Shark depredation rates in pelagic longline fisheries: a case study from the Northwest Atlantic

M. Aaron MacNeil, John K. Carlson, and Lawrence R. Beerkircher

A suite of modelling approaches was employed to analyse shark depredation rates from the US Atlantic pelagic longline fishery. As depredation events are relatively rare, there are a large number of zeroes in pelagic longline data and conventional generalized linear models (GLMs) may be ineffective as tools for statistical inference. GLMs (Poisson and negative binomial), two-part (delta-lognormal and truncated negative binomial, T-NB), and mixture models (zero-inflated Poisson, ZIP, and zero-inflated negative binomial, ZINB) were used to understand the factors that contributed most to the occurrence of depredation events that included a small proportion of whale damage. Of the six distribution forms used, only the ZIP and T-NB models performed adequately in describing depredation data, and the T-NB and ZINB models outperformed the ZIP models in bootstrap cross-validation estimates of prediction error. Candidate T-NB and ZINB model results showed that encounter probabilities were more strongly related to large-scale covariates (space, season) and that depredation counts were correlated with small-scale characteristics of the fishery (temperature, catch composition). Moreover, there was little evidence of historical trends in depredation rates. The results show that the factors contributing to most depredation events are those already controlled by ships' captains and, beyond novel technologies to repel sharks, there may be little more to do to reduce depredation loss in the fishery within current economic and operational constraints.

Keywords: bycatch, fisheries, zero-inflated models.

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Introduction

Sharks and cetaceans cause significant damage in pelagic longline operations worldwide, often as a consequence of bite-offs, loss of gear, catch displacement, reduced gear efficiency, and depredation of the catch (Gilman *et al.*, 2007). Depredation (when target species already captured are damaged by free-swimming predators) takes place in about half of all longline sets (Gilman *et al.*, 2007). At levels of 20% or more, economic losses from depredation can amount to thousands of dollars in lost revenue from a single set, so there is considerable motivation from fishers to avoid shark and cetacean interactions (Gilman *et al.*, 2008).

The dynamics of shark interactions in longline fisheries have generally been studied in terms of bycatch rates, where proportions of non-target species are modelled relative to suspected covariates of abundance (e.g. Francis *et al.*, 2001). In general, these models demonstrate notable bycatch rates of sharks, whales, and turtles attributable to both local (gear, temperature, depth) and regional (latitude, longitude, season) characteristics (Francis *et al.*, 2001; Beerkircher *et al.*, 2002; Gilman *et al.*, 2008). Some evidence has emerged to suggest that bycatch can be mitigated through changes in gear characteristics and fishing practices. Hook types, varying from previous use of "J" hooks to the now conventional use of "O" or circle hooks, have been

altered in many fisheries in response to demands for reduced commercial bycatch (Watson *et al.*, 2005b). Although such changes benefit pelagic ecosystems, gear and behavioural changes to reduce bycatch may have few positive effects for fishers; in contrast, depredation has a direct impact.

Although almost certainly related to bycatch dynamics, depredation events are scarcer in longline fisheries than the catch of many species and may be manifest through different processes from those determining bycatch rates. Whereas bycatch occurs through the same fishing processes as the other components of the catch, depredation takes place when species that are not part of the catch encounter hooked fish and attack them, rather than swallowing hooked bait. In addition, the size difference between a pelagic longline bait (usually squid or mackerel of 0.001–0.5 kg) and a caught fish (usually between 10 and 100 kg) is substantial, leading to potentially different processes influencing depredation and catch.

One of the main difficulties in modelling rates of depredation is the high incidence of zeroes in the data. Many zeroes can render traditional approaches to modelling bycatch inappropriate, particularly because such models fail to deal with the extensive over-dispersion that can be present. Two-stage models, such as a delta-lognormal, have been used to handle the zero and count

proportions of data separately (Lo *et al.*, 1992). An alternative approach for dealing with large numbers of zeroes is to model them explicitly, so that the presence or absence of a given phenomenon is specified through a Bernoulli distribution, and the number of occurrences is specified through another distributional form that has some density for zero observations, often as a Poisson (Hall, 2000), binomial (MacKenzie *et al.*, 2006), or negative binomial model (Minami *et al.*, 2007). Such models are often called "zero-inflated" or "mixture" models, highlighting the amalgamation of two distinct distributions to model simultaneously the presence/absence and count processes that may generate a set of observed data.

Depredation events are likely to fit the zero-inflated modelling approach well, because they occur in approximately half of observed longline sets and, when present, the number of depredated fish can range from 1 to 30 or more. The combination of a large number of zero observations along with the potential for large numbers of depredations on a given set are characteristic of previously successful fisheries studies that have employed the zero-inflated approach (Minami *et al.*, 2007). Here, we were specifically interested in (i) how different potential model and distributional assumptions could account for observed depredation rates, and (ii) what potential processes would be most related to depredation rates in the US Atlantic pelagic longline fishery. Our approach was to use a candidate set of models defined by the potential relationship of their covariates to specific biological processes and to compare this candidate set across distributional families.

Methods
Data collection
Data for the study were collected through the US Pelagic Observer Programme (USPOP), in which trained observers monitored randomly selected vessels undertaking commercial fishing and recorded detailed information on gear characteristics, location, environmental conditions, and the composition of the catch (Beerkircher *et al.*, 2004). Depredation events were recorded as "damaged", which included all forms of damage to the catch, including by cetaceans. We were unable to separate shark and whale damage in this study, but most of the depredated fish caught were likely to have experienced shark damage; discussions with active observers and a recent pilot study from the fishery found that cetacean damage accounted for <15% (170 of 1220) of depredation observations. As a result, we made the simplifying assumption that observations were the result of shark interactions. More detailed information regarding the USPOP is available in Beerkircher *et al.* (2004).

Candidate distributions
Because depredation data had not previously been modelled statistically, we employed five potential distributional forms to describe the observed depredation counts. A Poisson distribution is a frequent approach when analysing a set of count (integer-only) data and is among the most commonly used form of generalized linear models (GLMs; McCullagh and Nelder, 1989). The probability density function (PDF) for the Poisson is given by

$$f(y|\lambda) = \frac{\exp(-\lambda)\lambda^y}{y!}, \tag{1}$$

where λ is a shape parameter that describes both the mean and the variance of the distribution and y the number of depredations observed in n sets. Given available covariate information, the value of λ on any given set, i, can be estimated with a linear model structure:

$$\log(\lambda_t) = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n, \tag{2}$$

where $X_{i,\ldots,n}$ are the covariates of interest, and the values of β_i are their estimated coefficients. In cases where data are overdispersed relative to the Poisson distribution, the negative binomial distribution may provide a better fit (McCullagh and Nelder, 1989). The negative binomial differs from the Poisson by the inclusion of a scale parameter that describes the degree of overdispersion present relative to a Poisson, so adding substantial flexibility for describing count data (at the cost of estimating an additional parameter). The PDF for the negative binomial is given by

$$f(y|\mu, \theta) = \frac{\Gamma(\theta + y)}{\Gamma(\theta)y!} \left(\frac{\theta}{\theta + \mu}\right)^\theta \left(\frac{\mu}{\theta + \mu}\right)^y, \tag{3}$$

with mean μ and size parameter θ. The same linear model form as in Equation (2) can be used to estimate μ_i for any given set, and the negative binomial reduces to a Poisson as $\theta \to 1$ (Evans *et al.*, 2000).

When count data of length n contain a substantial number of zero observations, i.e. $n_{\text{zeroes}} > [(n_{\text{observations}})\exp(-\lambda)]$, the Poisson distribution fails to describe the zero portion of data well. Although statistically appropriate for rates rather than counts, a frequently used approach to dealing with excessive zeroes in fisheries models of catch per unit effort (cpue) or abundance data is the two-part delta-lognormal model (Delta-LN; Lo *et al.*, 1992; Stefánsson, 1996; Maunder and Punt, 2004). The approach splits the data into two datasets analysed separately, one giving the presence/absence of a response across all observations and a second a subset of only the positive counts observed. The presence/absence of depredation is described per set by a Bernoulli PDF:

$$y = \left\{ \begin{array}{l} 0, \text{ with probability } p \\ 1, \text{ with probability } 1 - p \end{array} \right\}, \tag{4}$$

where p can be modelled with covariates and a logit link:

$$\text{logit}(p_i) = \gamma_0 + \gamma_1 X_1 + \cdots + \gamma_n X_n. \tag{5}$$

Note that $1 - p$ represents the probability that at least one potentially depredating animal has encountered the gear and has attacked a caught fish. The count portion of the data is then assumed to be lognormally distributed:

$$f(y|\mu, \sigma) = \frac{1}{y\sigma(2\pi)^{1/2}} \exp\left(\frac{-\log(y - \mu)^2}{2\sigma^2}\right), \tag{6}$$

with μ and σ describing the mean and standard variation, respectively. As before, the values for μ_i can be modelled with covariates using a linear model approach:

$$\mu_i = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n. \tag{7}$$

Table 1. Candidate factors used to evaluate the inference weights for general processes affecting depredation rates in the US pelagic longline fishery.

Potential process	Factors used	Biological interpretation (hypothesis)
Effort	Soak time (h)	Longer soak times provide greater opportunity for the gear to be found
Gear	Proportion of lightsticks	More lights are more likely to attract animals, leading to depredation events
Environment	Depth (m), temperature (°C)	Ocean characteristics affect the dispersal of cues from distressed (caught) fish
Fishery	Target species	General fishing characteristics make depredation encounters more likely
Space	Latitude, longitude, management region	Some areas are more likely to have encounters owing to unmeasured characteristics; large-scale management regions contain differential depredation rates
Time	Year, season (winter = 1, summer = 0)	Increases or declines in predator populations through time lead to trends in depredation rates; seasonal migration trends may make caught fish more susceptible to depredation events
Catch	PCA$_1$, PCA$_2$	Catch compositions influence depredation events through the presence of depredating fish and/or favoured prey

A related two-part model more appropriate for discrete count data is the negative binomial hurdle model, where zeroes are governed by a Bernoulli process and counts modelled with a truncated delta-negative binomial distribution (O'Neill and Faddy, 2003). In this case, the lognormal distribution in Equation (6) is replaced by a truncated negative binomial (T-NB) for $y > 0$:

$$f(y|\mu, \theta) = \frac{\Gamma(\theta + y)}{\Gamma(\theta)y!} \left(\frac{\theta}{\theta + \mu}\right)^{\theta} \left(\frac{\mu}{\theta + \mu}\right)^{y} \left(\frac{1}{1 - (1 + \mu/\theta)^{-\theta}}\right),$$

(8)

where the probability of zero observations is only provided by the Bernoulli process and the negative binomial has probability only for counts ≥ 1 (Rose *et al.*, 2006).

An alternative approach for dealing with excess zero observations without partitioning data involves using a mixture of two distributional forms, a Bernoulli (zero) model for quantifying the presence or absence of positive counts, and a simultaneous count model of some other form for describing the distribution of positive observations. Unlike the Delta-LN approach, the count model includes some density for zero observations. These zero-inflated models are not part of the exponential family and are therefore not GLMs; however, they do allow covariate effects to be estimated for both the extra zero and count components of the data, similar to the GLM approaches above (Lewsey and Thomson, 2004). The most commonly used distribution mixture is to combine a Bernoulli distribution with a Poisson in a zero-inflated Poisson (ZIP) model (Lambert, 1992; Tu, 2002). In the context of depredation events, these components correspond to sets that have encountered animals available to depredate (with probability $1 - p$) and the number of depredations observed (with probability $\leq p$), given that such animals are there. The PDF is outlined by

$$y = \left\{ \begin{array}{l} 0, \text{ with probability } p \\ \text{Poisson}(\lambda), \text{ with probability } 1 - p \end{array} \right\}, \quad (9)$$

where the Poisson is specified as in Equation (1) (Tu, 2002). Given the availability of covariates for both the zero (Bernoulli) and count (Poisson) data, the full model is described through Equations (5) and (2), respectively.

Although ZIP models deal well with excess zeroes in a given dataset, observations can still be too overdispersed for the Poisson distribution to handle. As described in the GLM case

above, the zero-inflated negative-binomial (ZINB) may be more appropriate in these cases; the Poisson in Equation (9) is replaced by the negative binomial distribution in Equation (3), and linear models are specified for both the zero and count observations.

To evaluate their appropriateness for depredation data, each of the five distribution models were fitted by maximum likelihood (ML) in R (R Development Core Team, 2008) using the glm, hurdle, and zeroinfl algorithms from the stats and pscl libraries.

Candidate models

Although determining the appropriate distributional form for the depredation data was important, we also wished to understand the potential processes affecting depredation rates in the Northwest Atlantic. We grouped a subset of the covariates available from the observer data into seven process categories that described different aspects of the fishery (Table 1), based on their assumed importance in other studies and our own ideas on depredation. Owing to the dominance of particular target and bycatch species in the catch, community composition covariates were generated using the first- and second-axis principal components analysis (PCA) scores of the caught fish across all sets (Table 2; Jongman *et al.*, 1995). Covariates within a given process were grouped together in a base set of linear models to describe individual processes (Table 3) that were in turn combined into a larger set of candidate models for more complex interactions (Table 4).

Using the full set of 32 candidate models, we evaluated the weight of evidence for each one in each of the six potential model distribution structures using Akaike's Information Criterion (AIC; Akaike, 1974) and the full dataset. As they do not include an encounter model component, the candidate zero models were not run for the Poisson and negative binomial

Table 2. Dominant PCA factor loadings describing the catch composition of US Atlantic pelagic longline sets.

Species	PCA$_1$	PCA$_2$
Yellowfin tuna	**−0.149**	−0.169
Skipjack tuna	−0.007	−0.007
Bigeye tuna	0.030	−0.024
Dusky shark	−0.004	0.003
Night shark	0.009	0.004
Atlantic swordfish	0.486	**0.843**
Blue shark	**0.858**	**−0.506**
Cumulative variance	0.430	0.700

Highest and lowest loadings are shown emboldened.

Table 3. Basic candidate model set for depredation events in the US pelagic longline fishery.

Name	Potential process(es)	Zero model[a]	Count model
M0		β_0 (intercept only)	γ_0 (intercept only)
M1	E	$\beta_0 + \beta_1 SOK$	$\gamma_0 + \gamma_1 SOK$
M2	G,N	$\beta_0 + \beta_1 PLS + \beta_2 DEP + \beta_3 TMP$	$\gamma_0 + \gamma_1 PLS + \gamma_2 DEP + \gamma_3 TMP$
M3	F	$\beta_0 + \beta_{1\ldots n} TAR$[b]	$\gamma_0 + \gamma_{1\ldots n} TAR$[b]
M4	S	$\beta_0 + \beta_1 LAT + \beta_2 LON$	$\gamma_0 + \gamma_1 LAT + \gamma_2 LON$
M5	S	$\beta_0 + \beta_{1\ldots n} ARA$[b]	$\gamma_0 + \gamma_{1\ldots n} ARA$[b]
M6	T	$\beta_0 + \beta_1 YEA$	$\gamma_0 + \gamma_1 YEA$
M7	T	$\beta_0 + \beta_1 YEA + \beta_2 SEA$[b] $+ \beta_3 YEA \times SEA$[b]	$\gamma_0 + \gamma_1 YEA + \gamma_2 SEA$[b] $+ \gamma_3 YEA \times SEA$[b]
M8	C	$\beta_0 + \beta_1 PCA_1 + \beta_2 PCA_2$	$\gamma_0 + \gamma_1 PCA_1 + \gamma_2 PCA_2$

General processes represented include effort (E), gear (G), environmental (N), fishery (F), space (S), time (T), and catch (C). Factors used include: SOK, soak time; PLS, % lightsticks; DEP, depth; TMP, temperature; TAR, target species; LAT, latitude; LON, longitude; ARA, management area; YEA, year; SEA, season; PCA_1, first-axis PCA of catch; PCA_2, second-axis PCA of catch.
[a]Zero model component not run in Poisson and negative binomial GLMs.
[b]Fixed factor modelled with dummy variable(s).

Table 4. Complex candidate model set for depredation events in the US pelagic longline fishery.

Model	Potential processes	Zero model[a]	Count model
M9	E,S	M1 + M4	M1 + M4
M10	E,G,N,S	M1 + M2 + M4	M1 + M2 + M4
M11	E,G,N,S	M4	M1 + M2
M12	E,G,N,S	M1 + M2	M4
M13	F,C,S	M3 + M8	M4
M14	F,C,S	M4	M3 + M8
M15	F,C,S	M3 + M8	M5
M16	F,C,S	M5	M3 + M8
M17	S,T	M4 + M7	M4 + M7
M18	S,T	M5 + M7	M5 + M7
M19	S,T	M7	M4
M20	S,T	M7	M5
M21	E,G,N,C	M1 + M2 + M8	M1 + M2 + M8
M22	E,G,N,C	M1 + M2	M8
M23	E,G,N,C	M8	M1 + M2
M24	G,N,T,C	M2	M7 + M8
M25	G,N,T,C	M7 + M8	M2
M26	E,G,N,T,C	M1 + M2	M7 + M8
M27	E,G,N,T,C	M7 + M8	M1 + M2
M28	G,N,T,C,S	M2 + M5	M7 + M8
M29	G,N,T,C,S	M7 + M8	M2 + M5
M30	E,S,C	M1 + M5 + M8	M1 + M5 + M8
M31	E,G,N,S,C	M1 + M2 + M5 + M8	M1 + M2 + M5 + M8
M32	S,C	M5 + M8	M5 + M8

General processes represented include effort (E), gear (G), environmental (N), fishery (F), space (S), time (T), and catch (C). Linear model structures are given by specified combinations of the basic candidate model set provided in Table 3.
[a]Zero model component not run in Poisson and negative binomial GLMs.

distributions. In each case, model fits were compared with a null (intercept-only) model using a likelihood ratio test (LRT), where test-statistic values near zero (<0.01) were considered to be evidence of model structure with some support in the data. Residual plots were used to determine the adequacy of model fits. Although the AIC allowed us to compare model-based evidence within each distributional family, it did not allow us to select among distributional forms to decide which had the most appropriate fit.

To compare the relative model fits among distributions, we initially plotted the observed against the predicted distributions

for the full dataset to see which count residuals were most susceptible to high levels of dispersion. Although those results revealed strong differences among distribution forms, they provided no indication of how the models would perform outside the observed data. In an attempt to assess the robustness of our modelling results and to further compare among distribution forms, we conducted a bootstrap cross-validation (BCV; the k-fold procedure of Efron and Tibshirani, 1993) of the best-fitting linear model within each distribution family. Half the dataset (3714 sets) was used to calculate parameter estimates that were then used to predict the remaining half of the observations. This was repeated for 300 random samples of the data with the percentage prediction error at each count (between the observed and predicted data) and the resulting parameter estimates stored at each iteration. This allowed us both to determine the relative prediction error given each model structure and to build-up bootstrap distributions of parameter estimates that were subsequently used to calculate 95% percentile intervals of parameter uncertainty.

Results

Depredation events in the US Atlantic pelagic longline fishery were relatively common, occurring in 53% of all sets between 1992 and 2006; the true number of depredations may have been slightly higher, as leader bite-offs averaged 2.3% of recorded hooks. However, the distribution of events was highly skewed, with large numbers of zeroes and ones (71% of all sets) and a few (1.2%) observations of >10 depredations per set (Figure 1). The species breakdown of depredation events showed that caught tuna and sailfish experienced the greatest levels of depredation, whereas sharks tended to have the lowest (Table 5). Of the species readily identified, bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) were the most commonly depredated species, whereas blue shark (*Prionace glauca*) was frequently caught but experienced a very low level of depredation. The exceptionally large (77%) proportion of unidentified *Thunnus* spp. depredations was attributable to near-complete consumption of the animal, leading to difficulty in identification.

Model covariates were examined for correlation before analysis of the candidate model set, with no correlations >0.6 found among the factors used. The synthetic PCA variables developed from the set vs. species matrix of the catch implicated three species of importance related to catch composition: yellowfin tuna, swordfish (*Xiphias gladius*), and blue shark. Combined, the first and second axes were associated with 70% of the total
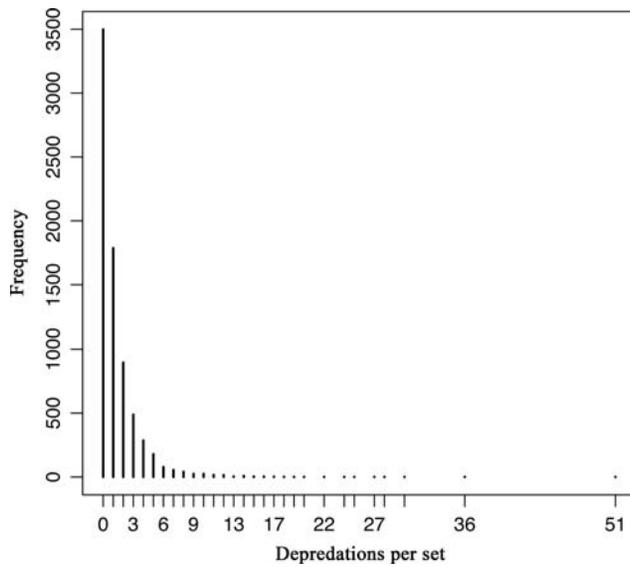
Figure 1. Observed frequency distribution for depredations per set in the US Atlantic pelagic longline fishery, 1992–2006.

Table 5. Species breakdown of depredation events for species with >200 observations in the US pelagic longline fishery.

Species	Observed	Depredations	Proportion
Thunnus spp.	668	512	0.766
Istiophorus spp.	543	53	0.098
Thunnus obesus	12 952	964	0.074
Thunnus albacares	38 801	2 852	0.074
Alepisaurus spp.	9 818	631	0.064
Rhizopriodon terraenovae	204	13	0.064
Thunnus alalunga	5 816	323	0.056
Acanthocybium solandri	1 844	91	0.049
Trichiuridae	433	21	0.048
Xiphias gladius	69 667	3 268	0.047
Thunnus atlanticus	2 204	94	0.043
Thunnus thynnus	1 712	71	0.041
Lepidocybium flavobrunneum	7 126	209	0.029
Ruvettus pretiosus	1 152	32	0.028
Istiophorus albicans	2 075	56	0.027
Carcharhinus signatus	1 719	41	0.024
Sphyraena spp.	331	7	0.021
Unknown	2 182	44	0.020
Makaira nigricans	2 044	41	0.020
Sphyrna lewini	865	17	0.020
Katsuwonus pelamis	1 534	28	0.018
Cubiceps spp.	221	4	0.018
Tetrapturus albidus	3 359	53	0.016
Brama spp.	546	8	0.015
Coryphaena hippurus	22 323	302	0.014
Carcharhinus spp.	257	3	0.012
Euthynnus alletteratus	350	4	0.011
Tetrapturus pfluegeri	203	2	0.010
Isurus oxyrinchus	3 085	27	0.009
Tetrapturus spp.	257	2	0.008
Unclassified sharks	1 737	13	0.007
Carcharhinus falciformis	3 844	27	0.007
Sphyrna spp.	572	4	0.007
Carcharhinus obscurus	2 278	14	0.006
Alopias superciliosus	704	3	0.004
Alepisaurus spp.	236	1	0.004
Prionace glauca	30 615	83	0.003
Mola spp.	684	1	0.001
Carcharhinus plumbeus	939	1	0.001
Galeocerdo cuvier	1 381	1	0.001
Raja spp.	8 082	5	0.001

TL is total length (cm).

variation in the community matrix, demonstrating that they were appropriate descriptors of the observed catch.

Among the five distributions used, only the ZINB and T-NB model structures adequately described both the large numbers of observed ones and zeroes as well as the highly right-skewed number of depredation events (Figure 2a). The excess zeroes observed caused both the Poisson and negative binomial GLMs to grossly underestimate the observed numbers of ones and twos in the data. Although the Delta-LN model accounted directly for the probability of encounter, it consistently overestimated the number of ones and underestimated the number of twos among the positive counts from the truncated (positive) data. By design, the Delta-LN did a better job of describing the observed zeroes than either the Poisson or the negative binomial model (Figure 2b). The second two-part model, the T-NB approach, performed substantially better than the Delta-LN model, accurately characterizing both the count and zero portions of the data. Similarly, both the ZIP and ZINB mixture distributions accurately described the observed proportion of zeroes in the data, and both models captured the distribution of the positive counts better than many of the other models.

Overall prediction error was highest in the Poisson and negative binomial models, which consistently overestimated zero counts and underestimated ones by ~40% (Figure 3). Neither model adequately described both the large numbers of zeroes and the long-tailed distribution of counts >10. The Delta-LN model showed a somewhat improved fit, particularly for the zeroes, but it consistently over-predicted ones and under-predicted twos by ~60%. That model also consistently predicted an excess of counts from two to five. As for the full dataset, both the zero-inflated and T-NB models had better predicted fits than the other distributions in the BCV results. Yet, despite such improvements, the ZIP model consistently predicted 9% more ones than were observed in the remaining data and under-predicted counts from two to four by 2–5%. The ZINB model fared better, having a positive prediction error only for the ones, and only of 1–2%. Finally, the T-NB model demonstrated the lowest prediction error of any of the

model structures, showing little to no prediction error across the entire range of depredation events.

Given the substantially improved fit and reduced prediction error, the ZINB and T-NB models were selected for subsequent inference about sources of longline depredation in the US Atlantic. M31 was the top-ranked model in all distribution forms, with ΔAIC values of 8 or more in every case (Table 6). LRT values were <0.001 in the ZINB and T-NB models, indicating that they had some level of support in the data, and residual plots demonstrated adequate model fit. Model M31 was among the most complex in the candidate model set, suggesting that the selected covariate set was appropriate and that most of the factors included were informative about depredation rates. This assertion was largely supported by parameter estimates for ZINB M31 (Table 7), where 14 of the 24 estimated parameters had 95% confidence intervals that did not span zero, indicating
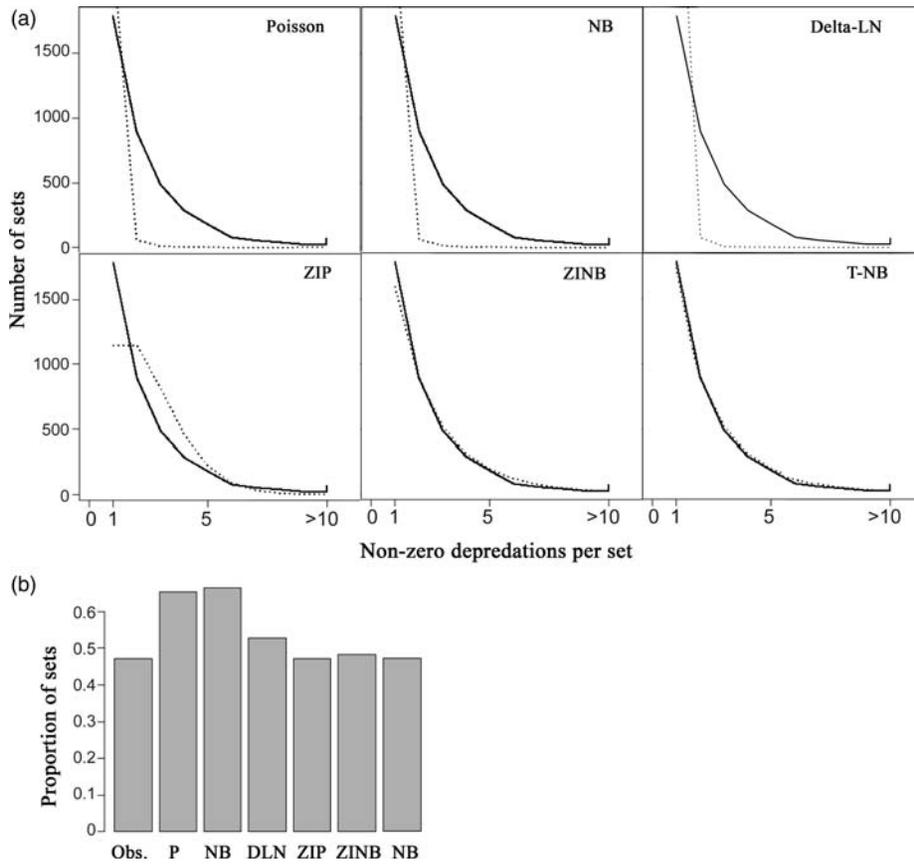
Figure 2. Observed and predicted frequencies of depredation events per set in the US Atlantic pelagic longline fishery. Plots include frequencies of (a) positive counts and (b) zeroes.
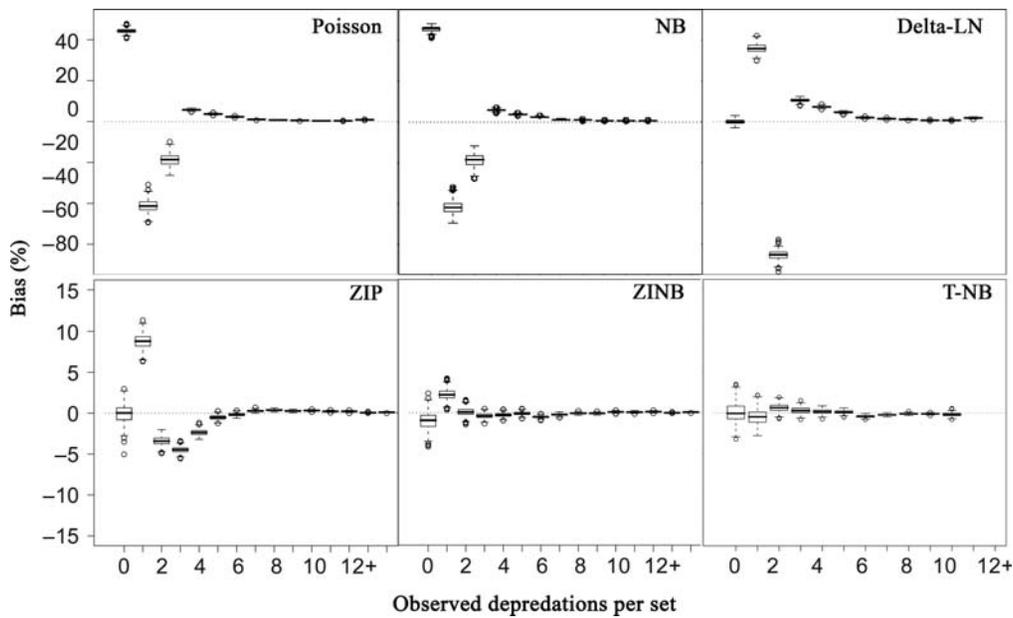

Figure 3. Relative bias plots between observed and predicted depredations from the best-fitting Poisson, negative binomial (NB), Delta-LN, ZIP, ZINB, and T-NB models, based on 300 resamples of the US pelagic longline observer dataset. For each iteration, model parameters estimated from half the dataset were used to predict the remaining observations, with bias calculated as the discrepancy between predicted and observed values.

Table 6. Model selection results for top-ranked Poisson (P), negative binomial (NB), Delta-LN, ZIP, ZINB, and T-NB models of depredation events in the US pelagic longline fishery.

Model	P	NB	Delta-LN$_{zero}$	Delta-LN$_{count}$	ZIP	ZINB	T-NB
M31	27 782 (0)	22 970 (0)	9 961 (0)	8 038 (0)	22 486 (0)	21 525 (0)	22 820 (0)
M21	27 850 (68)	22 993 (23)	10 034 (73)	8 046 (8)	22 594 (109)	21 728 (202)	22 901 (81)
M14	27 972 (190)	23 050 (80)	10 037 (75)	8 174 (136)	22 780 (294)	–	23 016 (196)
M30	28 117 (335)	23 085 (115)	10 048 (87)	8 080 (41)	22 648 (163)	21 656 (131)	22 936 (116)
. . .							
M0	29 049 (1267)	23 393 (423)	10 276 (315)	8 236 (197)	23 138 (652)	22 177 (652)	23 316 (496)

Values are AIC, with DAIC given in parentheses; model statistics for both the binomial and lognormal components of Delta-LN. Linear model structures provided in Tables 3 and 4.

Table 7. Parameter estimates for the best-fitting ZINB model of depredation events in US pelagic longlines.

Parameter	Zero	Count
ML		
Intercept	−1.52 [−10.58, 7.52]	−0.49 [−0.97, −0.02]
Soak time	−0.95 [−1.32, −0.58]	0.01 [−0.01, 0.03]
Proportion of lightsticks	0.20 [−1.19, 1.58]	−0.61 [−0.72, −0.50]
Depth	−0.024 [−0.01, −0.00]	−0.007 [−0.01, −0.001]
Temperature	−0.03 [−0.05, −0.02]	0.010 [0.007, 0.012]
PCA$_1$	−0.06 [−0.08, −0.03]	0.01 [0.007, 0.013]
PCA$_2$	−0.04 [−0.07, −0.01]	0.016 [0.012, 0.019]
Latitude	0.46 [0.29, 0.63]	0.016 [0.012, 0.023]
Longitude	0.15 [0.09, 0.22]	0.00 [−0.01, 0.01]
Season	6.00 [3.74, 8.26]	0.02 [−0.11, 0.16]
Year	0.11 [0.02, 0.21]	−0.01 [−0.02, 0.00]
Season × year	0.13 [−0.02, 0.27]	0.13 [−0.02, 0.17]
BCV		
Intercept	3.32 [−15.11, 18.46]	−0.58 [−1.62, 0.43]
Soak time	−0.95 [−1.74, −0.36]	0.02 [0.001, 0.100]
Proportion of lightsticks	−0.01 [−2.34, 2.28]	−0.59 [−0.71, −0.45]
Depth	−0.024 [−0.14, 0.056]	−0.007 [−0.012, −0.002]
Temperature	−0.03 [−0.07, −0.02]	0.010 [0.007, 0.013]
PCA$_1$	−0.06 [−0.10, −0.03]	0.010 [0.005, 0.014]
PCA$_2$	−0.04 [−0.08, −0.01]	0.016 [0.011, 0.020]
Latitude	0.43 [0.11, 0.78]	0.015 [0.003, 0.030]
Longitude	0.19 [0.08, 0.31]	0.00 [−0.01, 0.01]
Season	6.33 [3.65, 12.43]	0.04 [−0.16, 0.21]
Year	0.10 [−0.16, 0.23]	−0.011 [−0.03, 0.00]
Season × year	0.18 [−0.04, 0.59]	0.01 [−0.01, 0.03]

Coefficients are given for the ML estimates from the full dataset and the BCV values for the binomial (probability of zero; on logit-scale) and negative binomial (count) portions of model M31 (Table 4). ML, mean [2.5%, 97.5% confidence interval]; BCV, mean [2.5%, 97.5% percentile interval]. ZINB q (dispersion) parameter estimates were 0.873 and 0.885 for ML and BCV, respectively.

Table 8. Parameter estimates for the best-fitting T-NB model of depredation events in US pelagic longlines.

Parameter	Zero	Count
ML		
Intercept	−2.40 [−3.14, −1.66]	−0.50 [−1.24, 0.23]
Soak time	0.098 [0.05, 0.15]	0.01 [−0.02, 0.02]
Proportion of lightsticks	−0.53 [−0.68, −0.38]	−0.77 [−0.95, −0.60]
Depth	−0.01 [−0.02, −0.00]	−0.007 [−0.01, −0.002]
Temperature	0.014 [0.011, 0.017]	0.011 [0.007, 0.015]
PCA$_1$	0.02 [0.013, 0.028]	0.010 [0.006, 0.014]
PCA$_2$	0.03 [0.023, 0.033]	0.014 [0.010, 0.019]
Latitude	0.00 [−0.01, 0.01]	0.007 [−0.003, 0.018]
Longitude	−0.02 [−0.03, −0.01]	0.001 [−0.003, 0.007]
Season	0.29 [0.10, 0.47]	−0.06 [−0.26, 0.15]
Year	−0.00 [−0.02, 0.02]	−0.02 [−0.04, −0.001]
Season × year	−0.03 [−0.05, −0.01]	0.03 [0.01, 0.05]
BCV		
Intercept	−2.44 [−3.11, −1.67]	−0.72 [−2.11, 0.40]
Soak time	0.10 [0.05, 0.15]	0.00 [−0.001, 0.11]
Proportion of lightsticks	−0.53 [−0.68, −0.37]	−0.74 [−0.96, −0.55]
Depth	−0.009 [−0.01, −0.004]	−0.007 [−0.015, −0.002]
Temperature	0.014 [0.01, 0.02]	0.010 [0.006, 0.017]
PCA$_1$	0.017 [0.01, 0.02]	0.009 [0.002, 0.015]
PCA$_2$	0.028 [0.024, 0.033]	0.015 [0.009, 0.021]
Latitude	0.002 [−0.01, 0.01]	0.008 [−0.007, 0.030]
Longitude	−0.02 [−0.025, −0.016]	0.00 [−0.01, 0.01]
Season	0.28 [0.10, 0.48]	−0.07 [−0.02, 0.14]
Year	0.00 [−0.16, 0.02]	−0.023 [−0.04, −0.001]
Season × year	−0.03 [−0.05, −0.02]	0.02 [0.004, 0.05]

Coefficients are given for the ML estimates from the full dataset and the BCV values for the binomial (probability of zero; on logit-scale) and T-NB (count) portions of model M31 (Table 4). ML, mean [2.5%, 97.5% confidence interval]; BCV, mean [2.5%, 97.5% percentile interval]. T-NB q (dispersion) parameter estimates were 0.351 and 0.364 for ML and BCV, respectively.

tractable relationships. Similar results were observed for T-NB M31 (Table 8), with 16 of the 24 parameters failing to span zero. In both models, the BCV results generally supported the parameter estimates from model predictions of the full data (i.e. the GLM estimates from R), although a positive trend in encounter probabilities per year was marginal in the BCV estimates. Note that the bootstrap percentile intervals were based on half the data at each iteration and were therefore more conservative than the ML-estimated confidence intervals based on the full dataset.

In general, the zero component of ZINB M31 was most related to spatial, seasonal, and catch composition factors, but relatively

unrelated to effort, environment, and fishery characteristics. The logit-scale coefficient estimate for season (6.33) showed that encounter (non-zero) probabilities increased appreciably in summer (May–September; Figure 4a). Encounter probabilities were higher in western than in eastern areas, and there was some evidence for lower encounter probabilities in the north. Moreover, encounters were more likely in cooler water, particularly in areas with large numbers of blue sharks (PCA$_1$) and swordfish (PCA$_2$). Longer soak times were associated with greater encounter probabilities, but from plots of expected encounter probabilities per soak hour, it was clear that that trend was driven primarily by low encounter probabilities in the first two
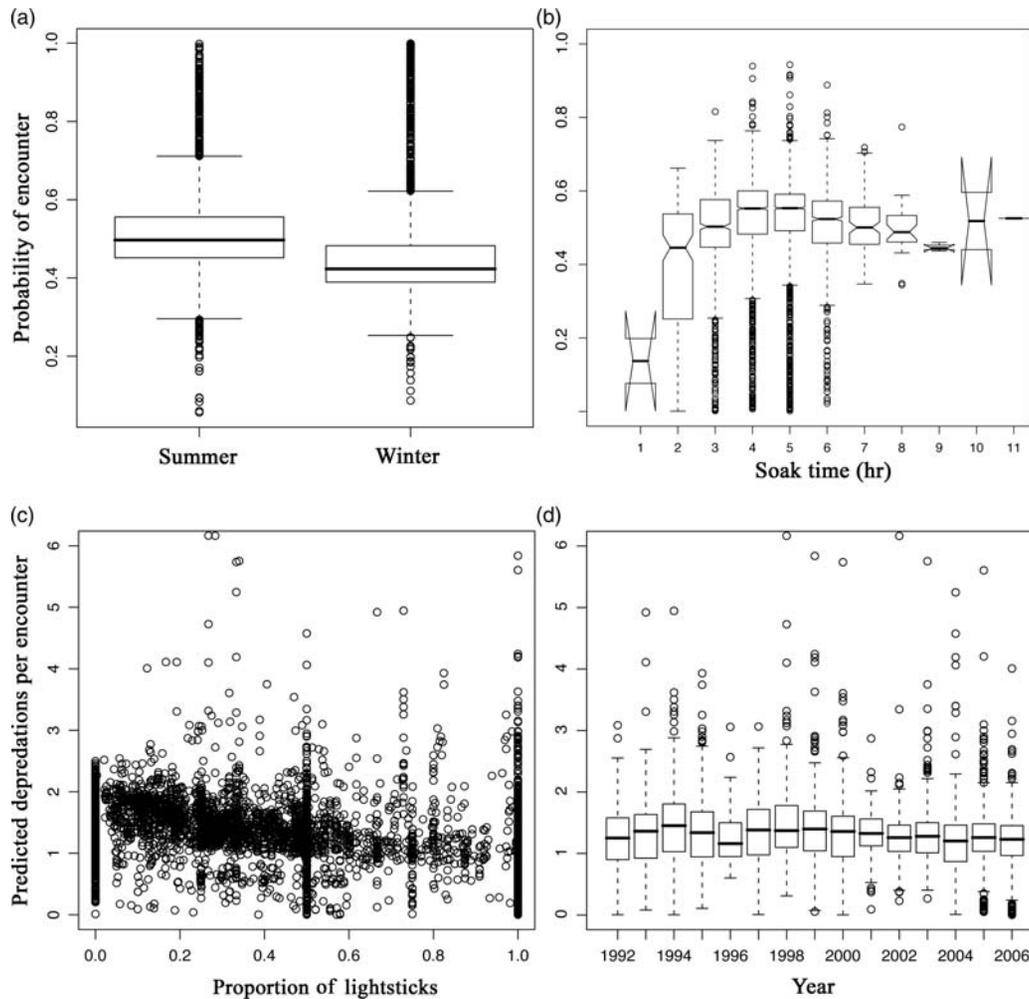
Figure 4. Marginal estimates of probability of encounter and depredation counts given encounter in the US Atlantic pelagic longline fishery, 1992–2006, using a ZINB approach. Estimates include the effects of (a) season and (b) year on encounter probabilities, and the effects of (c) proportion of lightsticks and (d) year on depredation counts. The lower panels have been truncated for presentation purposes; fewer than 1% of predicted counts were >6. Parameter estimates are provided in Table 6.

soak hours (Figures 4b and 5b). Finally, the percentage of lightsticks on a given set was positively associated with encounters, and there was little evidence of a positive or negative trend in encounter probabilities through time.

The T-NB M31 zero model parameter estimates differed from the ZINB estimates, with substantial differences in multiple parameters between models; soak time, year, and the catch PCA axes were negative in the ZINB model and positive in the T-NB model, whereas longitude was positive in the ZINB model and negative in the T-NB results (Table 8). Moreover, both the proportion of lightsticks used (Figure 5b) and a year × season interaction showed some evidence of being negative in the T-NB model. Finally, the strong seasonal effect on zero catches from the ZINB model was greatly reduced (from 6.00 to 0.29) in the T-NB approach.

Contrary to the encounter parameters, there was considerable agreement between the ZINB and T-NB M31 results. Sets with positive depredation counts were more associated with effort and gear characteristics than space or season, and catch composition was an important correlate of depredation. The model-predicted percentages of lightsticks used were negatively associated

with depredation counts (Figures 4c and 5c). Additional factors included effort, with longer soak times leading to more depredations, and catch composition, where large numbers of blue sharks and swordfish were correlated with larger numbers of depredations. As for encounter probabilities, the numbers of depredation events were greater in northern waters, and there was little evidence of an annual trend in depredation numbers (Figures 4d and 5d). To confirm this lack of annual trend, we ran a *post hoc* ZINB model using the general structure of M31, but with each sampling year as an individual fixed factor. This model had a substantially poorer fit (ΔAIC > 16), with few years showing substantial departure from the 1992 mean values.

Discussion

Most studies investigating shark interactions with pelagic longlines have dealt explicitly with bycatch (e.g. Francis *et al.*, 2001; Megalofonou *et al.*, 2005; Watson *et al.*, 2005b). Here, however, we utilize a unique set of depredation data to estimate trends and sources of variation in an additional component of a well-studied pelagic fishery. The first, and most potentially problematic,
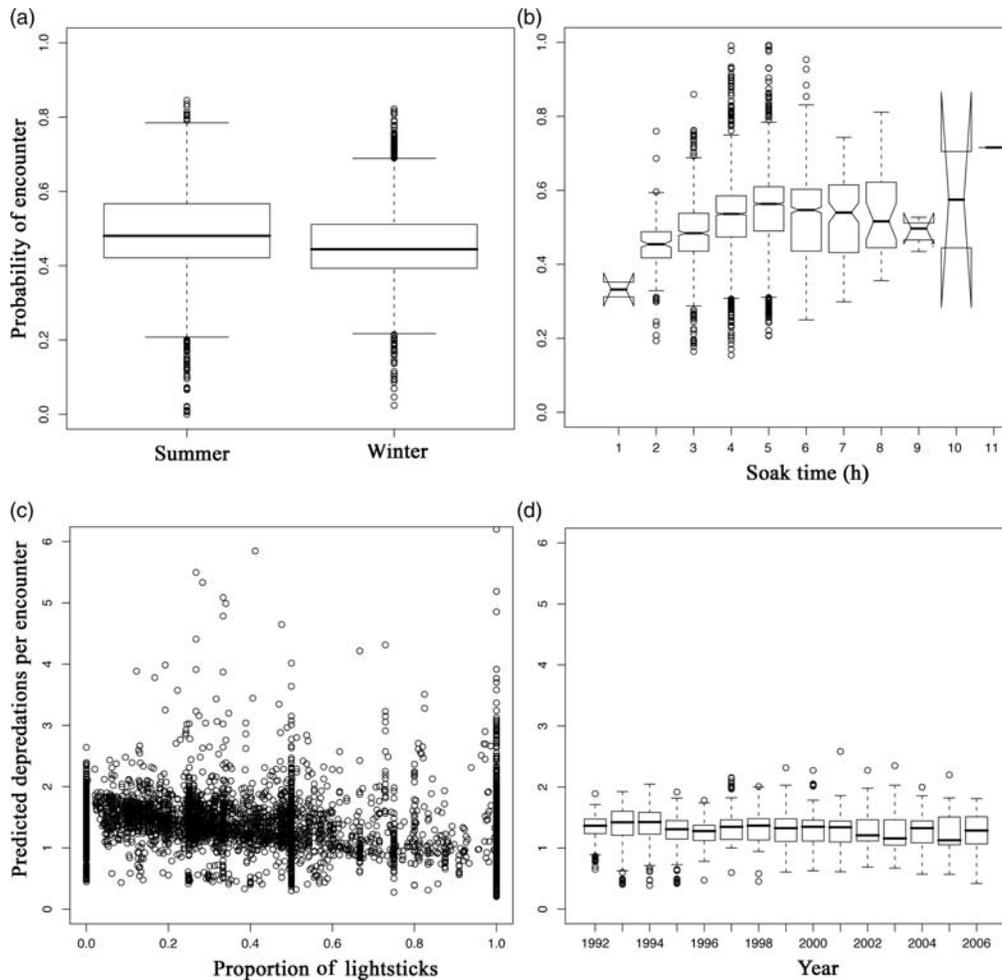
Figure 5. Marginal estimates of probability of encounter and depredation counts given encounter in the US Atlantic pelagic longline fishery, 1992–2006, using a T-NB approach. Estimates include the effects of (a) season and (b) year on encounter probabilities, and the effects of (c) proportion of lightsticks and (d) year on depredation counts. The lower panels have been truncated for presentation; fewer than 1% of predicted counts were >6. Parameter estimates are provided in Table 7.

issue with depredation data is to specify an appropriate distributional form for structuring the variation in the statistical model. Depredation data are somewhat complex to analyse because (i) approximately half the data are zeroes, (ii) a significant proportion are ones, and (iii) there are a few high depredation counts that lead to highly right-tailed data distributions. These conditions appear to overwhelm Poisson and negative binomial models through the excess of zeroes, and Delta-LN models through the excess of ones.

Zero-inflated and two-part mixture models are appropriate for dealing with depredation data, particularly in a negative binomial form. Negative binomial models are well known for accommodating more severe overdispersion in count data better than Poisson models (Ridout *et al.*, 2001), and when combined with a binomial model for zero counts, the ZINB and T-NB structures handle both the large number of zeroes and ones and a long right-tailed skew far better than the other models. Although we consider non-nested distribution forms that do not allow likelihood information to be used to rank model fit, the BCV prediction error estimates provide strong evidence for the superior ZINB and T-NB fit, so these models appear to be flexible options for fisheries data that should be considered routinely by fisheries researchers (Minami *et al.*, 2007).

It should be noted that other animals, such as cetaceans, have been implicated in pelagic longline depredations in other fisheries (Gilman *et al.*, 2007) and that these animals likely contributed to some of the depredation events observed here. However, US longline observers generally report cetacean damage explicitly, because it is easily distinguished from shark damage through cetaceans tending to take the entire body of a caught fish, leaving only the hooked head. Sharks on the other hand, tend to take chunks from the sides of fish at their thickest point. As cetacean reports accounted for <15% of all depredations observed in the data, the majority of depredation events should be attributable to sharks.

Potential processes
Although the T-NB model demonstrated the best fit and lowest prediction error of all the models considered, the assumptions underlying two-part and zero-inflated models are different and must therefore be closely considered when approaching

depredation data. The T-NB model assumes that the zeroes observed arise from only the presence/absence (encounter) portion of the model, whereas the ZINB model assumes that, in some cases, potentially depredating individuals may encounter the longline set without leading to one or more depredations. At this point, there is no information available whether sharks encountering a longline always predate on caught fish. Given the generally sparse distribution on predators and prey in the pelagic environment, it may be a sound assumption to assume that they do, but this is nevertheless a speculative assumption. With the current state of knowledge, we suggest that both models be run on a dataset and that the parameter estimates be compared for inference.

The covariates of depredation outlined here are processes familiar to the study of any longline fishery, but differences in the component zero and count models also highlight different scales between encounter probabilities and depredation counts. Encounter probabilities appear to be associated with large-scale processes of space and time, whereas catch rates are associated with local-scale characteristics of the fishery. Such relationships make intuitive sense where, as vessels travel throughout a given geographic region, the probability of their encountering sharks likely to depredate the catch is driven by the spatial or temporal distribution of species at a regional scale. Once they are encountered, however, the gear used and the small-scale characteristics of each set determine how many depredations there will be. Although both gear dynamics and environmental conditions are important for understanding catch rates of many pelagic species (Bigelow and Maunder, 2007), they have not frequently been associated with different processes relating to encounter probability and catch (or depredation).

Seasonality in depredation encounter probabilities agrees in general with bycatch observations for sharks in the southwestern North Atlantic (Beerkircher et al., 2002). Studies from northern Canadian waters, however, have found little evidence of a seasonal effect on blue shark cpue (Campana et al., 2006), suggesting that seasonality in shark encounter events may be more likely in US waters than in Canadian territorial waters. There is some evidence to support this statement from fishery-dependent logbook data, where catch quarter (season) is positively correlated with both blue and mako shark (Isurus oxyrinchus) bycatch rates during summer (Cortés et al., 2007). Catches of pelagic sharks and billfish in Hawaiian territorial waters show a similar seasonal pattern (Bigelow et al., 1999). Beyond the observer and logbook data collected by NMFS, little is known about seasonal patterns of shark migration in the study region.

As expected for saturating gear, longer soak times were associated with higher encounter probabilities in the fishery, given the ZINB model. Initially, we hypothesized that this could be due to night sets being longer (in general) than day sets. However, several post hoc (i.e. post-analysis) models examining soak time against night/day interactions found no evidence of a time-of-day effect. By plotting the predicted encounter probabilities by soak hour, it was clear that this trend was driven primarily by the first two soak hours. When modelled through the T-NB approach, these effects largely disappeared, reflecting that a substantial portion of the T-NB predicted encounters were excluded in short (1–2 h) sets in the ZINB model. Despite these differences between models, the higher encounter probabilities in longer sets reflect the time required for fish within the region around a set to encounter longline gear.

The data support catch composition as an important process affecting depredation levels in the US Atlantic pelagic longline fishery. Given that the species responsible for depredation are also susceptible to the gear itself, this result is hardly surprising. Yet the relationship between catch composition and depredation levels is worth exploring in detail. Of the three species that dominated the catch community matrix, two (swordfish and yellowfin tuna) are primary target species of the fishery, and the other (blue shark) is the most abundant shark species captured on US Atlantic longlines, comprising almost 20% of the total catch (Beerkircher et al., 2004). Both yellowfin tuna and swordfish are important target species that define distinct subcomponents of the fishery. Despite target species being included as fixed factors in several models (M3 and derivatives), there was little evidence to support catch target as a significant factor influencing depredation rates. This suggests that the species encountered play a more important role in determining depredation rates than the general characteristics of the fishery set up to catch them.

It is, however, likely that community composition may not represent only the depredating animals, but also their prey. Observers in the northeast US Atlantic have reported that, although many blue sharks are caught in a lot of the sets, it may be the larger shark species (e.g. mako) that contribute most to depredations (S. Gulak, pers. comm.). To seek just such an effect, we ran a series of additional post hoc models that replaced PCA_1 and PCA_2 with yellowfin tuna, swordfish, and mako shark abundance covariates. None implicated mako sharks with increased levels of depredation. At this point, it is difficult to determine which shark species are responsible for most depredation events but, as suggested by others (Ward et al., 2004), the association between large numbers of blue sharks and higher levels of depredation makes them a leading candidate.

Prey species on the other hand were readily identifiable within the data, with tuna and sailfish being the species most commonly targeted by scavengers. The 3.9% overall (sharks and whales combined) depredation rate we observed was similar to the 2.9% level observed for the western and central Pacific, where tuna species were also the dominant depredated group (Lawson, 2001). Ward et al. (2004) hypothesized that smaller animals, such as tunas, were more likely to be targeted by scavenging predators than larger active sharks, a result supported by our analysis. Together, the implications of these two studies are that longer soak times lead both to higher catch rates of sharks and more depredations on target species, suggesting an important trade-off between soak time and catch for smaller target tuna species.

The association between animals in the catch and animals that depredate on a given set is further supported by a negative association between counts and the percentage of lightsticks present. When many lightsticks are present on a given line, the sharks encountered by the set may be more likely to take a bait near a lightstick than to prey on fish caught already. The more the lightsticks, the greater the probability of catching a fish or shark, and the less likely those individual animals are to attack caught fish. The evidence presented here suggests that increased use of lightsticks to catch more fish may have the unexpected effect of reducing damage to the catch through increased bycatch.

The dominance of set-scale effects on catch should be unsurprising; fishers know well that bait and gear characteristics greatly affect what is caught on an individual set. Directed studies examining bycatch rates in pelagic longlines have found significant interactions between shark bycatch and the bait types

used, demonstrating that squid baits can in some cases reduce shark bycatch by ~9–18% (Watson *et al.*, 2005a; Gilman *et al.*, 2007). It has been shown previously that shark catch rates are reduced significantly when circle hooks are used instead of J-hooks (Watson *et al.*, 2005b), and when monofilament leaders are used in place of wire (Branstetter and Musick, 1993; Stone and Dixon, 2000; Ward *et al.*, 2008). However, over the range of years of data used for this study, US pelagic longliners were required to use only circle hooks as a management measure to reduce bycatch, and only 12 sets used wire leaders (Beerkircher *et al.*, 2004). The near total use of monofilament leaders means that our depredation estimates could be low, with smaller species being removed completely by predators (Ward *et al.*, 2004); at most this would approach the 2.3% bite-off rate of all sets—a potentially substantial proportion on some sets.

Many bycatch studies have demonstrated that cooler temperatures correlate with increased shark catches (Bigelow *et al.*, 1999; Watson *et al.*, 2005b; Bigelow and Maunder, 2007), and often suggest that more sharks are caught at shallower depths (Bigelow *et al.*, 2006; Bigelow and Maunder, 2007). Our results supported some of these results, finding lower levels of depredation (but higher encounter probabilities) on deeper sets and greater encounter probabilities in colder water. These results support the intuition of longline captains who anecdotally report larger shark catches on the cold side of a thermal gradient. Yet the relationship between gear sets and the physical characteristics of the ocean can be more complex than the linear relationship we assume. There are strong, non-linear relationships between depth and the catch of pelagic fish in the Pacific, where catch rates are correlated with physical characteristics of the ocean that can be non-linear through depth (Bigelow and Maunder, 2007). Additionally, the way in which gear is set has an influence on catch rates, because the positions of hooks within the physical structure of the ocean can lead to complex relationships affecting the fishing effort of each hook (Rey and Muñoz-Chápuli, 1991; Bigelow *et al.*, 2006).

Given previous studies that have noted declines in many shark species throughout the US Atlantic and Gulf of Mexico (Baum and Myers, 2004; Cortés *et al.*, 2007), the absence of an annual trend in depredation rates since 1992 is of note. Although no single species can be directly implicated in depredation events, the lack of a temporal trend suggests little change in the apex sharks responsible for longline depredations. If, as discussed above, blue sharks are the most likely candidate depredators, these results support previous assessments of static blue shark population trends since 1992 (Anon., 2008). If multiple species are responsible for the depredations observed, it may well be that downward trends in some large shark species have been compensated for by upward trends in others, meaning that there is some indication of stability in the apex predator complex throughout the US Atlantic since 1992. However, depredation rates are an indirect measure of such trends and have had little empirical study to date; conclusions from these data should therefore be regarded as tentative. Moreover, these data represent a relatively short timespan, and it may be that the species most likely to depredate have already experienced historical declines, making the stability we observe an artefact of shifting baselines in the Northwest Atlantic (Baum and Myers, 2004).

Conclusions

Although the economic costs associated with longline depredation can be substantial (Lawson, 2001), depredation is an inevitable part of conducting longline operations in the open ocean. Many of the fishing areas and characteristics used to target tunas and billfish also attract sharks likely to prey on the fish hooked. Although the large-scale spatial and temporal characteristics of a given fishery are unlikely to be changed to decrease depredation events (the costs would likely outweigh the benefits), local-scale characteristics of a fishing operation can be altered in beneficial ways. The warmer or deeper waters favoured by target billfish and tunas are areas likely to encounter high levels of depredation, so it is likely that captains are aware of these characteristics and may pull up their gear when the placement of a particular set goes awry. Future analyses of depredation may benefit from a closer examination of the site-specific environmental characteristics that have benefited catch and bycatch studies.

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