multimodel inference. Results from the best-fitting zero-inflated negative binomial model showed that standardized CPUE of oceanic whitetip sharks decreased by about 90% during 1995–2010 because of increased zero catch sets and decreased CPUE on sets with positive catch. Our model selection approach provides an objective way to address the question of how to treat zero catches when analyzing bycatch CPUE.

Résumé : Un des grands défis associés à la normalisation des captures par unité d'effort (CPUE) des espèces constituant des prises accessoires est la modélisation des observations de prises nulles par activité de pêche. La proportion de prises nulles est typiquement élevée et les nombres de prises peuvent s'avérer surdispersés. Nous avons mis au point une approche de sélection de modèle et d'inférence multi-modèle pour la normalisation des CPUE dans une étude de cas des prises accessoires de requins à longues nageoires (*Carcharhinus longimanus*) dans la pêche pélagique à la palangre basée à Hawaii. Différentes hypothèses concernant les prises de requins par palangre ont été caractérisées à l'aide du rapport de la variance à la moyenne de la distribution des nombres. Différents modèles, de Poisson avec et sans inflation de zéros, binomial négatif et delta-gamma, ont été ajustés à des données de pêche recueillies par des observateurs en utilisation la sélection de variables pas à pas. L'inférence multi-modèle a été utilisée pour comparer les différentes hypothèses. Les résultats du modèle binomial négatif avec inflation de zéros, celui qui colle le mieux aux données, montrent que les CPUE normalisées de requins à longues nageoires ont diminué d'environ 90 % de 1995 à 2010 en raison de l'augmentation des palangres avec prises nulles et de la diminution des CPUE de palangres avec prises positives. Notre approche de sélection de modèle constitue une façon objective d'aborder la question du traitement des prises nulles dans l'analyse des CPUE de prises accessoires. [Traduit par la Rédaction]

Introduction

Trends in the relative abundance of oceanic pelagic sharks are often inferred from time series of standardized catch rates (Maunder and Punt 2004; Camhi et al. 2008*a*; Clarke et al. 2013). Typically, shark catch rates are standardized using generalized linear models (GLMs), with the time series of year effect coefficients or predicted catch per unit effort (CPUE) interpreted as indices of relative abundance (Maunder and Punt 2004; Camhi et al. 2008*a*; Aires-da-Silva et al. 2008; Baum and Blanchard 2010). Standardized catch rates are used to estimate trends in relative shark abundance because most fishing nations do not conduct fishery-independent surveys for sharks and have not historically allocated resources needed for detailed stock assessments of nontarget species such as sharks (Camhi et al. 2008*a*; Stevens 2010).

Standardizing catch rates of oceanic pelagic sharks can itself prove challenging for several reasons. The first problem is underreporting of catches. In large-scale terms, this reflects a lack of shark catch reporting requirements among many fishing nations, presently or in the past (Clarke 2008; Dulvy et al. 2008; Stevens 2010). Even on a much smaller scale, significant underreporting of blue shark (*Prionace glauca*) bycatch[1] (Walsh et al. 2002) was documented in the logbook data from the Hawaii-based pelagic longline fishery despite virtually optimal monitoring circumstances (Walsh et al. 2005, 2007). A second, related problem is that shark catches may be pooled and not reported in species-specific formats (Dulvy et al. 2008; Stevens 2010), or they may be reported in vague categories (e.g., "large", "small") that preclude estimation of catch rates of individual species (Camhi et al. 2008*b*). Third, the effects of directive factors (sensu Fry 1971), such as thermocline depth, can differ between nontargeted sharks and targeted teleost species and result in vastly different catchabilities for nontarget and targeted species with longline gear.

Received 22 February 2013. Accepted 18 August 2013.

Paper handled by Associate Editor Ray Hilborn.

J. Brodziak. NOAA Fisheries, Pacific Islands Fisheries Science Center, Honolulu, HI 96822, USA.
W.A. Walsh. University of Hawaii, Joint Institute for Marine and Atmospheric Research, Pacific Islands Fisheries Science Center, Honolulu, HI 96822, USA.
Corresponding author: Jon Brodziak (e-mail: jon.brodziak@noaa.gov).

[1]We define bycatch as "discarded catch of any living marine resource plus retained incidental catch and unobserved mortality due to a direct encounter with fishing gear", which is consistent with the NOAA Fisheries National Bycatch Reduction Strategy but differs from the definition stated in the Magnuson–Stevens Fishery Conservation and Management Act.

As a result of these and possibly other factors, longline fishery data often contain a high percentage of zero catch observations for shark species (Maunder and Punt 2004; Minami et al. 2007; Tavares et al. 2012). The expected high percentage of zero catch observations may require special data evaluation (Nakano and Clarke 2006) and modeling techniques for standardizing shark rates (Maunder and Punt 2004). One important feature in this context is that the catch observations may include more zero observations than would be expected under a standard catch count distribution, such as the Poisson distribution. Such "extra" zero catches could be attributable to reporting error or misidentifications, survey error (in which sharks were present at the site of a longline set but were not observed because the gear deployment did not overlap with the depth distribution of sharks or did not attract sharks), or both. In what follows, we describe alternative models for standardizing shark CPUE, including zero-inflated models to account for extra zeros, and we also show how one can generally evaluate alternative models for handling zero catch observations of bycatch species.

In this paper, we develop GLM analyses to standardize catch rates for bycatch species and apply model selection and multimodel inference to account for structural uncertainty in the treatment of zero catch observations. We begin by providing some background for the fishery data of oceanic whitetip shark (*Carcharhinus longimanus*) catches in the Hawaii-based pelagic longline fishery. We then use a large, high-quality data set collected by fishery observers, in which under-reporting was not expected to be substantial, to achieve two goals. The first goal was to develop a candidate set of alternative standardized CPUE time series as potential relative abundance indices for oceanic whitetip shark in this fishery, because nominal values were judged insufficient for stock assessment and fishery management purposes (Walsh et al. 2009). The second goal was to apply multimodel inference to the problem of model selection for the CPUE standardization of a bycatch species using oceanic whitetip shark as a case study. In general, this paper shows how multimodel inference can be applied to CPUE standardization of bycatch species, where the quality of data may be more problematic than for typical CPUE standardization approaches applied to target species.

We also compare these results with recent findings from the western and central Pacific Ocean (Rice and Harley 2012; Clarke et al. 2013). This species was designated as a high priority for assessment by the Scientific Committee of the Western and Central Pacific Fisheries Commission (WCPFC) (Clarke and Harley 2010; Clarke et al. 2011). In response, a stock assessment was recently conducted under WCPFC auspices, and it was concluded that the stock was overfished and was experiencing overfishing (Rice and Harley 2012). Clarke et al. (2013) also documented declines in standardized catch rates and sizes of oceanic whitetip sharks across a very broad expanse of the Pacific Ocean.

Methods

Data sources

Catch and operational data were collected by Pacific Islands Regional Observer Program (PIROP) observers aboard Hawaii-based longline vessels on 3524 commercial fishing trips that deployed 47 140 longline sets over a 16-year period (1995–2010). Observer protocols for tallying catches and recording operational details are in the field manual published by the NOAA Fisheries Pacific Islands Regional Office (2011).

PIROP was established in 1994 and has since become the largest national pelagic longline observer program in the Pacific Ocean (Walsh et al. 2009). The observers record species-specific catch tallies from each longline set, along with a large suite of operational details. After returning to port, they are debriefed and their records thoroughly checked. As a result, concerns regarding catch data accuracy and underreporting are minimized, opportunities for exploratory analyses of operational parameters are maximized, and within-species trends are estimable.

Shark catches in the fishery

Observer data were used to describe shark catches in the Hawaii-based pelagic longline fishery for 1995–2006 (Walsh et al. 2009). The shark catch included at least 20 species from 11 genera in seven families from three orders and constituted about 16% of the total observed catch in numbers. Oceanic whitetip shark was common, comprising 3% of the shark catch, but it was unknown whether the CPUE values were an accurate measure of the relative abundance of oceanic whitetip sharks owing to the high frequency of zero catch counts (Walsh et al. 2009).

Empirical patterns in the fishery

Summaries of the PIROP data were made to provide an empirical description of the nominal fishery data. Summaries of the catch counts and CPUE of oceanic whitetip shark by fishery sector (deep set and shallow set) and fishing region provide an overview of the spatial distribution of the species in the western and central North Pacific Ocean. Oceanic whitetip shark catches and nominal mean CPUE were depicted using nonconfidential data[2] aggregated on 5° × 5° squares. Temporal trends in nominal CPUE and percentage of sets with zero catch by fishery sector were also summarized to show the empirical patterns in the observed data.

Alternative hypotheses for capture probabilities

We evaluated five alternative hypotheses for the catch response variable, which was the count of oceanic whitetip shark reported to be captured per hook in a set. These were formulated as probability of capture models, which reflected alternative hypotheses about whether the spatial distribution of sharks was more uniform or more clumped throughout the fishing area. The alternative hypotheses also described how zero catch observations were generated from the longline capture process for oceanic whitetip shark. The response variable for these models was a count of the catch of a bycatch species per set, which was typically zero but occasionally included catches of a few to many oceanic whitetip sharks (Walsh et al. 2009). Four of the alternative distributions were count processes (Table 1; Appendix A); these were the Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial (Zuur et al. 2009). Of these, the Poisson distributions represented more uniformly distributed shark catches, while the negative binomial distributions represented an overdispersed, or more clumped, distribution of shark catches. We also investigated models that could account for higher than expected zero catches because of observation or sampling errors that occur during data collection (Martin et al. 2005; Zuur et al. 2009). In particular, zero-inflated models were applied to account for the potential that there were more zeros than expected under a Poisson or negative binomial distribution. In this context, if there were sharks present, then the number of sharks captured would be a random process depending on the depth distribution of the sharks, the depth distribution of the fishing gear, and other characteristics of the fishing process. Captured sharks may also be misreported or misidentified as well, and it is the combination of all processes leading to extra zero observations that produces the zero-inflated component.

We also considered a non-count distribution, the delta-gamma (Table 1; Appendix A), as the fifth alternative for which there was

[2]Confidentiality requirements were met by pooling the data from all years and then plotting data from those 5° × 5° squares where ≥3 permitted vessels fished during the study period. This required removal of 0.2% of the data.

Table 1. Alternative hypotheses about the capture probability of ocean whitetip shark catch (C) for CPUE standardization in the Hawaii-based longline fishery, including the probability mass or density function for catch, the expected value ($E(C)$), the variance ($\mathrm{Var}(C)$), and the variance to mean ratio (VMR) for the Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial, and delta-gamma distributions, where π is the probability of an extra zero catch per set, p is the probability of a positive catch per set, and μ, k, and λ are parameters (see Appendix A).

Alternative hypothesis	Probability function	Expected value	Variance	Variance to mean ratio
Poisson	$\Pr(C=c)=\dfrac{\mu^c\cdot\exp(-\mu)}{c!}$	μ	μ	1
Negative binomial	$\Pr(C=c)=\dfrac{(c+k)!}{k!(c+1)!}\left(\dfrac{k}{k+\mu}\right)^k\left(\dfrac{\mu}{k+\mu}\right)^c$	μ	$\mu+\dfrac{\mu^2}{k}$	$1+\dfrac{\mu}{k}$
Zero-inflated Poisson	$\Pr(C=0)=\pi+(1-\pi)\exp(-\mu)$	$(1-\pi)\mu$	$(1-\pi)(\mu+\pi\mu^2)$	$1+\pi\mu$
	$\Pr(C=c\mid c>0)=(1-\pi)\dfrac{\mu^c\cdot\exp(-\mu)}{c!}$			
Zero-inflated negative binomial	$\Pr(C=0)=\pi+(1-\pi)\left(\dfrac{k}{k+\mu}\right)^k$	$(1-\pi)\mu$	$(1-\pi)\left(\mu+\dfrac{\mu^2}{k}\right)+\mu^2(\pi+\pi^2)$	$1+\dfrac{\mu}{k}+\dfrac{\mu\pi(1+\pi)}{(1-\pi)}$
	$\Pr(C=c\mid c>0)=(1-\pi)\dfrac{(c+k)!}{k!(c+1)!}\left(\dfrac{k}{k+\mu}\right)^k\left(\dfrac{\mu}{k+\mu}\right)^c$			
Delta-gamma	$\Pr(C=0)=1-p$	$p\cdot\dfrac{k}{\lambda}$	$p^2\cdot\dfrac{k}{\lambda^2}$	$\dfrac{p}{\lambda}$
	$\Pr(C=c\mid c>0)=p\cdot\dfrac{\lambda^k c^{k-1}\cdot\exp(-\lambda c)}{\Gamma(k)}$			

a binomial distribution for the probability of observing a positive catch and a gamma distribution to describe the positive catch data (cf., Aitchison 1955). Last, we also included a comparative analysis of the delta-lognormal (Appendix A; Pennington 1983), another non-count distribution, because it is commonly used to standardize CPUE for some target fisheries (Lynch et al. 2012) and fishery research surveys (Stefánsson 1996) and has been used with blue sharks (Tavares et al. 2012). A more detailed description of each of the probability distributions used to model the capture of oceanic whitetip shark is provided in Appendix A.

CPUE standardization models

We used a stepwise variable selection approach (Chambers and Hastie 1993) to choose the explanatory variables for each CPUE standardization hypothesis. Six variables were used to standardize CPUE under the alternative hypotheses: year, quarter, region, set type, sea surface temperature (SST), and hooks deployed per set (H). The relative importance of each explanatory variable was assessed in terms of reductions of the null deviance and deviance reductions per degree of freedom. Stepwise model selection was applied with sequential χ^2 tests to determine the significance of a set of explanatory variables under each alternative hypothesis. Sample sizes were large, and as a result, we expected that some explanatory variables would be statistically significant but of little practical importance. Therefore, we required that the amount of deviance that an explanatory variable accounted for ($D_{\mathrm{explained}}$) be at least one-tenth of a percent of the null deviance (D_{null}) or Akaike information criterion (AIC) to be included in a GLM ($D_{\mathrm{explained}} \geq 0.001D_{\mathrm{null}}$; cf., Maunder and Punt 2004). Similarly, a reduction in the AIC was required to retain an explanatory variable in a GLM. Interactions were not included because the number of empty factor combinations was considered excessive (Searle 1987); in particular, the deep-set sector did not operate in the northerly Regions 7 and 8, the shallow-set sector did not operate in the southerly Regions 1 and 2, and the shallow-set sector was effectively closed during 2001–2004 under court order to reduce fishery interactions with protected sea turtles.

Explanatory factor variables tested for significance[3] were time (year and quarter), fishing region[4], and set type (i.e., deep-set or shallow-set). Year and quarter were chosen to be the initial entries into each GLM because estimating temporal changes in standardized CPUE was the focus of this study. Eight regions were defined by 10° latitudinal increments and a longitudinal separation at 160°W. The set types correspond to the two sectors of this fishery as defined in the Federal Register (Department of Commerce 2004). Deep sets use at least 15 hooks per float, whereas shallow sets use less than 15 hooks per float. Also, longline gear is typically deployed near dawn on deep sets but is deployed after dusk on shallow sets, about twice as many hooks are used on deep as on shallow sets, and the deep-set target depth generally exceeds that for shallow sets by over 100 m.

SST was used to represent a habitat temperature preference index for oceanic whitetip shark. The SST variable was a continuous explanatory variable that was tested as a linear, quadratic, or cubic polynomial as an indicator of habitat preference. The SST values were weekly means measured by an advanced, very high resolution radiometer borne by a NOAA satellite, as in Walsh et al. (2005, 2007)[5].

GLMs were fitted to standardize catch rates (counts per set) for oceanic whitetip sharks using methods described in Crawley (2007) and Zeileis et al. (2008). Examples of the Poisson analyses can be found in Crawley (2007), and examples of the negative binomial and zero-inflated analyses can be found in Zuur et al.

[3]Two additional factor variables, five bait and six hook types, were tested in preliminary analyses but did not meet the criteria for inclusion as explanatory variables.

[4]Region 1: 0°N–10°N, 140°W–160°W. Region 2: 0°N–10°N, 160°W–175°W. Region 3: 10°N–20°N, 135°W–160°W. Region 4: 10°N–20°N, 160°W–180°W. Region 5: 20°N–30°N, 135°W–160°W. Region 6: 20°N–30°N, 160°W–180°W. Region 7: 30°N–45°N, 125°W–160°W. Region 8: 30°N–45°N, 160°W–180°W.

[5]Five additional continuous variables, vessel length, begin-set time, soak duration, distance to the nearest land, and the El Niño–Southern Oscillation Index, were tested in preliminary analyses but did not meet the criteria for inclusion as explanatory variables.

(2009). The GLM analyses were conducted after deleting 4.6% of the observed longline sets that had missing or erroneous values for one or more explanatory variables. This led to a total sample of N = 44 969 longline sets. All GLM computations were performed in R Version 2.14.1 for Windows or R Version 2.10.0 for Linux (R Development Core Team 2008). The significance criterion for statistical tests was $P < 0.05$, except for multiple comparisons of GLM coefficients or correlation coefficients, when significance was defined by the Bonferroni principle at $P \leq 0.05$. The zero-inflated and negative binomial models were computed with the "pscl" and "MASS" libraries, respectively. In this context, the pscl library provided estimates of AIC for model selection but did not include estimates of model deviance for the fitted GLM object.

Model estimates of the expected catch rate differed under the alternative GLM hypotheses. Under the Poisson and negative binomial GLMs, the expected catch on the ith set (C_i) was estimated as

$$(1) \qquad E(C_i) = \mu_i \cdot H_i$$

where μ_i is the mean catch per hook and H_i is the number of hooks on set i. For both models, the mean catch μ_i was a log-linear function of the explanatory variables, X_{ij}, indexed by j, with intercept α_X and their estimated coefficients β_j and was expressed as

$$(2) \qquad \mu_i = \exp\left(\alpha_X + \sum_j \beta_j X_{ij}\right)$$

Under the zero-inflated Poisson and negative binomial GLMs, the expected catch on set i included an additional term for the probability of observing an extra zero π_i and was

$$(3) \qquad E(C_i) = (1 - \pi_i) \cdot \mu_i \cdot H_i$$

For both models, the extra zero probability was a logistic function of the set of explanatory variables, Y_{ik}, indexed by k, with intercept α_Y and their estimated coefficients γ_k and was expressed as

$$(4) \qquad \pi_i = \frac{\exp\left(\alpha_\pi + \sum_k \gamma_k Y_{ik}\right)}{1 + \exp\left(\alpha_\pi + \sum_k \gamma_k Y_{ik}\right)}$$

For the delta-gamma and delta-lognormal mixture models, the expected catch per set was

$$(5) \qquad E(C_i) = p_i \cdot \mu_i \cdot H_i$$

where p_i, the probability of a positive catch, was a logistic function of the set of explanatory variables and where the mean catch per hook was a log-linear function of the explanatory variables, X_{ij}, indexed by j, with intercept α_X and their estimated coefficients β_j and was expressed as

$$(6) \qquad \mu_i = \exp\left(\alpha_X + \sum_j \beta_j X_{ij}\right)$$

Under the delta-lognormal model, the mean was multiplied by the exponential of one-half the residual variance ϕ^2 to adjust for the transformation bias from fitting the logarithm of the positive catch under a lognormal distributional assumption.

Fishing effort was included in the CPUE standardization analyses through the use of an offset in the GLM estimation (Crawley 2007). In this context, the measure of relative fishing effort between longline sets was equal to the number of hooks deployed per set. The Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial GLMs were computed with effort (i.e., the logarithm of the number of hooks deployed) as an offset for the positive count component of the distribution. The gamma and lognormal components of the delta-distribution models also included an offset for the logarithm of the number of hooks per set.

Model diagnostics included the reduction in AIC by each explanatory variable, the median residual, a linear regression of observed on fitted values, histograms of Pearson residuals, and a pseudo-coefficient of determination (pseudo-R^2) computed as the percentage of null deviance explained where available for the non-inflated models. The consistency of the GLM estimates of standardized CPUE among alternative hypotheses was assessed by pairwise correlations of standardized CPUE time series.

Standardized CPUE, measured in sharks per set, was calculated based on the fitted P, NB, ZIP, and ZINB models by setting factor and continuous variables at their mean levels and then applying the fitted effect coefficients to predict the standardized annual CPUE time series mean and variance. For the two delta-distribution models, the standardized annual CPUE was the product of the mean predictions of the delta (Δ) or presence–absence component and positive catch component. The variance of standardized CPUE for the delta-distribution models was computed as

$$(7) \quad \mathrm{Var}(\Delta C) = \mathrm{Var}(\Delta)\mathrm{Var}(C) + \mathrm{Var}(\Delta)E(C)^2 + \mathrm{Var}(C)E(\Delta)^2$$

For comparison, nominal annual CPUE in year t ($\mathrm{CPUE}_{\mathrm{OBS},t}$) was calculated from the mean number of hooks per set ($\overline{H}_t$) and the mean number of sharks per hook ($\overline{S}_t$) as the product

$$(8) \qquad \mathrm{CPUE}_{\mathrm{OBS},t} = \overline{H}_t \cdot \overline{S}_t$$

Model selection and multimodel inference

Multimodel inference was applied to account for model selection uncertainty (Buckland et al. 1997; Burnham and Anderson 2002). In particular, the directed Kullback–Leibler distance between each model and the true state of nature was approximated using information from the maximum likelihood estimate (MLE) of the model parameters to the observed data set. We applied the AIC adjusted for sample size bias, denoted as $\mathrm{AIC_c}$ (Hurvich and Tsai 1989), to measure the goodness of fit of the alternative standardization models. The $\mathrm{AIC_c}$ value was extracted from the best GLM fit for each model. The $\mathrm{AIC_c}$ was equal to −2 times the value of the fitted log-likelihood (log L) at the maximum likelihood estimate ($\hat{\theta}$) plus two times the number of parameters (K) times a bias-correction term depending on K and the number of samples (n):

$$(9) \qquad \mathrm{AIC_c} = -2\log L(\hat{\theta}) + 2K\left(\frac{n}{n - K - 1}\right)$$

The alternative models, indexed by j (M_j), were ranked by their $\mathrm{AIC_c}$ differences. The best-fitting model (M^*) with the minimum value of AIC produced the best fit to the observed data. The difference in the value of $\mathrm{AIC_c}$ for the ith alternative model (AIC_i) and the model with the minimum $\mathrm{AIC_c}$ value ($\mathrm{AIC_{min}}$) was the AIC difference (Δ_i), which was

$$(10) \qquad \Delta_i = \mathrm{AIC}_i - \mathrm{AIC_{min}}$$

Table 2. Summary of (A) nominal fishing effort and fishery observer deployments at sea, (B) operational parameters of the deep- and shallow-set sectors, and (C) nominal catch statistics for oceanic whitetip shark in the Hawaii-based longline fishery in 1995–2010.

(A) Observer effort[a].

Sector	Trips	Sets	Hooks	Vessels	Observers	Mean experience
All	3 524	47 140	85 264 659	178	449	6.5 trips
Deep-set	2 872	36 407	75 802 847	169	443	7.8 trips
Shallow-set	659	10 733	9 461 812	72	225	2.9 trips

(B) Operational parameters.

Sector	Latitude (°N)	Longitude (°W)	Hooks per set	Hooks per float	Begin-set time	Target depth (m)
Deep-set	20.7 (5.9)	158.3 (5.7)	2 082 (398)	27.8 (3.1)	0738 HST (1 h 23 min)	181.5 (93.7)
Shallow-set	30.1 (3.9)	157.6 (8.3)	882 (168)	4.5 (0.9)	1905 HST (2 h 53 min)	48.5 (49.3)

(C) Catch statistics.

Sector	Catch	Catch per set	Nominal CPUE (sharks per 1000 hooks)	Percent positive catch sets
Deep-set	5 495	0.151 (0.534)	0.077 (0.284)	10.2 (0.2)
Shallow-set	1 144	0.107 (0.500)	0.125 (0.615)	6.9 (0.3)

Note: Observer effort includes total values except for the mean number of trips by fishery observers (mean experience). Operational parameters and catch statistics include means (top entries) and standard deviations (bottom entries in parentheses) by sector.

[a]The fishery-wide trips total is less than the sum from the two sectors because seven trips included deep and shallow sets. Similarly, the total number of all observers is less than the sum from the sectors because some observers worked in both.

The likelihood of the ith model given the data ($L(M_i \mid D)$) relative to the set of alternative models was proportional to the exponential of the Δ_i value:

$$L(M_i \mid D) \propto \exp\left(-\frac{\Delta_i}{2}\right) \tag{11}$$

We calculated the Akaike weights (W_i) over the set of alternatives as

$$W_i = \frac{\exp\left(-\frac{\Delta_i}{2}\right)}{\sum_k \exp\left(-\frac{\Delta_k}{2}\right)} \tag{12}$$

We used the Akaike weights to quantify the relative probability of each model given the sample data and based the decision process for multimodel inference on the fitted Akaike weights. We also assessed the evidence ratios between the best-fitting model and the alternatives. The evidence ratio for model i relative to model j ($E_{i,j}$) measured the strength of support for model i versus model j given the data and was calculated as the ratio of the Akaike weights:

$$E_{i,j} = \frac{W_i}{W_j} \tag{13}$$

Ratios greater than unity indicated that there was stronger evidence that the ith model was a better approximation than the jth model and also provided a measure of the relative odds of the two models being true given their fits to the data.

Results

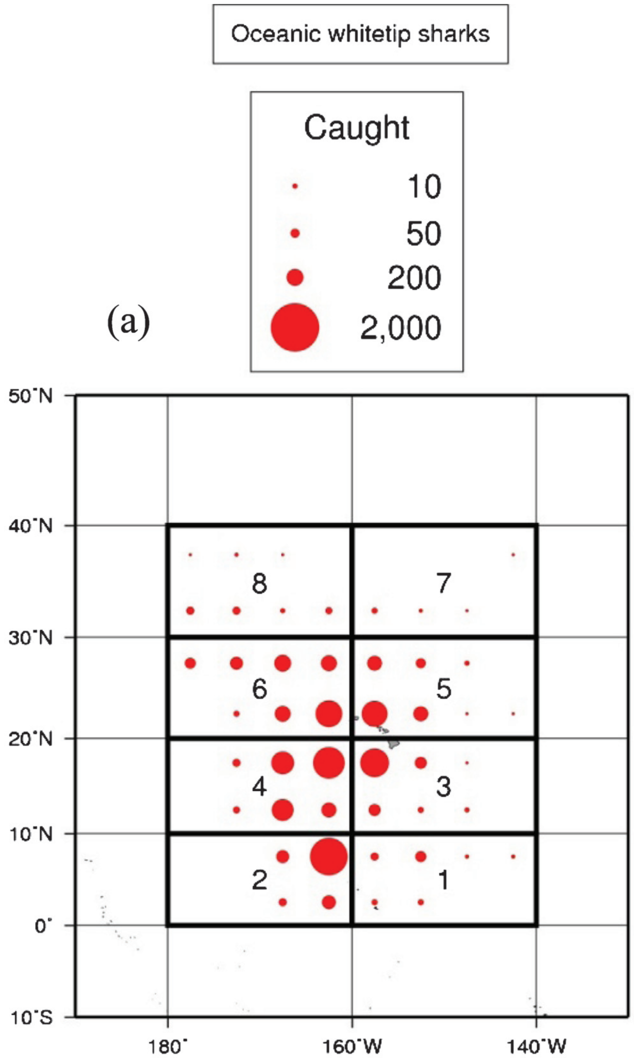
Empirical patterns in the fishery

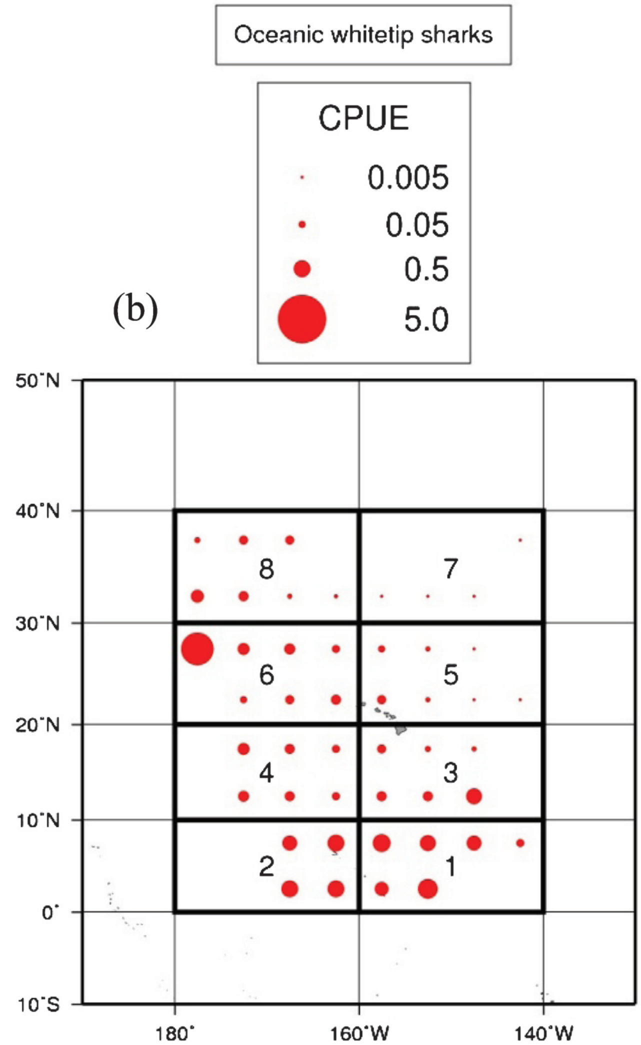
Summaries of the fishery observer activity, operational parameters on observed longline trips, and observed catch data show that the preponderance of oceanic whitetip sharks were caught in the deep-set longline sector from 1995 through 2010 (Table 2). The total catch was 6639 oceanic whitetip sharks, with the deep-set sector accounting for 83% of the total. Average effort in 1995–1999 was 523 observed sets per year. The PIROP began a major expansion in 2000, with average effort reaching 3761 observed sets per year in 2001–2006. Observer coverage increased to an average of 5133 sets per year in 2007–2010. Concomitantly, the geographic expanse of observed fishing increased by 75%, from approximately 17.3×10^6 km² in 1995 to 30.2×10^6 km² in 2010, as observer effort increased. A more detailed summary of Hawaii longline observer effort in 1995–2006 is presented in Walsh et al. (2009).

Oceanic whitetip sharks were caught on about 10% of the observed deep-set sector and 7% of the shallow-set sector sets (Table 2). Relatively large (5–15 sharks) catches were taken on only 0.2% of the sets, but comprised 8.5% of the total catch. The distributions of set types were closely related to latitude. Observed sets deployed south of 20°N included only 0.3% in the shallow-set sector. Deep sets comprised 79.2% from 20°N to 30°N and 24.0% of the effort above 30°N.

The spatial distributions of oceanic whitetip shark catches and nominal CPUE in the longline fishery differed (Fig. 1). Large oceanic whitetip shark catches were taken (Fig. 1*a*) from Region 2 in the rectangular area 5°N–10°N and 160°W–165°W (18% of the total) and from Regions 3, 4, 5, and 6 near Hawaii in the rectangular region 15°N–25°N and 155°W–165°W (39% of the total). Nominal CPUE (Fig. 1*b*) in tropical waters south of 10°N was generally greater than further northward, although the highest CPUE was observed between 25°N–30°N and 175°W–180°W and occurred on a small number (N = 66) of shallow sets. Conversely, the high catch between 5°N–10°N and 160°W–165°W (Fig. 1*a*) reflected a high level of observer effort (i.e., about 67% of all sets south of 10°N) rather than a particularly high CPUE; the mean from 5°N–10°N and 160°W–165°W (0.558 sharks per 1000 hooks) was nearly identical to that from 5°N–10°N and west of 165°W (0.546 sharks per 1000 hooks).

Fig. 1. Observed oceanic whitetip shark catches (*a*) and mean nominal CPUE (*b*) in the Hawaii-based pelagic longline fishery during 1995–2010 by fishing region and 5° square. All plotted data are nonconfidential and pooled from both the deep- and shallow-set sectors.





Variable selection for CPUE standardization models

The stepwise variable selection analyses produced a single best-fitting model for CPUE standardization under each of the five alternative hypotheses. The final best-fitting model for each alternative was selected based on the sequential likelihood ratio tests and the stepwise improvement in AIC, as indexed by the percent AIC reduction criterion.

The sets of explanatory variables that produced the best-fitting model under each of the five catch hypotheses were similar. The year effect was significant and important for all of the fitted model distributions. Similarly, the region and set type effects were significant and important for all of the fitted models except the binomial components of the zero-inflated models (ZIP and ZINB). The SST effect, either as a linear or quadratic term, was significant and important for all of the fitted models except the gamma component of the delta-gamma model. In comparison, the seasonal quarter effect was significant and important for all of the fitted models except for both components of the zero-inflated models. Overall, the alternative models showed consistency in the selection of explanatory variables that characterized the effects of temporal, regional, seasonal, fishery sector, and environmental effects on oceanic whitetip CPUE.

Last, we note that each of the best-fitting alternative models also showed a highly significant decreasing trend ($P < 0.0001$) in standardized CPUE during 1995–2010. For the best-fitting ZINB model, there was an annual mean decrease of about 4.1% per year (±0.4%). We also note that among the alternative models, the amount of null deviance explained by the Poisson, negative binomial, and delta-gamma models was consistent with the pattern of goodness of fit indicated by the AIC analyses. Overall, the negative binomial model had the highest pseudo-R^2 value of about 37% (Table A2-B), followed by the Poisson model at 34% (Table A2-A) and the delta-gamma model at 24% (Table A2-E).

Model selection and multimodel inference

The bias-corrected values of the AIC showed the relative goodness of fit of the alternative models to the fishery observer data. The highest value of AIC was AIC_{DG} = 29 976.2, which indicated that the delta-gamma model produced the most distant model from the observed CPUE process. The Poisson, negative binomial, and zero-inflated Poisson followed with increasing goodness of fit and decreasing AIC values of AIC_P = 29 565.5, AIC_{NB} = 28 626.1, and AIC_{ZIP} = 28 951.9, respectively. The best-fitting model was the zero-inflated negative binomial with AIC_{ZINB} = 28 558.0 and a total of 43 parameters, the most of the four count-based models.

The AIC differences for the alternative P, NB, ZIP, and DG models relative to the ZINB model all had values of $\Delta AIC > 50$ (Table 3), which indicated that there was virtually no support for the

Table 3. Summary of the model selection information from five oceanic whitetip shark GLM analyses, including the model structure, the CPUE predictors, the relative differences in Akaike information criterion (AIC) value between the *i*th and the best-fitting model (Δ_i), the model likelihoods $\left(\exp\left(-\frac{\Delta_i}{2}\right)\right)$, the Akaike weights ($W_i$), and the evidence ratio $\left(\frac{W_{\min\,\mathrm{AIC_c}}}{W_i}\right)$ for each model.

GLM hypothesis	Model structure	CPUE predictors	Δ_i	Model likelihood	Akaike weight	Evidence ratio
Poisson	Counts	Year, Quarter, Region, Set Type, SST (quadratic)	1007.52	0.00	0.00	>1 000 000
Negative binomial	Counts	Year, Quarter, Region, Set Type, SST (quadratic)	393.96	0.00	0.00	>1 000 000
Zero-inflated Poisson	Binomial and counts	Binomial: Year, SST (linear) Poisson: Year, Region Set Type, SST (linear)	68.13	0.00	0.00	>1 000 000
Zero-inflated negative binomial	Binomial and counts	Binomial: Year, SST (linear) Negative binomial: Year, Region Set Type, SST (linear)	0	1.00	1.00	1
Delta-gamma	Binomial and continuous	Binomial: Year, Quarter, Region, Set Type, SST (quadratic) Gamma: Year, Quarter, Region, Set Type	1418.25	0.00	0.00	>1 000 000

alternatives given the data. In particular, the model likelihoods of the four alternatives were effectively zero (Table 3). Furthermore, the evidence ratios of the P, NB, ZIP, and DG models relative to the ZINB model were highly improbable $\left(\frac{W_{\min\,\mathrm{AIC_c}}}{W_i} \gg 1000\right)$. As a result, we judged the ZINB model as clearly having the strongest support for CPUE standardization of oceanic whitetip shark using the Hawaii longline observer data.

Estimates of standardized oceanic whitetip shark CPUE from the best-fitting ZINB model and the alternative count models were generally quite similar. A comparison of the four count distribution models showed that the trends in CPUE were similar for the count models (Fig. 2*a*). Average CPUE for the negative binomial models NB and ZINB at the beginning of the time series (1995–1999) was about 9%–10% higher than that for the P and ZIP models, while average NB and ZINB CPUE was about 2% lower than that of the Poisson models at the end of the time series during 2006–2010. Thus differences among the ZINB and the alternative count models were more pronounced at the beginning of the CPUE time series. Similarly, the ZINB model and the delta-distribution models had similar trends in standardized CPUE (Fig. 2*b*) with strong concordance among the estimated time series from 2002 to 2010. The trends in standardized CPUE from the ZINB model and nominal CPUE were also similar (Fig. 2*c*), although there was more interannual variation in nominal values relative to the standardized estimates. In particular, the angular deviation between the ZINB time series and the nominal CPUE time series was about 6°, which was the second largest deviation among all pairs of time series estimates (Table A4). There was a highly significant positive pairwise correlation among all of the time series of estimates of standardized CPUE ($\rho > 0.98$; Table A4). Further, there was a high degree of collinearity among the time series of estimates of standardized CPUE, as measured by their angular deviations ($\theta \le 3.6°$; Table A4). Thus, although there was a substantial difference in goodness of fit between the alternative models and best-fitting ZINB model, there were moderate differences among the time series of estimates of standardized CPUE, and the standardized CPUE estimates were strongly collinear.

All estimated time series of standardized oceanic whitetip shark CPUE exhibited large declines between 1995 and 2010 (Fig. 2). Decreases in the 5-year average of mean standardized CPUE from 1995–1999 to 2006–2010 ranged from 88% to 89% declines for the P, NB, ZIP, DG, and best-fitting delta-gamma models. The mean nominal CPUE also declined by roughly 87.5% over the same time period. Overall, the conclusion that mean oceanic whitetip shark CPUE had declined substantially since the mid-1990s was robust and was consistent for the set of models analyzed.

Regional patterns in trends of standardized oceanic whitetip shark CPUE were also consistent. For example, the decreases in standardized CPUE of the deep-set sector from 1995 through 2010 were 83%, 91%, and 92% declines in Regions 2, 4, and 6 (Fig. 1), respectively. Similarly, decreases in the shallow-set sector were also observed and were 73%, 79%, and 92% in Regions 4, 6, and 8 (Fig. 1), respectively.

The regional and SST effects were confounded for both fishery sectors. However, we note that SST apparently did not fully account for the differences among the standardized CPUE trends. Predicted values of standardized CPUE for the deep-set sector in Region 6 with SST fixed at 27 °C showed that a 1 °C change in SST would account for about 37%–46% of the difference in CPUE trend from Region 4 (Fig. 3). Similarly, a 2 °C observed mean difference in SST between Regions 2 and 4 would account for about 56%–74% of the difference between predicted CPUE vectors. Similarly, for the shallow-set sector, a 1 °C increment in SST would account for about 38%–61% of the difference between the predicted CPUE vectors from Regions 6 and 8.

Discussion

This study developed a suite of GLM analyses that represented different hypotheses about the variance to mean ratio of the shark capture process and the interpretation of zero catch observations of oceanic whitetip sharks in the Hawaii-based pelagic longline fishery. Each of the alternative analyses documented a highly significant decline in relative abundance of oceanic whitetip shark in 1995–2010. This indicated that the evidence of a declining abundance trend was robust over the set of hypotheses we evaluated.

We applied model selection and multimodel inference based on the AIC to judge the alternative model hypotheses. In this application, model selection identified the ZINB model as providing the best-fitting representation of the CPUE observation process for oceanic whitetip shark. As a result, we did not attempt to construct a model-averaged estimate of standardized CPUE over the set of candidate models (Buckland et al. 1997; Burnham and Anderson 2002), but instead used the ZINB as the basis for inference. Overall, the modeling results indicated that there was an excess of zeros in the catch data and that an overdispersed model with zero inflation provided the best fit to the shark bycatch data.

The finding that quarterly effects on oceanic whitetip shark CPUE were statistically significant but of lesser relative importance than yearly effects was not surprising. Faunce and Barbeaux (2011) recently observed that use of quarter as a fixed effect in analyses of Alaskan groundfishes is unsatisfactory because fishery openings and closings do not conform to a quarterly schedule. Analogously, the quarterly schedule used for reporting purposes

Fig. 2. Comparisons of estimates of annual standardized CPUE (mean sharks per standardized longline set) for oceanic whitetip shark in the Hawaii-based pelagic longline fishery in 1995–2010 for the best-fitting model (ZINB) and the other count-based models (*a*), the best-fitting model and the two delta-distribution models (*b*), and the best-fitting model showing 95% confidence bars for the standard error of the mean CPUE and the nominal CPUE (*c*).

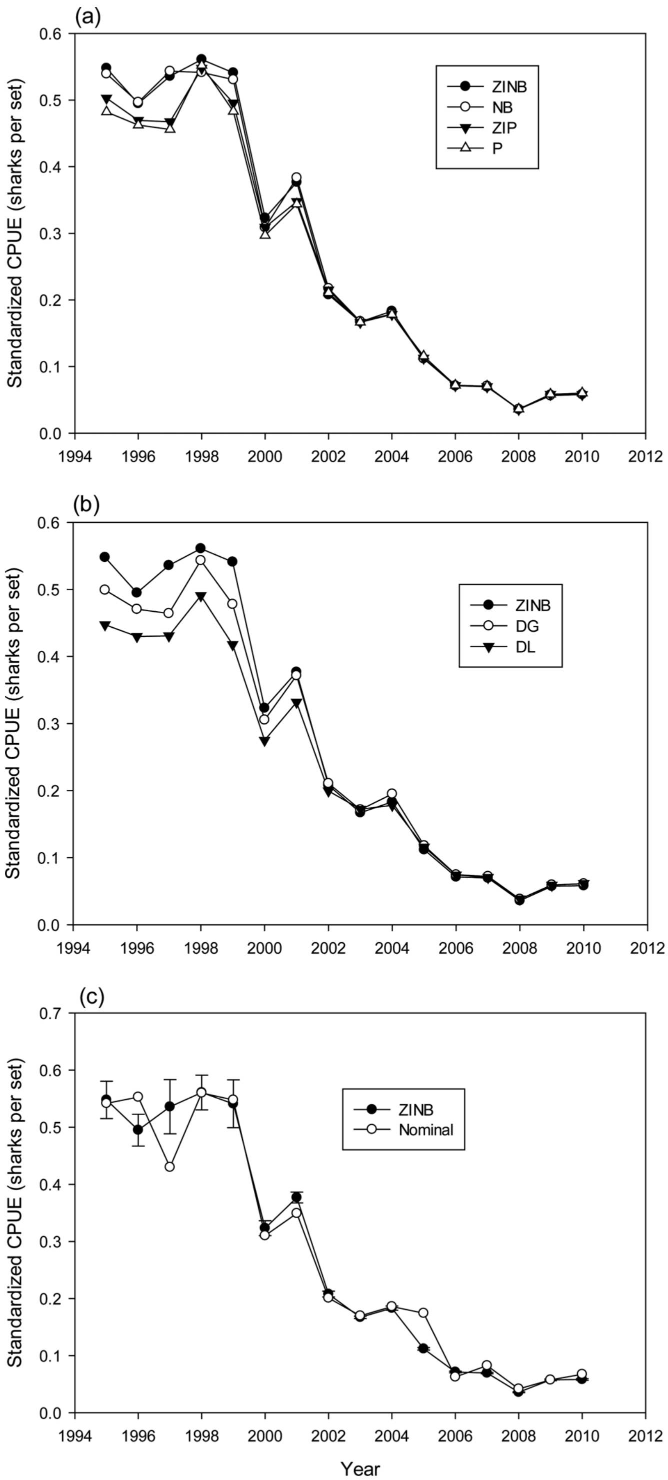
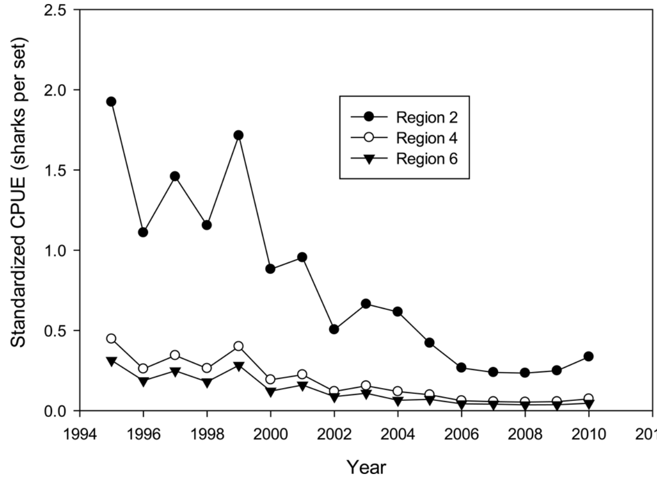


Fig. 3. Oceanic whitetip shark standardized CPUE for the deep-set sector as estimated by the best-fitting zero-inflated negative binomial model by fishing region.



in this fishery is not predicated upon the seasonal distributions of the targeted tunas or swordfish and may have little if any relationship with the life histories or movements of incidentally caught sharks.

The effects of the other explanatory variables were confounded; SST tends to vary inversely with latitude, and the set types were related to the fishing regions, with only deep-set fishing in tropical waters and mostly shallow-set fishing above 30°N. Nonetheless, the comparisons of standardized CPUE in which SST was manipulated indicated that the regions were not distinguished solely by their mean SST levels. Hence, there appear to be real differences among the regions as habitats that may be associated with oceanographic features or other extrinsic factors not included in the analyses. Similarly, the comparison between set types within regions (e.g., Regions 5 and 6) demonstrated the importance of this factor.

The highly significant effect of set types on CPUE of oceanic whitetip shark can be attributed to target depths. The median depth of the deepest hook on shallow sets was 60 m, whereas that for deep sets was 248 m (Bigelow et al. 2006). Musyl et al. (2011) recently used pop-up satellite tags to describe the behavior of several shark species and demonstrated that oceanic whitetip sharks remain in the near-surface mixed layer within 2 °C of the surface SST over 95% of the time. This finding is consistent with the observed distribution of oceanic whitetip shark catches in relation to SST in this study (Fig. 4). This also suggests that it may have low vulnerability to deep-set longline gear, except perhaps during the deployment or haulback as hooks pass through the near-surface mixed layer. This also emphasizes the importance of considering alternative hypotheses to represent the CPUE observation process (e.g., Lynch et al. 2012), including habitat-based standardization models that can account for habitat preference (e.g., statHBS: Hinton and Nakano 1996; Goodyear 2003; Maunder et al. 2006), delta-distribution models that can account for the proportion of zero catches (e.g., Aitchison 1955; Pennington 1983; Stefánsson 1996), and zero-inflated models that can account for the probability of observing extra zero catches (Zuur et al. 2009).

SSTs exerted dual effects on oceanic whitetip sharks, exemplified most clearly by the significant coefficients with different signs in the zero-inflated models. This was not a contradiction in relation to the lack of an SST effect in the lognormal model because the latter was fitted to a much smaller data set with a truncated SST range. This suggests that low SST acted as a thermal barrier for this species, but that within the preferred range CPUE was largely independent of SST. Moreover, SST appeared to act as a thermal barrier ~24 °C (Fig. 4; see also Musyl et al. 2011, their figure 5*c*), higher than the previously reported approximate lower limit ~20 °C (Bonfil et al. 2008).

Fig. 4. Oceanic whitetip shark catches and SST in the Hawaii-based pelagic longline fishery in 1995–2010. The upper panel (*a*) shows the percent frequency distribution for SST from all sets; the lower panel (*b*) shows the percentages of the oceanic whitetip shark catch relative to SST.

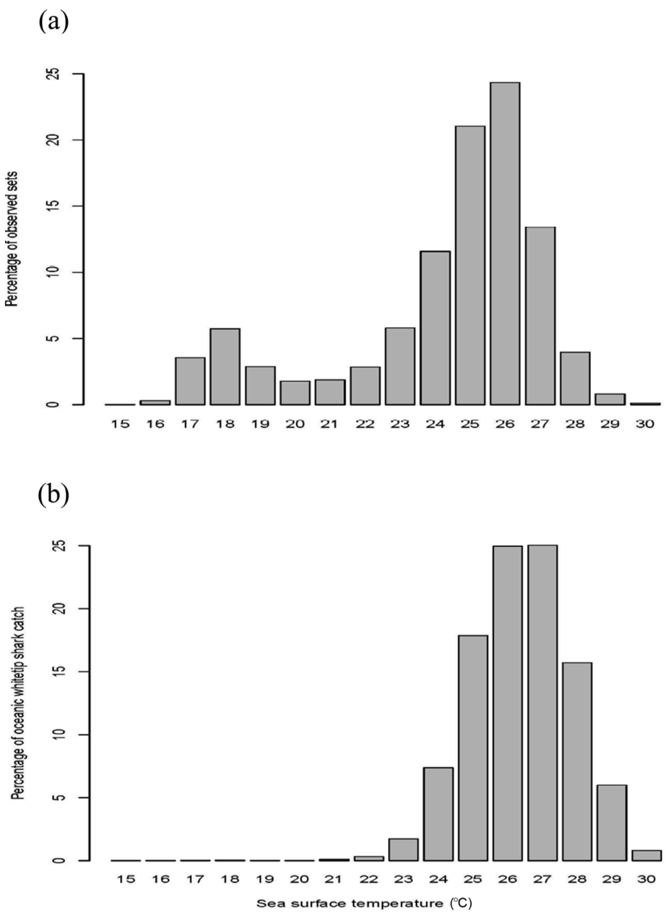
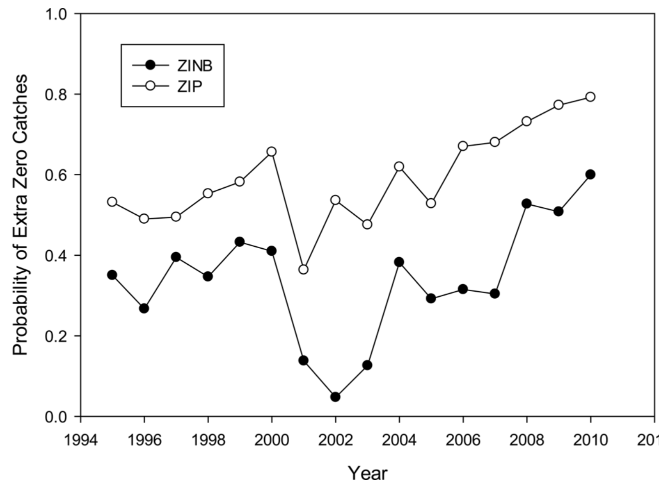


Fig. 5. A comparison of annual probabilities of extra zero catches of oceanic whitetip shark for the zero-inflated negative binomial (ZINB) and the zero-inflated Poisson (ZIP) models.



Set type, regional, and SST effects were confounded, but comparisons within regions between set types and within regions between SST levels indicate that their effects on oceanic whitetip shark CPUE were real and distinguishable. In general, SST exerted a strong positive effect on the probability of oceanic whitetip shark catches. SST also affected CPUE if all sets were considered, but had no significant effect in an analysis restricted to sets with catch and a truncated SST range.

Exploratory tests of several candidate explanatory variables were inconclusive. The nonsignificant exploratory test results (e.g., hook and bait types, long soak times, distance from land) cannot be regarded as definitive indicators of absence of effects on oceanic whitetip sharks. Because the operational parameters were not manipulated experimentally, their effects were confounded with and inextricable from those of other aspects of fishing. Hence, results from this study neither support nor refute findings such as those from Curran and Bigelow (2011), who reported significant reductions in catches and catchability for blue shark and catches of bigeye thresher (*Alopias superciliosus*) in fishing experiments that tested large (18/0) circle hooks against tuna or J-hooks.

The selection of the ZINB model provided some insight into the observation that the shark capture process could include extra zero catches and be overdispersed. The estimates of annual probabilities of observing extra zero catches were important for the ZINB model, as well as for the ZIP model, but the latter model did not include overdispersion (Fig. 5). This interpretation of the extra zero catches is consistent with several aspects of observing the shark capture process. First and foremost, many of the hooks deployed in one set of deep-set sector longline gear are at about 50–250 m and do not consistently overlap with the more shallow depth range of oceanic whitetip shark, which may be expected to be on the order of 10–100 m (Musyl et al. 2011). This lack of vertical overlap between the sampling gear and the bycatch species leads to the noncatchability of some oceanic whitetip sharks that are present but not distributed in the depth range available to the longline gear, giving rise to the presence of extra zero observations. Second, low SST values were associated with many zero catch observations. Third, observers collecting fishery information are not perfectly recording all of the catch in the pelagic longline fishery because of prioritization of sampling for protected species, such as false killer whales in the 2010s and probably even more so with sea turtles in the shallow-set sector during the 1990s, as well as other duties. This may be especially true for a bycatch species that is rapidly discarded at sea to allow for efficient processing of targeted catch. Nonetheless, we note that the actual cause or causes of the zero-inflation of oceanic whitetip shark catches have not yet been determined.

The declining trends in oceanic whitetip shark relative abundance, estimated with a mixture model, two counts models, and two zero-inflated models, were very consistent, with high positive correlation coefficients and relatively small angular deviations among the CPUE vectors. The nominal CPUE trends were also highly correlated with the various standardized trends. Thus, the downward trend in the nominal CPUE was not changed appreciably by removing the effects of extrinsic factors. In short, CPUE standardization did not engender an appreciably more optimistic population status scenario.

The magnitude of the decline in oceanic whitetip shark CPUE (~90%) alone would represent meaningful grounds for concern. More importantly, however, the declining trend in the observer data from Hawaii with a species traditionally considered highly abundant is similar in both trajectory and magnitude to the decrease in standardized CPUE as estimated from longline observer data across a vast expanse of the Western and Central Pacific Ocean (Clarke et al. 2013). It must be recognized that the closeness of the agreement between the trends in Hawaii and the Western and Central Pacific Ocean is partly an artifact because some Hawaii longline observer data were included in the latter analysis (Lawson 2011), but tuna purse seine fishery data documented a similar (79%) decrease in oceanic whitetip shark catches from 20°S to 20°N and 150°W to 130°E between 1999 and 2010

(Lawson 2011). As recently as 2008, oceanic whitetip shark was considered the second-most abundant oceanic shark (Bonfil et al. 2008). Blue and oceanic whitetip sharks were believed to have co-evolved in the oceanic realm, with the former species predominant in temperate waters and the latter in subtropical regions (Bonfil et al. 2008). Newly published analyses in a recent stock assessment (Rice and Harley 2012) in the WCPFC region concluded that the oceanic whitetip shark stock was overfished and was subject to overfishing, while Clarke et al. (2013) reported size decreases in oceanic whitetip sharks in the tropical core area. Overall, it is clear that oceanic whitetip shark abundance has declined substantially in the Pacific.

The aspect of pelagic longline fishing most closely associated with shark mortality is finning (Clarke et al. 2006*a*, 2006*b*; Clarke 2008; Dulvy et al. 2008; Stevens 2010). Very large numbers of sharks are finned in pelagic fisheries each year (Dulvy et al. 2008; Stevens 2010), but the estimates of finned sharks are highly imprecise because carcasses discarded at sea are often not reported (Clarke et al. 2006*b*; Clarke 2008). It is clear, however, that oceanic whitetip shark is strongly affected by the shark fin trade. In a detailed study of species composition of the Hong Kong shark fin market in 2000 (Clarke et al. 2006*a*), oceanic whitetip shark fins from three widely separated locales ranked eighth in importance at 1.8% of the identified fins. It is also notable that the practice of shark finning was banned in the Hawaii-based longline fishery in the early 2000s.

The combination of a decline in oceanic whitetip shark standardized CPUE and well-documented economic demand for their fins met by widely separated sources of supply represents grounds for concern about this species' resilience in relation to fishing pressure worldwide. Its intrinsic rebound potential lay in the midrange of 27 shark species (Au et al. 2008), but it is taken as both a nontarget species in tropical pelagic tuna longline fisheries and the target species in some small-scale fisheries (Bonfil et al. 2008).

The possibility that oceanic whitetip shark may be insufficiently resilient to withstand current or future levels of fishing pressure raises additional questions about the potential for ecological effects associated with removal of apex predators. In general, sharks are believed capable of top-down influence on food webs by direct predation, by generating risk of predation that evokes changes in behavior of prey species with consequent negative effects on their fitness, and by initiating trophic cascades (Heithaus et al. 2010).

Kitchell et al. (2002) used an Ecopath with Ecosim model to investigate fishing effects on and the ecological importance of "brown sharks" (i.e., oceanic whitetip and silky (*Carcharhinus falciformis*) sharks) in North Pacific food webs. They concluded that these sharks were not keystone species in this ecosystem, where food webs are dominated by fast-growing, highly productive tuna species. Rather, longline fishing itself functioned in the manner expected of a keystone species, and sharks were also subject to such strong predatory effects. Overall, the trend in oceanic whitetip shark relative abundance in the Hawaii-based longline fishery is consistent with the predictions from the Ecopath with Ecosim model (Kitchell et al. 2002). Although the outset of decline was not identified in this study, the relative abundance of this species was clearly in decline within a few years of the expansion of this longline fishery. The potential effects of heavy fishing pressure on oceanic pelagic sharks have been extensively discussed for more than two decades (Compagno 1990; Stevens et al. 2000; Dulvy et al. 2008; and many others). The basis for concern is the low productivity typical of elasmobranchs, which enhances their susceptibility (Smith et al. 1998; Camhi 2008).

The decline in oceanic whitetip shark relative abundance during 1995–2010 was related to decreases in both the probability of positive catch and CPUE on sets with positive catch, as shown by the empirical patterns in the nominal fishery catch rates. Furthermore, the consistent CPUE standardization results generated by a suite of GLM analyses representing different hypotheses regarding the nature of observed zero catches reinforce the inference that oceanic whitetip shark has undergone a large decrease in relative abundance on the order of 90% since the mid-1990s. Oceanic whitetip shark was recently approved for listing in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora in March 2013 (http://www.cites.org/).

The similarity between our results for the Hawaii longline fishery and those from the Western Pacific Ocean indicates that the decline in relative abundance of oceanic whitetip shark has not been a localized phenomenon near Hawaii. Rather, it appears to have occurred concomitantly with declines in multiple regions of the Pacific Ocean. As such, the full stock assessment conducted under WCPFC auspices (Rice and Harley 2012), which incorporated previous estimates of relative abundance developed by Walsh and Clarke (2011), provided an important initial step in estimating the magnitude of oceanic whitetip shark decline in the Western and Central Pacific Ocean.

Our study has demonstrated the value of model selection and multimodel inference in the context of CPUE standardization. This approach may be particularly relevant for oceanic pelagic sharks because the data available for analyses may support alternative hypotheses on the quality and information content of fishery-dependent observations. Overall, this study provides an advancement of techniques used to standardize catch rates of oceanic pelagic sharks and other bycatch species and has also provided information on the relative abundance of oceanic whitetip shark from the Hawaii-based longline fishery.

Acknowledgements

The authors thank Karen Sender for preparing catch and CPUE maps; Gerard DiNardo, Pierre Kleiber, Hui-Hua Lee, Kevin Piner, and two anonymous reviewers for commenting on earlier versions of this manuscript; and S. Joseph Arceneaux and Eric Forney of the PIROP for data checks. This work was supported in part by cooperative agreement NA17RJ1230 between NOAA and the Joint Institute for Marine and Atmospheric Research of the University of Hawaii. Last, we thank John Hampton and especially Shelley Clarke for facilitating this project.

References

Aires-da-Silva, A.M., Hoey, J.J., and Gallucci, V.F. 2008. A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. Fish. Res. **92**: 41–52. doi:10.1016/j.fishres.2007.12.019.

Aitchison, J. 1955. On the distribution of a positive random variable having a discrete probability mass at the origin. J. Am. Stat. Assoc. **50**: 901–908. doi:10.1080/01621459.1955.10501976.

Au, D.W., Smith, S.E., and Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. *In* Sharks of the open ocean: biology, fisheries, and conservation. *Edited by* M.D. Camhi, E.K. Pikitch, and E.A. Babcock. Blackwell Publishing Ltd., Oxford. pp. 298–308.

Baum, J.K., and Blanchard, W. 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fish. Res. **102**: 229–239. doi:10.1016/j.fishres.2009.11.006.

Bigelow, K., Musyl, M.K., Poisson, F., and Kleiber, P. 2006. Pelagic longline gear depth and shoaling. Fish. Res. **77**: 173–183. doi:10.1016/j.fishres.2005.10.010.

Bonfil, R., Clarke, S., and Nakano, H. 2008. The biology and ecology of the oceanic whitetip shark, *Carcharhinus longimanus*. *In* Sharks of the open ocean: biology, fisheries, and conservation. *Edited by* M.D. Camhi, E.K. Pikitch, and E.A. Babcock. Blackwell Publishing Ltd., Oxford. pp. 128–139.

Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an integral part of inference. Biometrics, **53**: 603–618. doi:10.2307/2533961.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Camhi, M.D. 2008. Conservation status of pelagic elasmobranchs. *In* Sharks of the open ocean: biology, fisheries, and conservation. *Edited by* M.D. Camhi, E.K. Pikitch, and E.A. Babcock. Blackwell Publishing Ltd., Oxford. pp. 397–417.

Camhi, M.D., Pikitch, E.K., and Babcock, E.A. (*Editors*). 2008*a*. Trends in catches and abundance of pelagic sharks: Introduction. *In* Sharks of the open ocean: biology, fisheries, and conservation. Blackwell Publishing Ltd., Oxford. pp. 163–165.

Camhi, M.D., Lauck, E., Pikitch, E.K., and Babcock, E.A. 2008*b*. A global overview of commercial fisheries for open ocean sharks. *In* Sharks of the open ocean: biology, fisheries, and conservation. *Edited by* M.D. Camhi, E.K. Pikitch, and E.A. Babcock. Blackwell Publishing Ltd., Oxford. pp. 166–192.

Chambers, J., and Hastie, T. (*Editors*). 1993. Statistical models in S. Chapman and Hall, New York.

Clarke, S. 2008. Use of shark fin trade data to estimate historic total shark removals in the Atlantic Ocean. Aquat. Living Resour. **21**: 373–381. doi:10.1051/alr:2008060.

Clarke, S., and Harley, S.J. 2010. Western and Central Pacific Fisheries Commission. Scientific Committee Sixth Regular Session, 10–19 August 2010. Nuku'alofa, Tonga. A proposal for a research plan to determine the status of the key shark species. WCPFC-SC6-2010/EB-WP-01.

Clarke, S.C., Magnussen, J.E., Abercrombie, D.L., McAllister, M.K., and Shivji, M.S. 2006*a*. Identification of shark species composition and proportion in the Hong Kong shark fin market based on molecular genetics and trade records. Conserv. Biol. **20**: 201–211. doi:10.1111/j.1523-1739.2005.00247.x. PMID:16909673.

Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H., and Shivji, M.S. 2006*b*. Global estimates of shark catches using trade records from commercial markets. Ecol. Lett. **9**: 1115–1126. doi:10.1111/j.1461-0248.2006.00968.x. PMID:16972875.

Clarke, S., Harley, S., Hoyle, S., and Rice, J. 2011. Western and Central Pacific Fisheries Commission. Scientific Committee Seventh Regular Session, 9–17 August 2011. Pohnpei, Federated States of Micronesia. An indicator-based analysis of key shark species based on data held by SPC-OFP. WCPFC-SC7-2011/EB-WP-01.

Clarke, S.C., Harley, S.J., Hoyle, S.D., and Rice, J.S. 2013. Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. Conserv. Biol. **27**: 197–209. doi:10.1111/j.1523-1739.2012.01943.x. PMID:23110546.

Compagno, L.J.V. 1990. Shark exploitation and conservation. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. *Edited by* H.L. Pratt, Jr., S.H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS 90. pp. 391–414.

Crawley, M.J. 2007. The R book. John Wiley & Sons, Ltd., The Atrium, Southern Gate, Chichester, England.

Curran, D., and Bigelow, K. 2011. Effects of circle hooks on pelagic catches in the Hawaii-based tuna longline fishery. Fish. Res. **109**: 265–275. doi:10.1016/j.fishres.2011.02.013.

Department of Commerce. 2004. Fisheries off West Coast states and in the western Pacific; highly migratory species fisheries. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Federal Register 69(67): 50 CFR Parts 223, 224, and 660.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., and Valenti, S. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat. Conserv. Mar. Freshw. Ecosyst. **18**: 459–482. doi:10.1002/aqc.975.

Faunce, C.H., and Barbeaux, S.J. 2011. The frequency and quantity of Alaskan groundfish catcher-vessel landings made with and without an observer. ICES J. Mar. Sci. **68**: 1757–1763. doi:10.1093/icesjms/fsr090.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish physiology. Vol. VI. Environmental relations and behavior. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–98.

Goodyear, C.P. 2003. Test of the robustness of habitat-standardized abundance indices using simulated blue marlin catch-effort data. Mar. Freshw. Res. **54**: 369–381. doi:10.1071/MF01253.

Heithaus, M.R., Frid, A., Vaudo, J.V., Worm, B., and Wirsing, A.J. 2010. Unraveling the ecological importance of elasmobranchs. *In* Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation. *Edited by* J.C. Carrier, J.A. Musick, and M.R. Heithaus. CRC Press. Boca Raton, Fla. pp. 611–637.

Hinton, M., and Nakano, H. 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with application to blue marlin (*Makaira nigricans*) catch and effort data from Japanese longline fisheries in the Pacific. Int.-Am. Trop. Tuna Comm. Bull. **21**: 171–200.

Hurvich, C., and Tsai, C.-L. 1989. Regression and time series model selection in small samples. Biometrika, **76**: 297–307. doi:10.1093/biomet/76.2.297.

Kitchell, J.F., Essington, T.E., Boggs, C.H., Schindler, D.E., and Walters, C.J. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. Ecosystems, **5**: 202–216. doi:10.1007/s10021-001-0065-5.

Lawson, T. 2011. Estimation of catch rates and catches of key shark species in tuna fisheries of the Western and Central Pacific Ocean using observer data. Scientific Committee Seventh Regular Session, 9–17 August 2011. Pohnpei, Federated States of Micronesia. A progress report on the shark work plan. WCPFC-SC7-2011/EB-IP-02.

Lynch, P.D., Shertzer, K.W., and Latour, R.J. 2012. Performance of methods used to estimate indices of abundance for highly migratory species. Fish. Res. **125–126**: 27–39. doi:10.1016/j.fishres.2012.02.005.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., and Possingham, H.P. 2005. Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. Ecol. Lett. **8**: 1235–1246. doi:10.1111/j.1461-0248.2005.00826.x. PMID:21352447.

Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. **70**: 141–159. doi:10.1016/j.fishres.2004.08.002.

Maunder, M., Hinton, M., Bigelow, K., and Langley, A. 2006. Developing indices of abundance using habitat data in a statistical framework. Bull. Mar. Sci. **79**: 545–559.

Minami, M., Lennert-Cody, C.E., Gao, W., and Román-Verdesoto, M. 2007. Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. Fish. Res. **84**: 210–221. doi:10.1016/j.fishres.2006.10.019.

Musyl, M.K., Brill, R.W., Curran, D.S., Fragoso, N.M., McNaughton, L.M., Nielsen, A., Kikkawa, B.S., and Moyes, C.D. 2011. Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish. Bull. **109**: 349–368.

Nakano, H., and Clarke, S. 2006. Filtering method for obtaining stock indices by shark species from species-combined logbook data in tuna longline fisheries. Fish. Sci. **72**: 322–332. doi:10.1111/j.1444-2906.2006.01153.x.

Pacific Islands Regional Office. 2011. Hawaii Longline Observer Program Field Manual. Version LM. 09.11. Honolulu.

Pennington, M. 1983. Efficient estimators of abundance for fish and plankton surveys. Biometrics, **39**: 281–286. doi:10.2307/2530830.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rice, J., and Harley, S. 2012. Stock assessment of oceanic whitetip sharks in the western and central Pacific Ocean. WCPFC-SC8-2012/SA-WP-06 Rev 1.

Searle, S. 1987. Linear models for unbalanced data. John Wiley and Sons, New York.

Smith, S.E., Au, D.W., and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Mar. Freshw. Res. **49**: 663–678. doi:10.1071/MF97135.

Stefánsson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES. J. Mar. Sci. **53**: 577–588. doi:10.1006/jmsc.1996.0079.

Stevens, J.D. 2010. Epipelagic oceanic elasmobranchs. *In* Sharks and their relatives. II: Biodiversity, adaptive physiology, and conservation. *Edited by* J.C. Carrier, J.A. Musick, and M.R. Heithaus. CRC Press, Boca Raton, Fla. pp. 3–35.

Stevens, J.D., Bonfil, R., Dulvy, N.K., and Walker, P.A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES. J. Mar. Sci. **57**: 476–494. doi:10.1006/jmsc.2000.0724.

Tavares, R., Ortiz, M., and Arocha, F. 2012. Population structure, distribution and relative abundance of the blue shark (*Prionace glauca*) in the Caribbean Sea and adjacent waters of the North Atlantic. Fish. Res. **129–130**: 137–152. doi:10.1016/j.fishres.2012.06.018.

Walsh, W.A., and Clarke, S.C. 2011. Analysis of catch data for oceanic whitetip and silky sharks reported by fishery observers in the Hawaii-based longline fishery in 1995–2010. Pacific Islands Fisheries Science Center Admin. Rep. H-11-10.

Walsh, W.A., Kleiber, P., and McCracken, M. 2002. Comparison of logbook reports of incidental blue shark catch rates by Hawaii-based longline vessels to fishery observer data by application of a generalized additive model. Fish. Res. **58**: 79–94. doi:10.1016/S0165-7836(01)00361-7.

Walsh, W.A., Ito, R.Y., Kawamoto, K.E., and McCracken, M. 2005. Analysis of logbook accuracy for blue marlin (*Makaira nigricans*) in the Hawaii-based longline fishery with a generalized additive model and commercial sales data. Fish. Res. **75**: 175–192. doi:10.1016/j.fishres.2004.11.007.

Walsh, W.A., Bigelow, K.A., and Ito, R.Y. 2007. Corrected catch histories and logbook accuracy for billfishes (Istiophoridae) in the Hawaii-based longline fishery. NOAA Tech. Memo. NMFS-PIFSC-13.

Walsh, W.A., Bigelow, K.A., and Sender, K.L. 2009. Decreases in shark catches and mortality in the Hawaii-based longline fishery as documented by fishery observers. Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci. **1**: 270–282. doi:10.1577/C09-003.1.

Zeileis, A., Klieber, C., and Jackman, S. 2008. Regression models for count data in R. J. Stat. Softw. **27**(8): 1–25.

Zuur, A.E., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Zero-truncated and zero-inflated models for count data. *In* Mixed effects models and extensions in ecology with R. Springer Science + Business Media, LLC, New York. pp. 261–293.

Appendix A

This appendix provides supplementary information for the article. The summary information includes information on the empirical patterns in the fishery (Fig. A1) and a description of each of the alternative CPUE standardization models along with the delta-lognormal model. It also includes fishery statistics of the oceanic whitetip shark catch by fishery sector in the Hawaii-based longline fishery (Table A1), time series of estimates of standardized oceanic whitetip CPUE (sharks per set) during 1995–2010 for each alternative hypothesis about zero catches (Table A3), and histograms of Pearson residuals for oceanic whitetip shark CPUE for each alternative hypothesis (Fig. A2).

Fig. A1. Oceanic whitetip shark catch trends in the Hawaii-based pelagic longline fishery in 1995–2010 for the deep-set sector (solid line) and shallow-set sector (dashed line). Shallow-set sector data are not plotted for 2001–2004 because it was closed all or part of these years. Annual mean nominal CPUE for the two sectors (*a*), as well as annual mean nominal CPUE on sets with positive catch (solid lines) and percentages of zero catches (dashed lines) in the deep-set sector (*b*) and shallow-set sector (*c*) are presented.

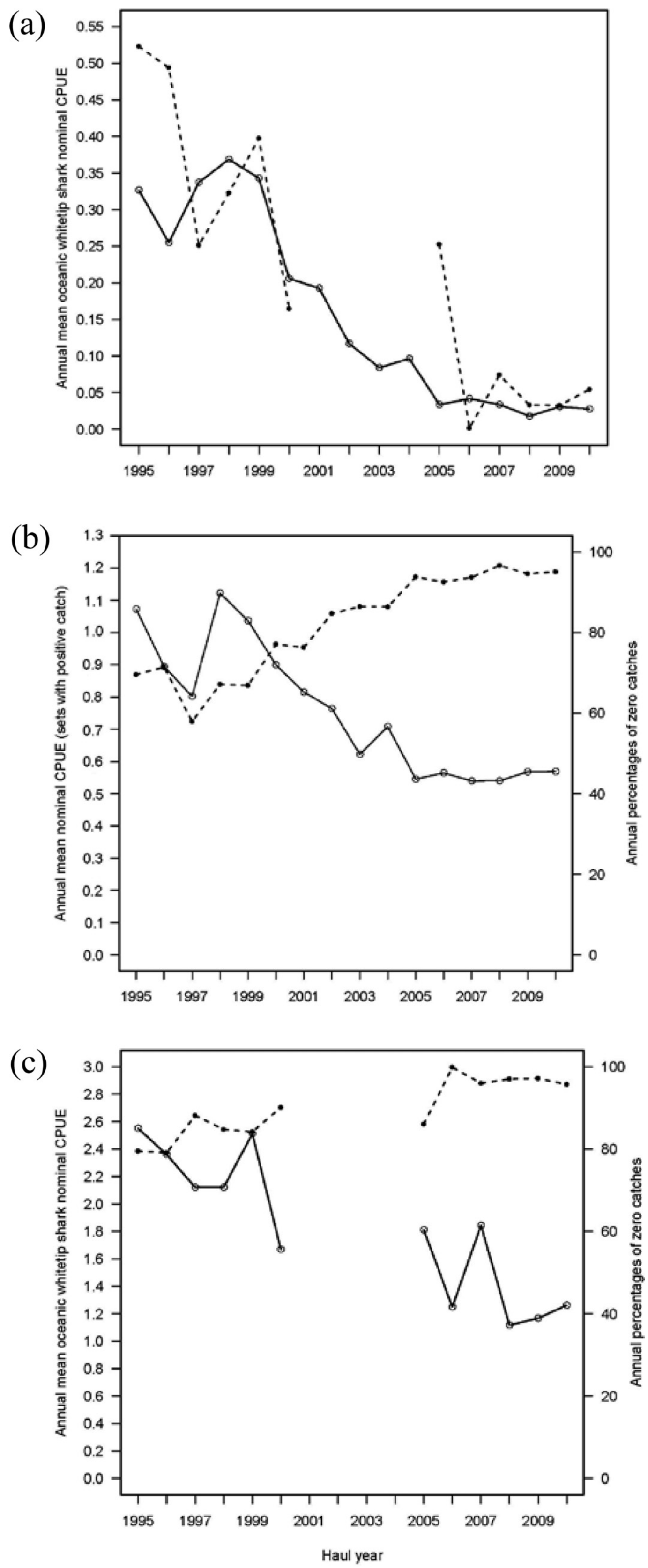


Table A1. Summary of the total catch of oceanic whitetip shark (number of sharks), mean nominal oceanic whitetip shark CPUE (sharks per 1000 hooks), and nominal fishing effort (number of sets) in the Hawaii-based longline fishery by sector, region, and quarter during 1995–2010.

Region	Parameter	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Deep-set sector					
Region 8	No. of sharks	—	—	—	—
	Mean CPUE	—	—	—	—
	Fishing effort	22	61	488	58
Region 7	No. of sharks	—	—	—	—
	Mean CPUE	—	—	—	—
	Fishing effort	7	40	1095	85
Region 6	No. of sharks	113	112	59	336
	Mean CPUE	0.058	0.080	0.058	0.081
	Fishing effort	960	739	532	2128
Region 5	No. of sharks	52	23	113	300
	Mean CPUE	0.014	0.006	0.014	0.028
	Fishing effort	1939	1758	3839	5232
Region 4	No. of sharks	368	603	365	419
	Mean CPUE	0.081	0.090	0.138	0.120
	Fishing effort	2150	3131	1315	1569
Region 3	No. of sharks	231	257	165	340
	Mean CPUE	0.066	0.070	0.088	0.106
	Fishing effort	1651	1913	1001	1745
Region 2	No. of sharks	509	377	251	266
	Mean CPUE	0.527	0.447	0.451	0.818
	Fishing effort	324	386	255	131
Region 1	No. of sharks	36	55	104	21
	Mean CPUE	0.460	0.271	0.505	0.808
	Fishing effort	20	76	95	15
Shallow-set sector					
Region 8	No. of sharks	1	6	57	1
	Mean CPUE	0.002	0.023	0.171	0.019
	Fishing effort	591	246	362	23
Region 7	No. of sharks	6	—	3	1
	Mean CPUE	0.002	—	0.063	0.001
	Fishing effort	3386	188	53	828
Region 6	No. of sharks	5	498	50	6
	Mean CPUE	0.009	0.319	0.852	0.166
	Fishing effort	621	1801	72	33
Region 5	No. of sharks	6	196	62	43
	Mean CPUE	0.018	0.157	0.731	0.559
	Fishing effort	329	1358	101	73
Region 4	No. of sharks	—	4	22	9
	Mean CPUE	—	0.856	1.036	1.274
	Fishing effort	0	5	25	8
Region 3	No. of sharks	—	18	150	—
	Mean CPUE	—	1.058	1.965	—
	Fishing effort	0	22	79	5
Region 2	No. of sharks	—	—	—	—
	Mean CPUE	—	—	—	—
	Fishing effort	0	0	0	0
Region 1	No. of sharks	—	—	—	—
	Mean CPUE	—	—	—	—
	Fishing effort	0	0	0	0

Note: A long dash (—) indicates no shark catch or CPUE.

Empirical patterns in the fishery

Trends in nominal CPUE of oceanic whitetip shark were similar for the deep-set and shallow-set sectors (Fig. A2*a*) and were significantly positively correlated (ρ = 0.81, $P < 0.002$). The temporal trends in nominal CPUE and nominal CPUE on sets with positive catch were negative, while the percentages of sets with zero observed catches increased in 1995–2010 in both fishery sectors (Fig. A2). Nominal CPUE (Fig. A2*a*) decreased on average by 1.9% and 2.9% per year in the deep- and shallow-set sectors, respectively. Nominal CPUE on sets with positive catch (Fig. A2*b*) decreased by 3.1% per year in the deep-set sector (Fig. A2*b*) and 4.1% per year in the shallow-set sector (Fig. A2*c*), while the number of sets with zero observed catches increased from 69.1% to 95.1% in the deep-set sector (Fig. A2*b*) and from 76.3% to 95.7% in the shallow-set sector (Fig. A2*c*). Thus, the substantial declines in oceanic whitetip shark nominal CPUE reflected both increases in proportions of sets with zero observed catch and decreases in numbers of sharks taken on sets with positive catches.

Summaries of the effects of fishery sector and fishing regions on quarterly nominal CPUE of oceanic whitetip shark nominal CPUE showed important spatial and seasonal variation (Table A1). There was substantial overlap of fishing effort in both fishery sectors in Regions 5 and 6, where the mean nominal shallow-set CPUE was generally greater and more variable than that in the deep-set sector. Regional effects were exemplified by the large differences (threefold to eightfold higher catch rates) between mean nominal

Table A2. Summaries of all GLM variable selection analysis of deviance methods used in this study: (A) Poisson, (B) negative binomial, (C) zero-inflated Poisson, (D) zero-inflated negative binomial, and (E) delta-gamma binomial.

(A) Poisson GLM[a].

Parameter	df	Pr>|χ^2|	ΔAIC	Percent AIC	ΔAIC per df	Median residual
Intercept	1	—	—	—	—	–0.527
Year	15	<0.0001	3943.1	9.8%	262.9	–0.392
Quarter	3	<0.0001	443.6	1.1%	147.9	–0.383
Region	7	<0.0001	3531.0	8.8%	504.4	–0.341
Set type	1	<0.0001	1271.9	3.2%	1271.9	–0.330
SST (quadratic)	2	<0.0001	1303.9	3.3%	652.0	–0.303

(B) Negative binomial GLM[b].

Parameter	df	Pr>|χ^2|	ΔAIC	Percent AIC	ΔAIC per df	Median residual	*k*
Intercept	1	—	—	—	—	–0.456	0.160
Year	15	<0.0001	2292.6	6.4%	152.8	–0.370	0.287
Quarter	3	<0.0001	347.6	1.0%	115.9	–0.360	0.299
Region	7	<0.0001	2326.0	6.5%	332.3	–0.326	0.548
Set type	1	<0.0001	968.3	2.7%	968.3	–0.319	0.686
SST (quadratic)	2	<0.0001	1054.4	3.0%	539.7	–0.291	0.870

(C) Zero-inflated Poisson GLM.

Parameter	df	Pr>|χ^2|	ΔAIC	Percent AIC	ΔAIC per df	Median residual
Counts model[c]						
Intercept	1	—	—	—	—	–0.297
Year	15	<0.0001	2358.8	6.5%	157.3	–0.258
Region	7	<0.0001	2512.6	6.9%	358.9	–0.241
Set type	1	<0.0001	1174.1	3.2%	1174.1	–0.229
SST (linear)	1	<0.0001	1056.6	2.9%	1056.6	–0.218
Zeros model						
Year	15	<0.0001	77.6	0.2%	5.2	–0.215
SST (linear)	1	<0.0001	265.6	0.7%	265.6	–0.201

(D) Zero-inflated negative binomial GLM.

Parameter	df	Pr>|χ^2|	ΔAIC	Percent AIC	ΔAIC per df	Median residual	*k*
Counts model[d]							
Intercept	1	—	—	—	—	–0.277	0.160
Year	15	<0.0001	2292.6	6.4%	152.8	–0.247	0.287
Region	7	<0.0001	2456.2	6.9%	350.9	–0.231	0.536
Set type	1	<0.0001	984.8	2.7%	984.8	–0.222	0.667
SST (linear)	1	<0.0001	1085.8	3.0%	1085.8	–0.208	0.817
Zeros model							
SST (linear)	1	<0.0001	182.9	0.5%	182.9	–0.204	0.963
Year	15	<0.0001	56.7	0.2%	3.8	–0.201	1.117

(E) Delta-gamma binomial GLM.

Parameter	df	Pr>|χ^2|	ΔAIC	Percent AIC	ΔAIC per df	Median residual
Gamma GLM: counts model[e]						
Intercept	1	—	—	—	—	–0.438
Year	15	<0.0001	389.3	1.0%	26.0	–0.277
Quarter	3	<0.0001	81.6	0.2%	27.2	–0.247
Region	7	<0.0001	109.8	0.3%	15.7	–0.208
Set type	1	<0.0001	310.1	0.8%	310.1	–0.179
Binomial GLM: zeros model[f]						
Intercept	1	—	—	—	—	–0.457
Year	15	<0.0001	1955.8	5.0%	130.4	–0.356
Quarter	3	<0.0001	269.4	0.7%	89.8	–0.350
Region	7	<0.0001	2584.1	6.6%	369.2	–0.312
Set type	1	<0.0001	214.7	0.6%	214.7	–0.309
SST (quadratic)	2	<0.0001	993.4	2.5%	496.7	–0.279

Note: Summaries include degrees of freedom (df) associated with each variable, the *P* value of the sequential χ^2 test (Pr>|χ^2|), the reduction in AIC (ΔAIC), the percent reduction in AIC from the null model AIC (Percent AIC), the reduction in AIC per degree of freedom (ΔAIC per df), the median residual from the fitted model, and the MLE of the overdispersion parameter (*k*) (sections B and D).

[a]Residual deviance = 20 161.7, pseudo-R^2 = 34.4%, null AIC = 40 059.1.

[b]Residual deviance = 14 903.6, pseudo-R^2 = 36.8%, null AIC = 35 614.9.

[c]Null AIC = 36 397.2.

[d]Null AIC = 35 616.9.

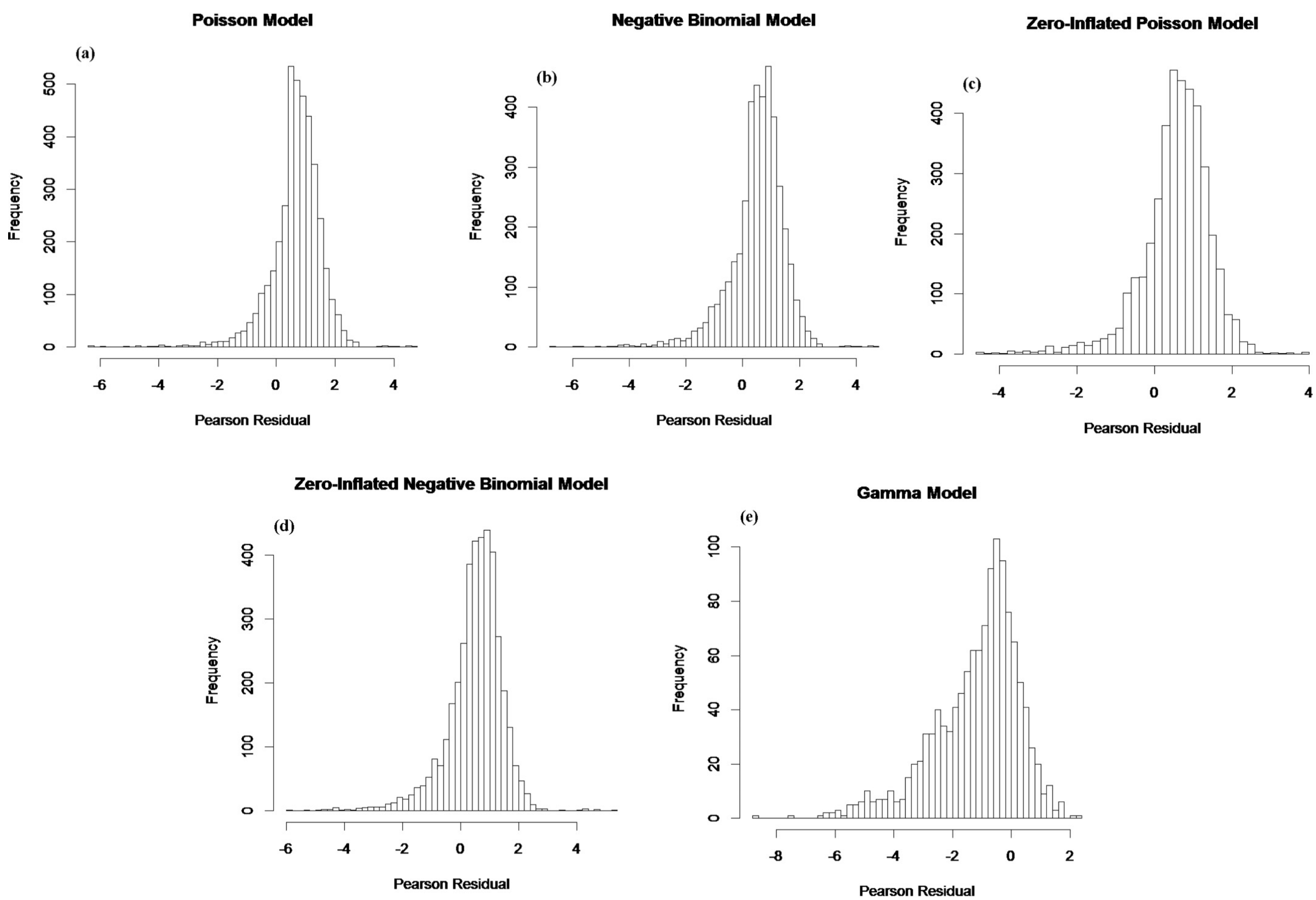
[e]Residual deviance = 964.4, pseudo-R^2 = 49.4%, null AIC = 38 997.3.

[f]Residual deviance = 22 066.6, pseudo-R^2 = 21.6%; combined gamma and binomial pseudo-R^2 = 23.5%.

Table A3. Estimates of annual mean standardized CPUE (μ, mean number of oceanic whitetip sharks caught per set) for the best-fitting ZINB model, four alternative standardization models, and the nominal mean CPUE along with corresponding estimates of the coefficient of variation of the mean CPUE (CV) and the sample size (n, number of sets per year).

Year	μ_{ZINB}	CV_{ZINB} (%)	μ_{P}	CV_{P} (%)	μ_{NB}	CV_{NB} (%)	μ_{ZIP}	CV_{ZIP} (%)	μ_{DG}	CV_{DG} (%)	$\mu_{NOMINAL}$	n
1995	0.548	6.0	0.482	5.5	0.539	6.0	0.503	5.3	0.499	3.7	0.542	477
1996	0.495	5.6	0.462	5.3	0.497	5.8	0.470	5.2	0.470	3.8	0.553	452
1997	0.536	8.9	0.456	8.3	0.543	9.1	0.467	7.7	0.464	5.1	0.430	351
1998	0.561	5.4	0.552	5.3	0.541	5.4	0.548	5.1	0.543	3.9	0.560	442
1999	0.541	7.7	0.483	7.8	0.531	8.0	0.496	6.9	0.478	5.6	0.548	352
2000	0.323	4.0	0.297	3.4	0.309	3.6	0.309	3.7	0.305	2.7	0.310	1061
2001	0.377	2.5	0.344	2.6	0.383	2.6	0.348	2.3	0.371	1.8	0.349	2406
2002	0.208	2.4	0.211	2.7	0.217	2.8	0.215	2.6	0.211	2.2	0.201	2767
2003	0.167	1.3	0.167	1.3	0.168	1.4	0.166	1.3	0.171	1.2	0.170	2959
2004	0.183	2.1	0.178	1.6	0.179	1.6	0.178	1.9	0.195	1.2	0.186	4051
2005	0.112	1.9	0.116	1.9	0.112	2.0	0.112	1.7	0.118	1.7	0.174	4997
2006	0.071	2.0	0.072	1.9	0.071	2.0	0.071	2.2	0.074	1.8	0.063	4143
2007	0.069	1.8	0.070	1.9	0.071	1.9	0.070	1.9	0.072	1.8	0.082	5093
2008	0.036	1.9	0.036	1.8	0.036	1.9	0.036	1.7	0.038	1.8	0.042	5366
2009	0.057	2.6	0.058	2.2	0.056	2.3	0.058	2.6	0.059	2.1	0.058	5139
2010	0.058	2.3	0.060	2.1	0.058	2.2	0.058	2.2	0.061	2.0	0.067	4913

Fig. A2. Histograms of Pearson residuals for oceanic whitetip shark CPUE values under the (*a*) Poisson, (*b*) negative binomial, (*c*) zero-inflated Poisson, (*d*) zero-inflated negative binomial, and (*e*) delta-gamma models.



CPUE in tropical waters (i.e., Regions 1 and 2) and all regions above 10°N. Very few oceanic whitetip sharks were caught in the deep-set sector above 30°N, and several species identifications were found to be questionable. As a result, deep-set sector sets above 30°N were not included in subsequent CPUE standardization analyses. The overall seasonal pattern consisted of a lower mean nominal CPUE in the first quarter (0.052 sharks per 1000 hooks), when the SST averaged 21.9 °C, than in quarters 2 through 4, when mean SST ranged from 24.6 to 25.9 °C and nominal mean CPUE ranged from 0.076 to 0.128 sharks per 1000 hooks.

Table A4. Matrix of Pearson correlation coefficients (ρ, below the diagonal) and angular deviations (θ, above the diagonal) between the annual mean nominal oceanic whitetip CPUE and the annual effect coefficients vectors from the GLM analyses.

Analysis	Delta-gamma	Poisson	Negative binomial	Zero-inflated Poisson	Zero-inflated negative binomial	Annual mean nominal CPUE
Delta-gamma	—	1.6°	3.4°	1.7°	3.1°	5.3°
Poisson	$\rho > 0.99$; $P < 0.001$	—	3.6°	1.0°	3.1°	5.0°
Negative binomial	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	—	3.0°	1.2°	6.4°
Zero-inflated Poisson	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	—	2.4°	4.9°
Zero-inflated negative binomial	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	$\rho > 0.99$; $P < 0.001$	—	6.0°
Annual mean nominal CPUE	$\rho = 0.99$; $P < 0.001$	$\rho = 0.99$; $P < 0.001$	$\rho = 0.98$; $P < 0.001$	$\rho = 0.99$; $P < 0.001$	$\rho = 0.98$; $P < 0.001$	—

Note: Significance values are from t tests of the correlation coefficients with 16 degrees of freedom.

Alternative models for capture probabilities

The Poisson (P) model consisted of a Poisson distribution with a mean catch rate parameter (μ). For a given longline set, the P model represented shark catch (C) as

$$\text{(A.1)} \qquad \Pr(C = c) = \frac{\mu^c \cdot \exp(-\mu)}{c!}$$

Given the P model, the expected catch C per hook was equal to the mean catch rate parameter, which was also equal to the variance of the catch

$$\text{(A.2)} \qquad E(C) = \mu = \mathrm{Var}(C)$$

Under the P model, the variance to mean ratio (VMR), or index of dispersion, is VMR = 1. As a result, the distribution of shark capture events is assumed to be more or less random in space and time. It was also hypothesized that the oceanic whitetip shark capture process generated only Poisson-distributed zero observations, the expected catch distribution was adequately approximated by a discrete Poisson random variable, and the predictors had an important influence on the expected catch distribution. The P model can be expressed as the limit of a large series of independent Bernouilli trials with a small constant probability of success. Under this interpretation, the Poisson model may provide an accurate approximation of the fishing process of longline gear deployment for a nontarget species in which thousands of hooks are deployed per set, with each hook having a small probability of capturing a shark. The P model was based on a standard probability distribution with a single parameter (μ) and a discrete response that accounted for zero counts. However, the variance of the capture process under the P model was inflexible because the VMR is identically unity with the capture process variance equal to the mean.

The negative binomial (NB) model consisted of a negative binomial distribution with a mean catch parameter (μ) and an overdispersion parameter (k). The NB model is a natural extension of the P model and arises as a way to represent the probability of observing a discrete number of captures (C) in a scaled time interval. For a given longline set, the NB model represented shark catch as

$$\text{(A.3)} \qquad \Pr(C = c) = \frac{(c + k)!}{k!(c + 1)!}\left(\frac{k}{k + \mu}\right)^k\left(\frac{\mu}{k + \mu}\right)^c$$

Assuming a negative binomial distribution for the capture process, the expected catch C per hook was equal to the mean catch rate parameter

$$\text{(A.4)} \qquad E(C) = \mu$$

and the variance of the catch C was

$$\text{(A.5)} \qquad \mathrm{Var}(C) = \mu + \frac{\mu^2}{k}$$

Under the NB model, the VMR is always greater than unity and is a decreasing function of k with

$$\text{(A.6)} \qquad \mathrm{VMR} = 1 + \frac{\mu}{k}$$

In this case, it was hypothesized that the oceanic whitetip shark capture process generated only negative binomially distributed zero observations, and it was also assumed that the expected catch was approximated by a discrete negative binomial random variable and that the predictive variables were adequate to fit the expected catch distribution. The NB model generalizes the P model by allowing for overdispersion in the catch process and is formally equivalent to a Poisson capture process with a time-varying mean catch rate parameter. As a result, the NB model has a much more flexible VMR for the capture process than the P model, and it explicitly accounts for both zero catch counts and potential overdispersion of catches.

The zero-inflated Poisson (ZIP) model was a mixture model that accounted for the observation of extra zeros in the catch data set. The ZIP model was composed of a binomial model, which measured the probability of observing an extra zero (π), times a Poisson count model with a mean catch rate parameter (μ) to measure the probability of Poisson-distributed catches of oceanic whitetip shark. In this context, extra zero catches, or excess zero observations, could have been due to multiple factors affecting observation error rates, for example, nondetection owing to the depth distribution of longline gear in comparison with shark habitat, misreporting of species, or nonobservation because the fishery observer was occupied by a protected species interaction or other task. Overall, the ZIP model was a mixture of binomial and Poisson distributions for which a zero catch could occur as an extra zero with probability π or as a Poisson-distributed zero with probability $1 - \pi$. This leads to the following expression for the ZIP distribution:

$$\text{(A.7)} \qquad \begin{aligned} &\Pr(C = 0) = \pi + (1 - \pi)\exp(-\mu) \\ &\Pr(C = c \mid c > 0) = (1 - \pi)\frac{\mu^c \cdot \exp(-\mu)}{c!} \end{aligned}$$

Given the zero-inflated Poisson assumption, the expected catch C per hook was equal to the probability of not observing an extra zero times the mean catch rate parameter:

$$E(C) = (1 - \pi)\mu \tag{A.8}$$

and the variance in catch was equal to

$$\mathrm{Var}(C) = (1 - \pi)(\mu + \pi\mu^2) \tag{A.9}$$

Under the ZIP model, the index of dispersion is always greater than unity and is an increasing function of the extra zero probability with

$$\mathrm{VMR} = 1 + \pi\mu \tag{A.10}$$

For the ZIP model, it was also hypothesized that the catch data for oceanic whitetip shark included both extra and Poisson zero observations, the expected catch was approximated with a discrete Poisson random variable, and the available predictors for standardizing effort were appropriate to fit both the extra zero probability and the expected catch distribution. The ZIP model was a two-parameter distribution (π, μ) that explicitly accounts for extra zeros. The ZIP model will exhibit some overdispersion for the binomial process generating extra zeros; however, the ZIP model provided less flexibility for modeling the mean–variance capture process than the NB model.

The zero-inflated negative binomial (ZINB) model was another mixture model that accounted for the possibility of observing extra zeros. The ZINB model was composed of a binomial model, which measured the probability of observing an extra zero (π), times a negative binomial count model with a mean catch rate parameter (μ) and an overdispersion parameter (k) to measure the probability of negative binomial zeros and positive catches of oceanic whitetip shark. As with the ZIP model, the ZINB model was a mixture of a binomial and a non-negative count distribution for which a zero catch could occur as an extra zero with probability equal to π or as a negative binomially distributed zero with probability equal to $1 - \pi$. This gives the ZINB distribution as

$$\begin{aligned} &\Pr(C = 0) = \pi + (1 - \pi)\left(\frac{k}{k + \mu}\right)^k \\ &\Pr(C = c \mid c > 0) = (1 - \pi)\frac{(c + k)!}{k!(c + 1)!}\left(\frac{k}{k + \mu}\right)^k\left(\frac{\mu}{k + \mu}\right)^c \end{aligned} \tag{A.11}$$

Given the zero-inflated negative binomial assumption, the expected catch C per hook was equal to the probability of not observing an extra zero times the mean catch rate parameter

$$E(C) = (1 - \pi)\mu \tag{A.12}$$

and the variance of the catch was

$$\mathrm{Var}(C) = (1 - \pi)\left(\mu + \frac{\mu^2}{k}\right) + \mu^2(\pi + \pi^2) \tag{A.13}$$

Under the ZINB model, the index of dispersion is always greater than unity and is a decreasing function of k and an increasing function of the extra zero probability with

$$\mathrm{VMR} = 1 + \frac{\mu}{k} + \frac{\mu\pi(1 + \pi)}{(1 - \pi)} \tag{A.14}$$

For the ZINB model, it was also hypothesized that the catch data for oceanic whitetip shark included both extra and negative binomial zero observations, the expected catch was approximated with a discrete negative binomial random variable, and the available predictors for standardizing effort were appropriate to fit both the extra zero probability and the expected catch distribution. The ZINB model was a three-parameter distribution (π, μ, k), which explicitly models the occurrence of extra zeros. The ZINB model exhibits overdispersion for both the binomial process generating extra zeros and the positive count process. As a result, it is more flexible for modeling excess variability in the observed count data than the ZIP model.

The delta-gamma (DG) model is a mixture model with a continuous response. This mixture model is composed of a Bernoulli random variable that determines whether or not the sampled set included a positive shark catch and a positive random variable that measures the magnitude of the conditional positive catch rate of sharks caught per hook (Aitchison 1955), which is a gamma distribution in this application. For a given longline set, the DG model includes the probability (p) that a set had a nonzero shark catch (C) and a gamma distribution for the conditional positive catch per hook with a rate parameter (λ) and a shape parameter (k) as

$$\begin{aligned} &\Pr(C = 0) = 1 - p \\ &\Pr(C = c \mid c > 0) = p \cdot \frac{\lambda^k c^{k-1} \cdot \exp(-\lambda c)}{\Gamma(k)} \end{aligned} \tag{A.15}$$

Given the delta-gamma assumption, the expected catch C per hook was the positive catch probability times the expected value of the gamma distribution:

$$E(C) = p \cdot \frac{k}{\lambda} \tag{A.16}$$

and the variance in catch C was

$$\mathrm{Var}(C) = p^2 \cdot \frac{k}{\lambda^2} \tag{A.17}$$

Under the DG model, the variance to mean ratio was an increasing function of the probability of a positive catch and a decreasing function of the gamma distribution shape parameter with

$$\mathrm{VMR} = \frac{p}{\lambda} \tag{A.18}$$

As a result, the DG model could exhibit overdispersion or underdispersion depending on whether $p > \lambda$ or $p < \lambda$.

For the DG model, it was hypothesized that the oceanic whitetip shark capture process included only binomially distributed zero observations, and it was also assumed that the conditional positive catch was approximated with a continuous gamma-distributed random variable and that the available predictors for standardizing effort were appropriate to fit both the positive catch probability and the expected catch distribution. In this case, the DG model approximated a discrete number of shark captures per set with an explicit approximation error in which a continuous variable was being used to model a discrete catch response. Overall, the DG model provided a three-parameter distribution (p, λ, k) with a very flexible mean–variance capture process that also allowed for wide tails in the response variable.

The delta-lognormal (DL) model is also a mixture model, composed of a Bernoulli random variable for whether or not the sampled set included a positive shark catch times a lognormal random variable that measured the magnitude of the conditional positive catch rate, indexed by the number of sharks caught per hook. For a given longline set, the DL model included the probability (p) that a set had a nonzero catch of shark (C) and a lognormal distribution for the conditional positive catch per hook with log-scale mean (ξ) and dispersion parameter (ϕ^2) as

$$\text{(A.19)} \quad \begin{aligned} &\Pr(C = 0) = 1 - p \\ &\Pr(C = c \mid c > 0) = p \cdot \frac{1}{c\phi\sqrt{2\pi}} \exp\left[\frac{-(\ln \xi - c)^2}{2\phi^2}\right] \end{aligned}$$

Given the delta-lognormal assumption, the expected catch C per hook was the positive catch probability times the expected value of the lognormal distribution:

$$\text{(A.20)} \quad E(C) = p \cdot \exp\left(\xi + \frac{\phi^2}{2}\right)$$

and the variance in catch C was

$$\text{(A.21)} \quad \mathrm{Var}(C) = p^2 \cdot \exp(2\xi)[\exp(2\phi^2) - \exp(\phi^2)]$$

Under the DL model, the index of dispersion was an increasing function of the probability of a positive catch with

$$\text{(A.22)} \quad \mathrm{VMR} = p \cdot \exp\left(\xi + \frac{\phi^2}{2}\right)[\exp(\phi^2) - 1]$$

For the DL model, it was hypothesized that the oceanic whitetip shark capture process included only binomially distributed zero observations, the conditional positive catch was approximated with a continuous lognormal random variable, and the available predictors for standardizing effort were appropriate to fit both the positive catch probability and the expected catch distribution. Thus, the application of the DL model to approximate a discrete number of shark captures per hook included an approximation error where a continuous variable was being used to model the discrete catch response. The DL model provided a three-parameter distribution (p, ξ, ϕ^2) with a flexible mean–variance capture process that also allowed for wide tails in the response variable. However, we could not directly compare the DL model with the other models using AIC because the lognormal component of the DL model was fit to log-transformed shark count data.

Variable selection for CPUE standardization models

Under the Poisson (Table A2-A) and negative binomial (Table A2-B) hypotheses, the selected predictors ranked by total reduction in AIC were year, region, quadratic SST, set type, and quarter. In comparison, the explanatory variables ranked by their relative reduction in AIC per degree of freedom were set type, quadratic SST, region, year, and quarter. This indicated that set type and SST included important information to explain variation in CPUE despite explaining less total deviance than the temporal and regional effects under both the P and NB models. The median residual declined by 43% and 36% in the fitting of the P and NB models, respectively (Tables A2-A and A2-B), which indicated that both models were progressively reducing the central tendency of the residual distribution. For the NB model, the overdispersion parameter increased about fivefold from the null to the best-fitting model, which indicated that the variance of the predicted catch decreased with k (Table 1). Overall, the P model explained about 34% of the deviance, while the NB model explained about 3% more, or 37% of the null deviance.

For the positive count distribution of the zero-inflated P (Table A2-C) and NB (Table A2-D) models, the two most important predictors for accounting for reductions in total AIC were region and year. The next two selected predictors were set type and linear SST, whose inclusion led to similar reductions in AIC. The explanatory variables ranked by their relative reduction in AIC per degree of freedom were set type and linear SST followed by region and year. In comparison with the P and NB models, we did not detect a significant effect of quarter on CPUE under the ZIP and ZINB count models. However, the results were consistent in showing that including set type and SST were important dimensions to help explain variation in CPUE despite accounting for less total deviance than the annual and regional effects.

There were two significant predictors for the extra zero process under the ZIP and ZINB models (Tables A2-C and A2-D). These were linear SST and year. Linear SST accounted for about threefold more variation than the year effect and was also much more important in explaining the amount of AIC per degree of freedom. Overall, the zero-inflated model results indicated that the SST effect was much more pronounced for explaining the extra zero process.

For the gamma positive catch distribution of the delta-gamma model, there were four predictors that explained a significant amount of deviance. These were, ranked in order of decreasing importance, year, set type, region, and quarter (Table A2-E). In terms of deviance explained per degree of freedom, the ranking was set type, quarter, year, and region. Thus, set type and season were important dimensions to account for in fitting the DG count model. In comparison with the best-fitting count models for the zero-inflated processes, the selected gamma positive catch distribution model did not included SST but instead included quarter. The lack of an SST effect reflected a major shift in the SST distributions of sets with positive catch (median: 26.2 °C) and zero catch sets (median: 24.1 °C) (Wilcoxon two-sample rank sums test: $P < 0.0001$). Because the gamma model included only positive catches, the SST range was effectively truncated as an explanatory variable.

Under the binomial positive catch probability of the delta-gamma model, there were a total of five significant explanatory variables in terms of total deviance explained. These were, ranked in order of decreasing importance, region, year, SST, quarter, and set type. In terms of deviance explained per degree of freedom, the ranking was SST, region, set type, year, and quarter. The binomial positive catch and the zero-inflated extra zero probability models each included SST, which reflected the importance of this environmental indicator of oceanic whitetip habitat.