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Killer whale (*Orcinus orca*) depredation effects on catch rates of six groundfish species: implications for commercial longline fisheries in Alaska

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Killer whale (*Orcinus orca*) depredation occurs when whales damage or remove fish caught on longline gear. This study uses National Marine Fisheries Service longline survey data from 1998–2011 to explore spatial and temporal trends in killer whale depredation and to quantify the effect of killer whale depredation on catches of six groundfish species within three management areas in Alaska: the Bering Sea, Aleutian Islands and Western Gulf of Alaska. When killer whales were present during survey gear retrieval, whales removed an estimated 54–72% of sablefish (*Anoplopoma fimbria*), 41–84% of arrowtooth flounder (*Atheresthes stomias*) and 73% (Bering Sea only) of Greenland turbot (*Reinhardtius hippoglossoides*). Effects on Pacific halibut (*Hippoglossus stenolepis*) and Pacific cod (*Gadus macrocephalus*) were significant in the Western Gulf only with 51% and 46% reductions, respectively. Overall catches (depredated and non-depredated sets) for all groundfish species significantly impacted by killer whale depredation were lower by 9–28% ($p < 0.05$). Effects on shortspine thornyhead (*Sebastolobus alascanus*) catches were not significant in any management area ($p > 0.05$). These results provide insight into the potential impacts of killer whale depredation on fish stock abundance indices and commercially important fisheries in Alaska and will inform future research on apex predator–fisheries interactions.

Keywords: depredation, groundfish, killer whales, longline, marine mammals, Pacific halibut, sablefish.

Introduction

Killer whale (*Orcinus orca*) depredation (whales removing or damaging fish caught on fishing gear) impacts longline fisheries in all ocean basins (Sivasubramaniam, 1964; Iwashita *et al.*, 1976; Yano and Dahlheim, 1995; Garrison, 2007; Visser, 2000; Clark and Agnew, 2010; Belonovich and Burkanov, 2012). Killer whale depredation can reduce overall catch rates by up to 30% and individual sets by 100% (Sivasubramaniam, 1964; Kock *et al.*, 2006; Dalla Rosa and Secchi, 2007; Roche *et al.*, 2007). Depredation has negative consequences for the fishermen through reduced catch rates and increased operating costs (Yano and Dalheim, 1995; Ashford *et al.*, 1996; Purves *et al.*, 2004; Goetz *et al.*, 2011). Depredation also has negative consequences for the whales through increased risk of vessel strike, gear entanglement, fisher aggression and altered foraging strategies (Ashford *et al.*, 1996; Northridge and Hofman, 1999; Roche *et al.*, 2007; Hernandez-Milian *et al.*, 2008). An additional management concern stems from the impact that whale depredation may have on the accuracy of fish stock abundance indices (Purves *et al.*, 2004; Kock *et al.*, 2006; Gillman *et al.*, 2006; Clark and Agnew, 2010; Hanselman *et al.*, 2010).

Killer whale depredation has been documented in four main regions in Alaska: the Bering Sea (BS), Aleutian Islands (AI), Western Gulf of Alaska (WGOA) and the coastal waters of Prince William Sound. The problem of killer whale depredation is particularly acute in western Alaska, where high-dollar longline fisheries are prosecuted in areas supporting some of the greatest densities of "fish-eating" or resident killer whales in the world (Yano and Dahlheim, 1995; Forney and Wade, 2006; Fearnbach, 2012). It was estimated in 2010 that a minimum of 1300 resident killer whales inhabit the BS, AI and WGOA (Angliss and Outlaw, 2010). However, more recent photographic mark-recapture assessments indicate that significantly more (perhaps twice that) fish-eating residents use the coastal waters around the eastern and central Aleutians alone in some years (Fearnbach, 2012). Alaskan resident killer whales have been observed feeding on Pacific salmon (*Oncorhynchus spp.*), Atka mackerel (*Pleurogrammus monopterygius*) and Pacific halibut (*Hippoglossus stenolepis)* (Ford *et al.*, 1998; Saulitis *et al.*, 2000; Herman *et al.*, 2005; Krahn *et al.*, 2007; Fearnbach, 2012). Resident killer whales in the BS, AI and WGOA show strong long-term associations consistent with a matrilineal pattern and have been shown to exhibit a high degree of site fidelity over time. Ranges are generally limited to around 200 km, although longer movements have been documented (Ford and Ellis, 2006; Forney and Wade, 2006; Matkin *et al.*, 2007; Fearnbach, 2012).

The goal of this study was to improve our understanding of the effect of killer whales on National Marine Fisheries Service (NMFS) longline survey catches, fish stock abundance indices, and commercial fisheries. Killer whales are known to depredate on sablefish (*Anoplopoma fimbria*), arrowtooth flounder (*Atheresthes stomias*), Pacific halibut and Greenland turbot (*Reinhardtius hippoglossoides*) (Matkin, 1988; Yano and Dahlheim, 1995). There is also some evidence suggesting killer whales may interact with Pacific cod (*Gadus macrocephalus)* longline fisheries in the BS (Perez, 2006). Exact catch losses due to killer whales are difficult to quantify as there are a number of confounding variables that can also impact catch rates, such as habitat type, geographical region, set soak time, set depth and year (Clark and Agnew, 2010; Hanselman *et al.*, 2010). Therefore, we used a generalized modelling approach to address two specific objectives: (i) to quantify temporal and spatial trends in killer whale depredation, and (ii) to quantify the effect of killer whale depredation on catch rates of six commercially important groundfish during longline surveys off Alaska.

Material and methods

Data collection

Data on killer whale depredation were collected during the annual NMFS sablefish longline survey 1998–2011. Stations were surveyed in the BS during odd years, in the AI during even years and in the WGOA every year from June to August 1998–2011. Stations in the BS (odd years) and AI (even years) were fished from approximately 31 May–14 June, while WGOA stations were fished each year from 16–30 June. Survey stations generally overlapped with sablefish commercial longline fishing grounds along the continental slope and were systematically spaced approximately 30–50 km (Figure 1) apart at depths ranging from 150–1000 m (Sigler *et al.*, 2008). The survey followed a systematic design, with stations fished in the same location each year. A station was fished from shallow to deep and consisted of two sets hauled end to end. The basic unit of gear was a skate; there were 80 or 90 skates per set depending on the management area. Each skate consisted of 45 hooks, baited with squid, spaced 2 m apart. Stations in the BS had 180 skates for a total of 8100 hooks fished per day, while AI and WGOA stations had 160 skates for a total of 7200 hooks per day. Species-specific catch data were tallied for each hook retrieved. A fish was labelled as "depredated" if only lips or torn, punctured fish remnants were brought aboard (Figure 2). Length and sex information were recorded for major species such as sablefish, Pacific cod, Greenland turbot, arrowtooth flounder, giant grenadier (*Albatrossia pectoralis*), and others. Sea surface temperature (SST) was measured immediately prior to gear retrieval at each station.

Catch was calculated for each species by summing the total number of individuals caught per skate. Catch per unit effort (cpue) was then calculated by dividing the catch by the number of effective hooks per skate. Hooks were deemed "ineffective" if they were straightened, snarled, bent or in any way unable to fish properly. Mean latitude and longitude for each set was computed by averaging the latitude and longitude of the set start and set end. Depth was recorded every fifth skate and interpolated for all other skates. An alternative depth index (depth stratum) was also used to identify broad depth ranges (Stratum 1: 0–100 m, Stratum 2: 101–200 m, Stratum 3: 201–300 m, Stratum 4: 301–400 m, Stratum 5: 401–600 m, Stratum 6: 601–800 m, Stratum 7: 801–1000 m, Stratum 8: 1001–1200 m). Killer whale depredation data were recorded at the skate level. The vessel captain and chief scientist recorded the time and skate number when killer whales were first sighted within ~ 300 m of the vessel. Skates were labelled as "depredated" if whales were sighted near the vessel and there was evidence of depredation (e.g. damaged fish observed on the skate).

Data analysis

The first objective of this study, quantifying spatial and temporal trends in killer whale depredation, was addressed by examining the proportion of skates depredated by station and year, and modelling depredation as a function of time, fishery or environmental variables. The second objective, exploring the effect of killer whale depredation on catch rates, was addressed by comparing cpue between sets with and without killer whale depredation, and modelling the catch per set as a function of station, year, presence of killer whales, and other relevant covariates using a generalized modelling approach. All analyses were done using R Statistical Computing Software (version 2.15.0).

Spatial and temporal trends in killer whale depredation

The average proportion of skates depredated was calculated for each station and year by dividing the number of skates depredated by killer whales by the total number of skates fished. To assess temporal trends in killer whale depredation in each management area, a logistic regression was used to determine if there was a significant trend in the proportion of depredated skates (π) over time. The logistic regression was fitted into a Generalized Linear Modelling (GLM) framework assuming a binomial distribution for the response variable (Hardin and Hilbe, 2007). The response variable was the presence (1) or absence (0) of depredation on a given set, where "0" meant that no skates were depredated on the set and "1" meant that at least one skate was impacted by killer whale depredation. The binomial response variable was linked to the linear predictor, which included year and station as explanatory variables, through the logit function $\{\log[\pi/(1-\pi)]\}$. Two models were compared to examine trends in the proportion of

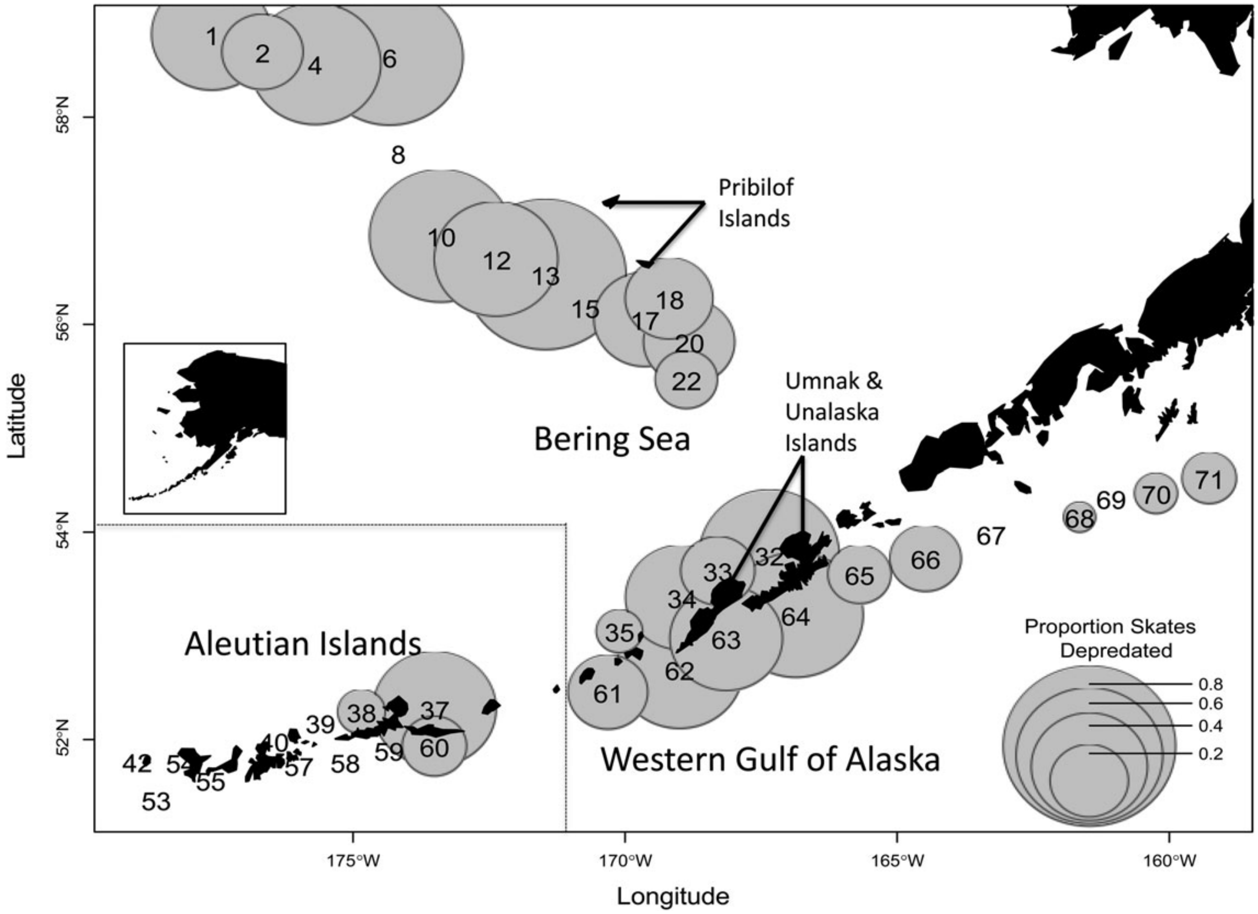

Figure 1. Stations surveyed (numbered 1–71) in the Bering Sea, Aleutian Islands and Western Gulf of Alaska (NMFS longline survey 1998–2011). Symbol sizes (grey circles) are equivalent to the average proportion of skates depredated by killer whales at each station.

depredated skates over time: one that estimated annual means across all years i and station means across all stations j, and a second model that estimated station means and a simple linear trend (slope β_1) in the proportion of depredated skates over time:

$$\log\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \beta_0 + year_i + station_j$$

$$\log\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \beta_0 + station_j + \beta_1(year)$$

where π_{ij} is the estimated proportion of skates depredated at station j in year i. Each management area was modelled separately. Stations that experienced no depredation in any year were removed. Confidence intervals were reported as $\pm 1.96 \times$ s.e.

To examine the effects of environmental and fishery-related variables on the frequency of killer whale depredation, the above models were extended to include smooth, non-parametric functions of potentially important covariates in a Generalized Additive Model (GAM; as implemented in the R package "mgcv") (Wood, 2006; Zuur *et al.*, 2009). Explanatory variables considered included SST, killer whale social cluster, gear soak time, depth, set haul time, latitude, longitude, distance fished, and ineffective hooks (Table 1). Year was treated as a categorical variable. As a measure of local abundance, sablefish cpue, Pacific halibut cpue, and arrowtooth flounder cpue were averaged by station for all skates not affected by depredation. For this analysis, each station was assigned to one of three killer whale social clusters, based on social connectivity and geographic range, as defined by Fearnbach (2012). Social cluster was included to account for possible differences in depredation rates between different social groups of killer whales.

SST, soak time, haul time, distance fished, depth and cpue for sablefish, Pacific halibut and arrowtooth were averaged by station and year for this analysis. Pairwise correlations were computed between all variables to check for collinearity. When significant collinearity occurred (Pearson's correlation test; $r > 0.5$, $p < 0.05$) one of the two variables was dropped from the final model based on lowest AIC score.

$$\begin{aligned}
&(\mathit{proportion\ skates\ depredated})\\
&\quad = year_i + whale\ cluster_k\\
&\qquad + f_1(Lat,\ Long)\\
&\qquad + f_2(SST) + f_3(depth) + f_4(soak\ time)\\
&\qquad + f_5(haul\ time) + f_6(distance\ fished)\\
&\qquad + f_7(inef\ fective\ hooks) + f_8(Sable\ CPUE)\\
&\qquad + f_9(Hal\ CPUE) + f_{10}(Arrow\ CPUE) + \varepsilon
\end{aligned}$$

The maximum degree of freedom for the smooth terms was restricted to 3 to accommodate biologically reasonable

Figure 2. Killer whale depredation evidence (a) juvenile killer whale approaching to dive on the longline gear NMFS Permit Number 14122, (b) Pacific halibut, arrowtooth flounder and sablefish damaged by killer whales, (c) fisherman with killer whale photographed near longline vessel in background, (d) evidence of bite marks, crushed tissue and lip remnants demonstrate varying degrees of damaged sablefish.

relationships with linear, dome-shaped or sigmoidal shapes (Goetz *et al.*, 2011). Geographic differences were modelled by including location (latitude/longitude) as a covariate, hence data from all three management areas were combined in the analysis. Outliers were identified and removed if Cook's distance exceeded 0.5 (Cook, 2000). The best model was selected based on stepwise regression and lowest Akaike information criterion (AIC) values (Hardin and Hilbe, 2007; Zuur *et al.*, 2009).

Catch reductions of groundfish species

To quantify the effect of killer whales on catches of groundfish species we used a statistical modelling approach to analyse NMFS longline survey data for 1998–2011 and to compare cpue between sets with and without killer whales present. The response variable consisted of counts of sablefish, Pacific halibut, Pacific cod, arrowtooth flounder, shortspine thornyhead (*Sebastolobus alascanus*) and Greenland turbot (BS only) per skate or stratum, and was modelled using a GLM approach to estimate changes in catch associated with killer whale depredation (Zuur *et al.*, 2009; Clark and Agnew, 2010; Hanselman *et al.*, 2010). Years with no depredation (2004 in the AI; 1998, 1999 and 2001 in the WGOA) and stations where no killer whale depredation was observed in any year were excluded from the analysis. Due to limited catches, Strata 1 and 8 were removed for sablefish, Greenland turbot, shortspine thornyhead, and arrowtooth flounder. Strata 6–8 were removed for Pacific cod and Pacific halibut.

A number of distributions were initially considered to model the count data in a GLM framework including: Poisson, negative binomial (NB; as implemented in the R package "MASS") (Venables and Ripley, 2002), zero-inflated negative binomial (ZINB; as implemented in R package "pscl"), and hurdle or zero-adjusted negative binomial models (ZANB; "pscl") (Zeileis *et al.*, 2008). The Poisson distribution is commonly used to model count data, but initial model explorations indicated that the observed counts were overdispersed in all three areas for all fish species, which occurs when the variance of the counts is greater than their mean. The NB distribution accounts for overdispersion by adding an additional parameter to model the higher variance (Zeileis *et al.*, 2008; Zuur *et al.*, 2009; Hilbe, 2011). Fitting a NB GLM to the catch data resulted in a much-improved fit compared to the Poisson model based on AIC and model diagnostics. Due to the large number of zero catches in the data, ZINB

Table 1. Explanatory variables considered for modelling proportion of skates depredated by killer whales across 348 station/year combinations (GAM model input), and for modelling killer whale effects on catch rates across 57 043 skates fished between 1998 and 2011 (NB GLM model input).

Explanatory Terms	GAM Model Input	NB GLM Model Input	Descriptor
Year	factor	factor	even years AI, odd years BS, all years WG
Station	–	factor	sampling locations in each management area
Year: Station	–	interaction	year and station effect on catch rates
Killer whale depredation (Yes/No)	–	factor	presence of killer whales in conjunction with evidence of damaged fish on the set
Depth stratum (metres)	–	factor	broad depth ranges (0–100 m, 101–200 m, 201–300 m, 301–400 m, 401–600 m, 601–800 m, 801–1000 m, 1001–1200 m)
Depth (metres)	smoother	continuous	septh taken every 5th skate and interpolated for all other skates
Killer whale depredation: stratum	–	interaction	killer whale depredation effect by stratum
Killer whale depredation: interpolated depth	–	interaction	killer whale depredation effect by interpolated depth
Sea surface temperature (SST) °C	smoother	continuous	surface temperature taken at the start of the set
Haul time (minutes)	smoother	continuous	elapsed time between the start of gear haul and the end of gear haul
Soak time (minutes)	continuous	continuous	elapsed time between gear deployment and the end of gear haul
Distance fished (metres)	smoother	continuous	linear distance fished between haul start and haul end locations
Ineffective hooks	smoother	continuous	number of ineffective (straightened, snarled, bent) hooks per skate
Whale social cluster	factor	–	assigned whale cluster (2, 3, 4) based on Fearnbach (2012)
Groundfish cpue	smoother	–	number of individual fish caught per skate divided by the number of effective hooks per skate (for depredated and non-depredated skates only)
Latitude, longitude	smoother	–	coordinates for each station sampled

This table lists all GAM and NB GLM considered explanatory terms, whether they were included as continuous variables, smoother terms, factors or interaction terms, and their descriptions.

and ZANB models were also considered. However, ZINB and ZANB models failed to converge in most management areas (Hanselman *et al.*, 2010), hence we only present results based on the NB GLM.

Explanatory variables considered (Table 1) included station, year, depth stratum and killer whale depredation as categorical variables, and SST, haul time, distance fished, soak time and depth as continuous explanatory variables. Killer whale depredation was treated as a dummy variable consisting of "0" for skates with no depredation, and "1" for skates with depredation. Selected interaction terms such as year and station and the interaction between killer whale depredation and depth were examined (Ai and Norton, 2003). To adjust catches for differences in effort resulting from ineffective hooks, all models included an "offset" term as log(effective hooks) and used a log-link to model log(catch) as a function of the linear predictor. The global model without interaction terms, therefore, had the following form:

$$\begin{aligned}\log(catch) = \beta_0 &+ year_i + station_j \\ &+ killer\ whale\ depredation_k + stratum_l \\ &+ \beta_1(soak\ time) + \beta_2(SST) \\ &+ \beta_3(distance\ fished) \\ &+ log(effective\ hooks) + \varepsilon\end{aligned}$$

Outliers were excluded if Cook's distance exceeded 0.5 (Cook, 2000). The best reduced model for each management area and fish species was selected based on lowest AIC values (Hardin and Hilbe, 2007; Zuur *et al.*, 2009). Residual diagnostics from the initial NB GLM modelling approach showed strong spatial autocorrelation between successive skates (Durbin-Watson test, $p <$ 0.05), resulting in pseudo-replication and standard errors that were much too small. We addressed this issue by aggregating the data by depth stratum and modelled the aggregated number of fish caught per stratum at a given station and year using the same modelling approach as described above for catch per skate. Aggregating the catch data by stratum greatly reduced residual autocorrelation, and standard errors were more reasonable. Therefore, the aggregated NB GLM was selected for the final analyses.

Catch losses associated with killer whale depredation were quantified at two levels. First, for each fish species we estimated the overall average catch per stratum that would have been caught and the associated uncertainty had killer whales not been present at a given skate or station. The number of fish that would have been caught in the absence of depredation was estimated by setting the killer whale depredation variable to "0" and computing predicted catches per stratum for each station and year under this "no-depredation scenario". Differences between the observed and predicted catches by year and station were computed and graphically summarized by year and management area to illustrate killer whale effects on overall catch rates across both depredated and non-depredated sets. Second, the estimated reduction in catches for stratums with confirmed killer whale depredation was calculated using the model-estimated killer whale depredation coefficients. The killer whale depredation coefficient represents the average difference in catch (on the log scale) of a given fish species with and without killer whales present. Models were also fit separately for each year/stratum combination to compare variations in the killer whale depredation coefficient across individual years and strata for sablefish, arrowtooth flounder and Pacific halibut (primary depredated species).

Results

Spatial and temporal trends

A comparison of average catch rates for sablefish, Greenland turbot, Pacific halibut, Pacific cod, arrowtooth flounder and shortspine thornyhead rockfish suggested that there were significant reductions in catch rates for all groundfish species (Kruskal-Wallis test, $p < 0.001$) except shortspine thornyhead (Kruskal-Wallis test, $p = 0.708$) when depredating killer whales were present (Figure 3). From 1998–2011, a total of 57 043 skates (2 566 935 hooks) were fished in the BS, AI and WGOA. The total number of skates depredated for all three areas was 12 021 skates, and the percentage of skates depredated by killer whales across all years and areas was 20.9% ± 6.7%. Although effort differed between areas, both the number and percentage of affected sets was greatest in the BS, followed by the WGOA and the AI. Survey stations in the BS were located along the continental slope, and stations were generally fished trending northwest–southeast. Killer whale depredation was documented at 14 of 16 stations between 1998 and 2011 in the BS. The highest proportion of depredated skates in the BS was concentrated around stations 10, 12 and 13, approximately 180 km west of the Pribilof Islands (Figure 1). The average proportion of skates depredated for these three BS stations exceeded 55%. In the AI and WGOA, stations were generally fished from east to west around 50–55°N. In the AI, killer whale depredation was documented at only 5 of 14 stations. Killer whale depredation in the WGOA region was most common at stations 62–64 (45% skates depredated), approximately 70 km south of Unalaska Island in the Umnak and Unalaska basins (Figure 1).

The percentage of skates depredated ranged from 12.3–55.0% per year ($\bar{x} = 34.5\% \pm 2.3\%$) in the BS, from 0–19% per year ($\bar{x} = 6.6\% \pm 1.5\%$) in the AI and from 0– 41% ($\bar{x} = 18.9\% \pm 2.0\%$) in the WGOA. Based on AIC results and model diagnostics the models estimating station means and a simple linear trend in the proportion of depredated skates over time best summarized variability in depredation rates in the AI ($\Delta\text{AIC} = 3.16$) and BS ($\Delta\text{AIC} = -1.32$; Figure 4). The model estimating separate means by year resulted in a much lower AIC score in the WGOA ($\Delta\text{AIC} = 7.4$), and was thus selected for the final analysis in the WGOA only (Figure 4). There was a significant increase in the proportion of skates depredated in the AI ($p = 0.049$, %dev = 40.26) and significant differences among years in the WGOA (Likelihood ratio test; $\chi^2 < 0.001$, %dev = 52.06). The increasing trend in the BS was not significant ($p = 0.285$, %dev = 9.50; Figure 4).

Factors affecting depredation occurrence

Stepwise regression and AIC results suggest that the proportion of skates depredated was related to sablefish cpue, haul time and year (GAM; %dev = 32.50) and showed additional spatial variability not captured by these variables that could be described by a smooth spatial surface (f_1 term):

$$\text{Proportion skates depredated} = year_i + f_1(Lat, Long) + f_2(haultime) + f_3(sablecpue) + \varepsilon$$

The proportion of skates depredated decreased non-linearly with haul time and increased to an asymptote as sablefish cpue increased (Figure 5). The effect of year was not significant overall with all three management areas included ($p = 0.16$), however, there were significant differences between certain years. The proportion of skates depredated varied significantly between station locations with two primary "hotspots" evident: (i) along the Bering Sea slope southwest of the Pribilof Islands, and (ii) along the continental shelf north and south of the Unalaska and Umnak Islands. The proportion of depredated skates decreased to the east and west of these zones.

Catch reductions

The presence of killer whales was generally associated with lower catches of sablefish, arrowtooth flounder and Pacific halibut in all three management areas. Greenland turbot in the BS ($p < 0.001$) and Pacific cod in the WGOA ($p = 0.015$) were also affected by killer whale depredation (NB GLM; Table 2). Killer whales did not appear to affect Pacific cod catches in the BS or AI, or shortspine thornyhead catches in any management area

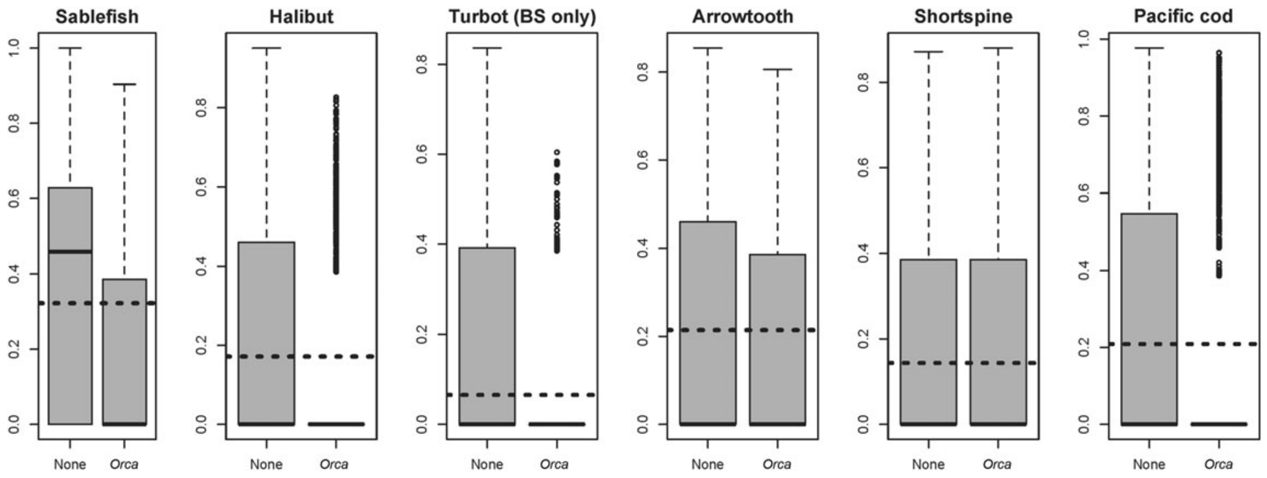

Figure 3. Groundfish cpue averaged over time and across all survey stations, with ("*Orca*") and without ("None") killer whales present, NMFS longline survey 1998–2011. Black bars denote median, dotted lines denote overall mean, grey boxes denote lower and upper quartiles, and whiskers extend to the closest observation that is <1.5 times the interquartile range from the upper quartile.

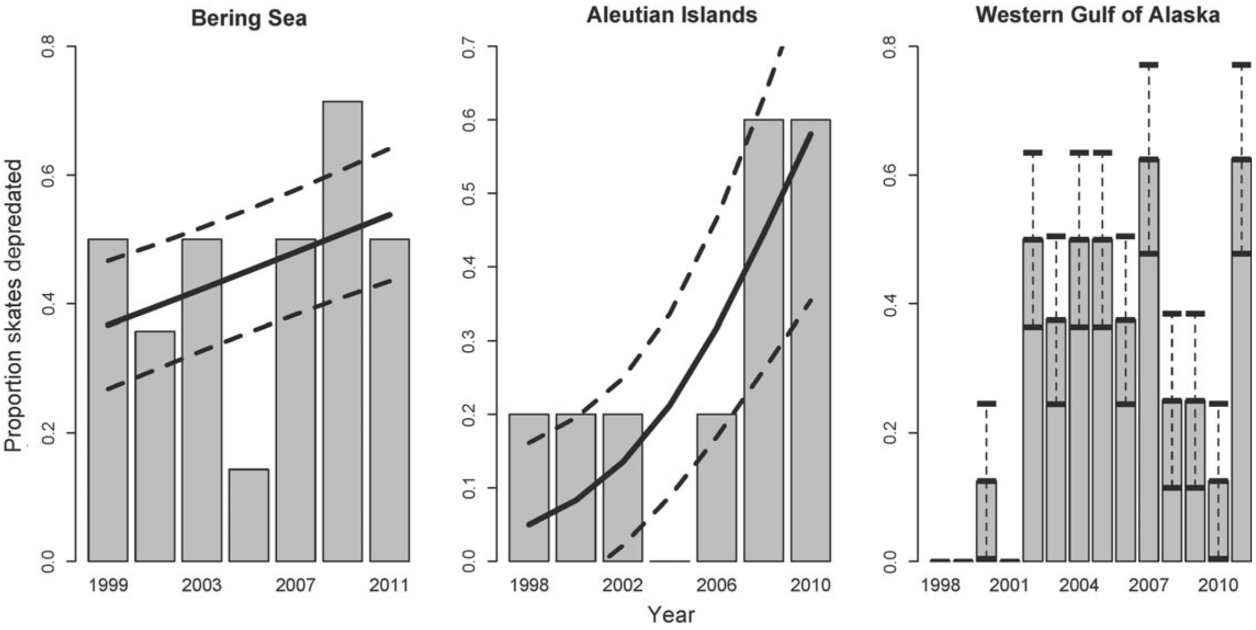

Figure 4. Observed and estimated proportion of skates depredated by killer whales ± 2 s.e. for each management area, NMFS longline survey 1998–2011, based on AIC-best model (see text). Temporal trend was significant for the Aleutian Islands ($p = 0.049$) and the difference between years in the Western Gulf of Alaska was significant ($p < 0.001$).

($p > 0.05$; Table 2). The best-performing model to evaluate the killer whale effect on groundfish catch rates included year and station and their interaction, killer whale depredation and depth stratum. Therefore, results from this model will be presented for each groundfish species in each management area:

$$\log(catch) = \beta_0 + year_i + station_j + (year{*}\text{station})_{\text{ij}} + \text{killer whale depredation}_{\text{k}} + stratum_l + log(effective\ hooks) + \varepsilon$$

Predicted mean annual catch reductions from 1998–2011 on all sets (depredated and non-depredated) ranged from 13.5–28.9% for groundfish species affected in the BS. Killer whale depredation also resulted in predicted overall catch reductions in the AI and WGOA for sablefish (23.6% AI, 10.5% WGOA) and arrowtooth flounder (21.8% AI, 10.2% WGOA; Table 2). Overall predicted catch reductions varied by both year and groundfish species in each management area (Figure 6). Sablefish catch losses calculated based on the killer whale coefficient (depredated sets only) were 72.0% in the BS and AI (Table 2). Depredated set catch losses were greatest in the BS for Greenland turbot (73.0%) and the AI for arrowtooth flounder (84.2%). Although depredated set catch losses were less severe in the WGOA for sablefish and arrowtooth flounder, Pacific halibut (51.8%) and Pacific cod (46.3%) incurred the highest catch losses in the WGOA (Table 2).

Discussion

Main findings

Killer whale depredation had a significant effect on NMFS longline survey catch rates for five of the six groundfish species evaluated in this study. Moreover, there were indications that the frequency of depredation increased after the late 1990s in the AI and during the mid-2000s in the WGOA (GLM; Figure 4), consistent with fishermen observations from these regions (MJP, unpublished data). Based on the results from the NB GLM, the highest overall catch reductions in each region generally occurred for sablefish (10.5–28.9%), followed by arrowtooth flounder (10.2–21.8%; Table 2). Although the percentage of skates depredated in the AI ($\bar{x} = 6.6\% \pm 1.5\%$) was lower than the BS ($\bar{x} = 34.5\% \pm 2.3\%$), killer whales in the AI were still highly effective at removing target groundfish from longline gear when they were present.

Sablefish cpue, gear haul time and location significantly impacted the proportion of skates depredated (GAM; Figure 5). Killer whales were more likely to depredate stations with higher average sablefish cpue, which may be consistent with optimal foraging efficiency and maximizing net rate of energy gain (Estes *et al.*, 2003). Killer whales also targeted stations southwest of the Pribilof Islands and north and south of Unalaska and Umnak Islands. Abundance data for killer whales are limited in these regions, however the increased prevalence of killer whale-fisheries interactions may be related to higher abundances of killer whales in these areas (Fearnbach, 2012). Killer whale depredation decreased with longer gear haul times. This may have occurred due to poor sea state conditions (vessels will often haul slower in poor weather conditions), combined with observations that killer whales may be less likely to depredate in stormy weather (Belonovich and Burkanov, 2012).

Pacific halibut catch reductions were statistically significant in the WGOA only (9.3%, $p < 0.001$). However, fishermen report that the BS and AI Pacific halibut commercial fisheries are heavily impacted by killer whale depredation. The failure of the Pacific halibut models in this study to show a significant effect on halibut catch rates in these areas, in spite of estimated effects that are of similar magnitude to the other regions, may be a result of low sample size (unaffected years and stations eliminated) and lower Pacific halibut catches overall (Table 2). Similar to

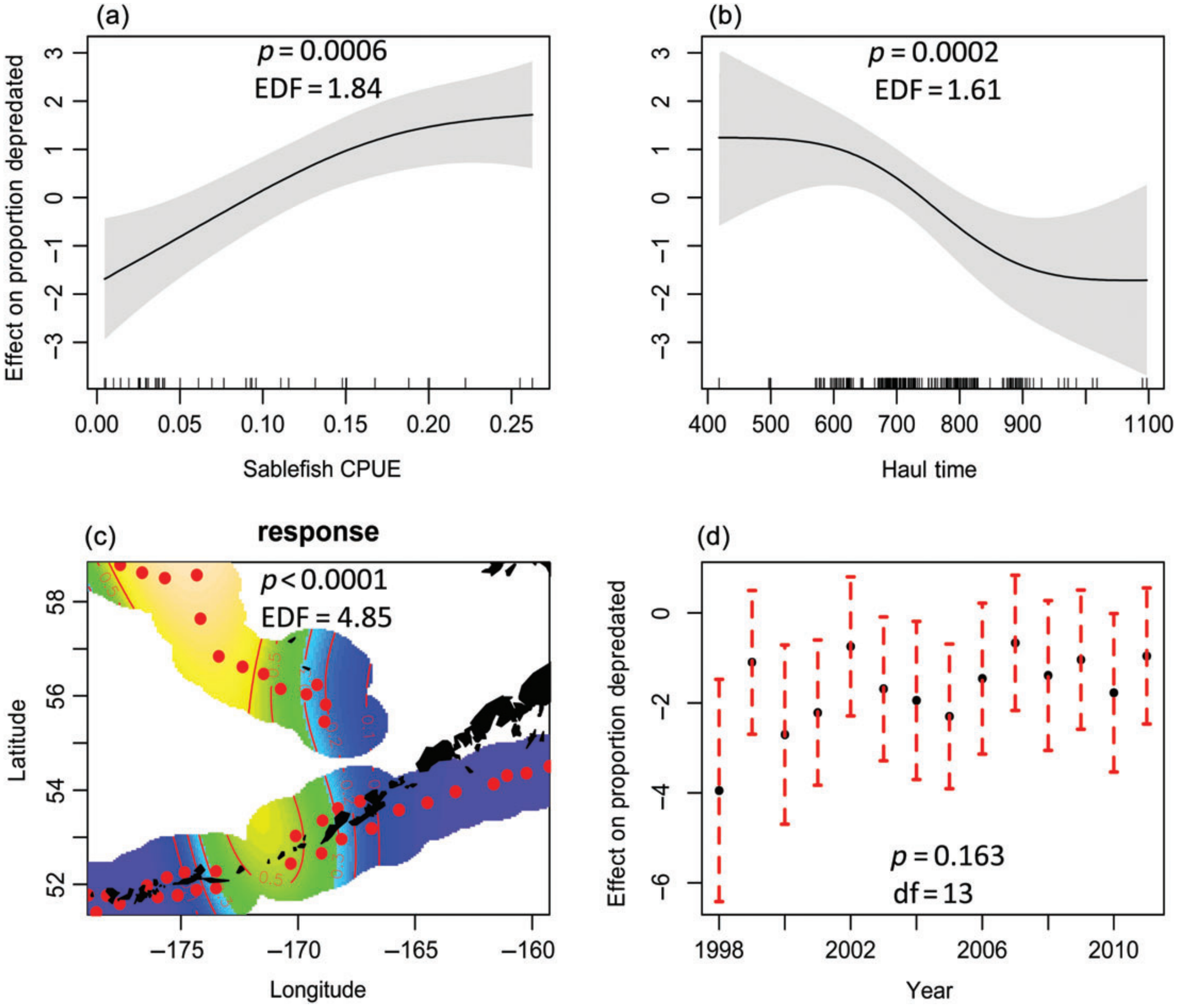

Figure 5. Additive effects of a) sablefish cpue, b) haul time, c) spatial location (latitude/longitude), and d) year on the proportion of depredated skates estimated using a generalized additive model with a binomial response. Shaded areas represent ~95% confidence bands. Estimated degrees of freedom and *p*-values associated with each term are shown in associated panel. Significance based on z-test for year and Chi-square test for sablefish cpue, haul time and latitude/longitude.

Pacific halibut, Pacific cod catch reductions were statistically significant in the WGOA only (10.5%, $p = 0.015$). Unlike Pacific halibut, overall catch reductions estimated in BS and AI Pacific cod models do not suggest that killer whales are removing Pacific cod from longline gear in either area (Table 2). Killer whale depredation on Pacific Cod in the WGOA has not previously been documented on the survey. Using observer data, Perez (2006) did find that a small percentage of longline caught Pacific cod in the BS was affected by killer whale depredation; however, the study concluded killer whales were likely selectively taking other groundfish species off the line. Although it seems unlikely that killer whales were targeting Pacific cod in the WGOA, it is possible that whales opportunistically removed Pacific cod from the longline gear during the survey.

Killer whale depredation in the WGOA was relatively common ($\bar{x} = 18.9\% \pm 2.0\%$) and increased from very low levels in 1998–2001 to very high levels in the last decade; however, the estimated percentage of overall catch taken by killer whales was lower than in the BS and AI for primary species affected (sablefish, arrowtooth flounder; Table 2). The increased frequency of the whale depredation behaviour is more recent in the WGOA, and it is possible killer whales in this area may be less effective "depredators" or that the behaviour is not as widespread among groups. However, catch rates of sablefish and Pacific halibut are much higher in the WGOA than in the BS or AI (Kruskal-Wallis test; $p < 0.05$), therefore, lower percentages of killer whale removals could be related to killer whales reaching a degree of satiation based on natural daily energy requirements (Perez *et al.*, 1993; Sigurjónsson and Víkingsson, 1997; Clark and Agnew, 2010). This is consistent with an asymptotic relationship between depredation and local sablefish abundance (Figure 5). Moreover, a significant gap in killer whale distribution between Kodiak Island and Unimak Pass may be contributing to lower overall depredation rates in the WGOA (Zerbini *et al.*, 2007).

The method used to quantify depredation during surveys may lead to biased estimates of the proportion of skates affected by

Table 2. The response variable, number of fish caught per stratum, followed negative binomial distribution.

Area	Species	Mean Pred. Annual Catch Lost (%)	Min Pred. Annual Catch Lost (%)	Max Pred. Annual Catch Lost (%)	KW coeff.	KW Effect (p-value)	d.f.	% dev	n	AIC	The-ta
Bering Sea	Sablefish	−28.9	−2.0	−50.6	−0.72	$p < 0.001$	105	86.6	475	2839	2.11
	Greenland turbot	−22.0	−0.8	−39.1	−0.73	$p < 0.001$	105	73.2	478	3018	1.53
	Arrowtooth flounder	−20.3	−1.8	−58.1	−0.51	$p < 0.001$	105	65.0	478	4353	2.49
	Pacific halibut	−13.5	−0.8	−26.0	−0.39	$p = 0.088$	97	63.3	455	3537	1.65
	Pacific cod	8.3	3.1	17.4	0.30	$p = 0.399$	97	83.7	455	3719	2.01
	Shortspine thornyhead	NA	NA	NA	0.21	$p = 0.527$	105	88.2	478	1987	3.15
Aleutian Islands	Sablefish	−23.6	−5.7	−62.0	−0.72	$p < 0.001$	37	69.5	172	1275	1.35
	Arrowtooth flounder	−21.8	−3.3	−63.1	−0.84	$p < 0.001$	37	56.1	178	1188	1.07
	Pacific halibut	−5.7	0.0	−26.0	−0.49	$p = 0.072$	36	79.6	172	1096	2.37
	Pacific cod	1.8	0.0	9.0	0.32	$p = 0.507$	37	93.4	178	1016	3.94
	Shortspine thornyhead	NA	NA	NA	−0.07	$p = 0.243$	38	84.9	172	758	2.60
Western Gulf of Alaska	Sablefish	−10.5	−2.6	−22.3	−0.54	$p < 0.001$	95	60.7	569	6028	2.17
	Arrowtooth flounder	−10.2	−1.8	−29.5	−0.44	$p < 0.001$	95	65.5	569	3840	2.03
	Pacific halibut	−9.3	−0.7	−24.9	−0.51	$p < 0.001$	93	75.1	484	3175	2.17
	Pacific cod	−10.5	−0.2	−25.9	−0.46	$p = 0.015$	93	91.8	484	2322	1.74
	Shortspine thornyhead	−7.1	−1.8	−12.1	−0.18	$p = 0.32$	95	44.5	569	4508	1.27

The results displayed include the mean and range of predicted annual catch losses associated with whale depredation, the model-estimated difference in catch between depredated and non-depredated skates, whether the killer whale depredation effect was signficant ($p < 0.05$), degrees of freedom (d.f.), percentage of deviance explained (%dev), the sample size (aggregated catch by stratum; n), Akaike Information Criterion (AIC) and the dispersion parameter (theta).

killer whale depredation. Skates were labelled as depredated if killer whales were sighted within 300 m of the vessel and there was evidence of depredation or damaged fish on the set. Killer whale presence can be difficult to confirm visually if sea surface conditions are rough or the whales are depredating far off the vessel, resulting in an underestimate of the number of affected skates. In contrast, it is possible that some damaged fish brought on board were damaged by sharks, other fish or sand fleas (High, 1980; Trumble *et al.*, 2000; Dalla Rosa and Secchi, 2007; Stahl and Holum, 2008), possibly resulting in an overestimate of affected skates. Despite the challenges inherent in confirming killing whale depredation, we are confident these results represent a reasonable, if not slightly conservative, estimate of the proportion of skates affected by killer whales on the longline survey and associated catch reductions of depredated groundfish species.

The NMFS longline survey spends a relatively short amount of time sampling in western Alaska each year, making it difficult to identify seasonal trends in killer whale depredation or to draw larger fleet-wide conclusions. There are also important differences between NMFS longline survey methods and the operations of the commercial sablefish or Pacific halibut fisheries. The longline survey fishes pre-determined stations at set times each day irrespective of the presence of depredating whales. The longline survey also fishes with a factory-processing vessel, which processes fish at sea and releases a stream of offal that may distract whales from the longlines. Conversely, many fishermen do not process at sea (delivering shoreside in the round) and employ a number of tactics to avoid depredating whales including dropping their gear to "wait the whales out," moving to a different fishing location or using deterrents such as seal bombs. These whale avoidance measures employed by longline fisheries likely reduce the overall number of skates affected by killer whales. Despite these differences, this analysis of killer whale depredation using NMFS sablefish longline survey data serves as an important first proxy for what the commercial fisheries could experience when depredating killer whales arrive during fishing operations.

Killer whale depredation in Alaska

Trends in predicted mean catch reductions associated with killer whale depredation concur with previous regional catch reduction assessments conducted in the 1980s. Killer whale depredation was studied in the BS and AI during the Japan–US cooperative longline survey from 1980–1989. Based on a comparison of annual average catch rates among years, killer whale depredation resulted in losses ranging from 14–60% for sablefish, 39–69% for Greenland turbot, and 6–42% for arrowtooth flounder (Yano and Dahlheim, 1995). The impact of killer whale depredation on a commercial fishery was studied in Prince William Sound in 1985 and 1986, where it was estimated that 25–35% of overall sablefish catch was lost to killer whales. Individual sets were affected by as much as 80–90% for sablefish and Pacific halibut (Matkin, 1986; Matkin, 1988), consistent with our results that average reductions in the three management areas ranged from 54–72% for sablefish. The authors are aware of no previous studies investigating killer whale depredation and catch reductions specific to the WGOA, likely because killer whale depredation in

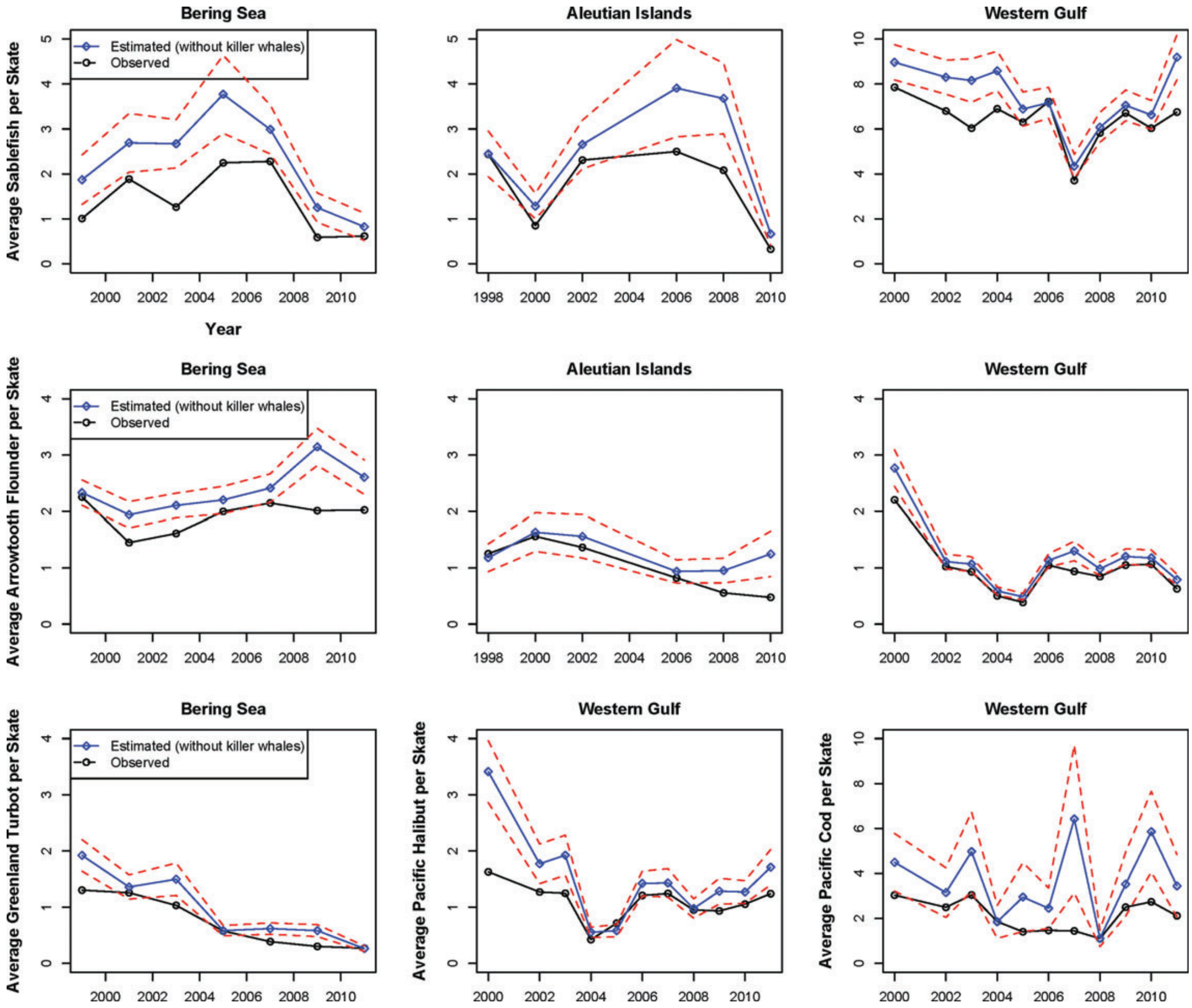

Figure 6. Observed (black lines) and model-estimated (blue lines) average annual catches of groundfish in the absence of killer whales with 95% confidence bands (red dashed lines) (NMFS longline survey 1998–2011).

this region has primarily been observed in more recent years (Yano and Dahlheim, 1995).

Killer whale social structure and distribution likely plays a critical role in shaping their interactions with longline fisheries in western Alaska. A recent study by Fearnbach (2012) evaluating movement and association patterns based on photo-identification data from 2001–2010 in western Alaska indicated four distinct clusters or groups of "resident" killer whales in western Alaska, likely composed of stable matrilineal groups with unique ranging patterns. Cluster 2 whales (central AI with north/south movements in the BS) formed the largest cluster identified in this study (Fearnbach, 2012). The extensive ranges and relative abundance of cluster 2 whales in the BS overlapped with the highest proportion of skates depredated and percentage catch reductions experienced on the NMFS longline survey. It is possible that individual whales within this cluster have learned to specialize in the depredation behaviour as a cooperative foraging strategy in this area (Tixier *et al.*, 2010). There is significant spatial overlap and, therefore, social connectivity between the four clusters of killer whales in northwest Alaska. In particular, cluster 2 (central AI and BS) and 3 (eastern AI) whales showed relatively extensive ranges (maximum distance between repeated encounter locations), averaging 236 km and 430 km, respectively. The spatial overlap and social connectivity between these groups of whales provides insight into how the depredation behaviour could spread throughout western Alaska through cultural transmission of the learned behaviour (Fearnbach, 2012).

Implications for commercial longline fisheries

Killer whale depredation was documented as early as the 1960s in the BS by Japanese longliners (Matkin, 1986; Dalheim, 1988), and whale depredation has played a major role in changing fishing practices of longline fleets, specifically: gear type, season timing, and proportion of total allowable catch harvested of certain groundfish in the BS. The sablefish fishery in the BS has seen a large number of vessels transitioning to pots as a result of killer whale depredation. In 2000, the pot fishery accounted for $<$ 10% of the fixed gear sablefish catch in the BS and AI, whereas in 2009 pot fishing accounted for $>$ 70% of sablefish catch in the BS (Hanselman *et al.*, 2011). The Greenland turbot longline fishery is forced to delay the start of the fishing season to avoid depredating killer whales (Ianelli *et al*., 2011). And for the first time in 2008, the proportion of Greenland turbot caught by trawlers exceeded the proportion of Greenland turbot caught by longlines (Ianelli *et al*., 2011). Additionally, BS sablefish, Greenland turbot and Pacific halibut fisheries have not been prosecuted to the full extent of the total allowable catch in recent years (Hanselman *et al*., 2011; Ianelli *et al*., 2011; NMFS RAM Division, 2012). Fishermen report that this is in part due to severe killer whale interactions in this area (MJP, unpublished data). Changes in gear type, such as the increased prevalence of sablefish pot gear in the BS (which is not depredated), could result in the transfer of additional killer whale depredation effort to other longline fisheries, such as Pacific halibut or Greenland turbot (which cannot be fished with pots to date).

WGOA fishermen accounts and model results from this study indicate that killer whale depredation in the WGOA became more severe between the late 1990s through 2007. In addition to the growing problem of killer whale depredation in the WGOA, commercial longline fisheries face an extra challenge with sperm whale interactions occurring in the same region. The killer whale effect was significant for both sablefish and Pacific halibut catch in the WGOA, and overall survey catches were reduced by 10.5% and 9.3%, respectively. Despite relatively moderate catch rate reductions in the WGOA, especially compared to the BS, the magnitude of the economic losses to the commercial fisheries in the WGOA could exceed that of the BS or AI in the WGOA when higher quotas and increased fishing effort are taken into account. For instance, in 2011 sablefish commercial catch in the WGOA was twice as large as BS or AI sablefish catch, and the Pacific halibut catch in the WGOA (Area 3B) was two to three times larger than that in the AI (Area 4A/4B) or BS (Area 4C/4D; (NMFS RAM Division, 2012). Pot fishing for sablefish is currently not legal in the Gulf of Alaska; however, the North Pacific Fishery Management Council is conducting reviews to determine the feasibility of reintroducing pot fishing for target groundfish species in the Gulf of Alaska.

A number of studies have investigated mitigation measures to reduce whale interactions, such as shifted fishing seasons, deterrents, physical catch protection, gear modifications and acoustic harassment devices (Mooney *et al*., 2009; Rabearisoa *et al*., 2009; McPherson and Nishida, 2010; Rabearisoa *et al*., 2012). In contrast to pelagic longline tuna and swordfish fisheries, killer whale depredation on demersal fisheries in Alaska typically occurs during haulback operations. Thus, physical catch protection for demersal fisheries could occur through gear modifications designed to protect the fish during gear retrieval. Catch protection devices such as the "umbrella-and-stone" Chilean longline system were tested on Patagonian toothfish fisheries in the Southwest Atlantic. Although these devices did reduce depredation, there may be a negative effect on cpue (Moreno *et al*., 2008; Goetz *et al*., 2011). Active or passive acoustic deterrents could be another method to deter killer whales away from fishing gear (Mooney *et al*., 2009). There is no single remedy against killer whale depredation to date, and it is possible that a combination of gear modifications, deterrents and adaptive management (such as shifted fishing seasons or altered season durations) will be necessary to reduce the frequency of the interaction.

Conclusions

This study provides new information on the potential effects of killer whale depredation on the NMFS longline survey and commercial groundfish fisheries in western Alaska. Killer whale depredation primarily impacts catch rates of sablefish, Greenland turbot, arrowtooth flounder and Pacific halibut, and there are indications that killer whale depredation may be getting more severe in the AI and WGOA. Results from this work are also relevant for the development of a correction factor for the annual fish stock abundance indices to account for depredation. The NMFS longline survey is currently forced to drop data from skates affected by killer whale depredation. This is particularly problematic for the BS and AI management areas where stations are only sampled every other year. The modelling methodologies from this research using NMFS longline survey data provides a framework for future studies of whale depredation on commercial fisheries operating in the region, and we are currently examining NMFS Fishery Observer data and surveying fishermen to gain further insights into the effect of depredation on fishing operations. Effective management of whale depredation in Alaska requires the establishment of baseline data on depredation rates, depredation trends and the impacts of depredation on catch rates in the NMFS longline survey and the commercial longline fisheries.

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