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Original Article

Whale depredation in the South Georgia Patagonian toothfish (*Dissostichus eleginoides*) fishery in the South Atlantic: a comparison of estimation methods

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Removal of fish from gear by marine predators, known as depredation, is a fishery dependent mortality that needs to be included in stock assessments for affected stocks to avoid misestimation of the assessed resource. Toothed whales engage regularly in depredation from longlines, and while in some regions they leave clear marks of depredation activity, in the longline fisheries in the Southern Ocean they often leave no trace of removal, making it necessary to estimate depredation through modelling approaches. Several modelling approaches have been developed over the past decade in affected Southern Ocean fisheries, and in this paper, we examine five applications of common CPUE model structures to the same dataset from the longline fishery around South Georgia. We then compare the estimates of depredation with those based on observed bycatch ratios. The different model structures estimated very similar annual depredation removals, with all approaches averaging around 5% of the catch removed throughout the entire fishery. While depredation varies spatially, the different modelling approaches consistently highlighted areas where the impact of depredation was highest.

Keywords: depredation, longline, marine mammal, modelling, odontocete, South Atlantic, South Georgia.

Introduction

In the marine environment, depredation on fishery catches occurs when animals exploit resources aggregated by humans. Examples include sharks (MacNeil *et al.*, 2009; Ryan *et al.*, 2019), colossal squid (Remeslo *et al.*, 2019), and various marine mammal species (Read, 2005; Werner *et al.*, 2015) depredating on catches associated with nets or longlines. Toothed whales (odontocetes), in particular, have regularly been observed engaging in depredation, from the Alaskan sablefish fishery, to fisheries in the tropics, and as far South as the Antarctic (e.g. Sivasubramaniam, 1964; Yano and Dahlheim, 1995; Kock *et al.*, 2006; Dalla Rosa and Secchi, 2007; Rocklin *et al.*, 2009; Peterson and Carothers, 2013; Rabearisoa *et al.*, 2018; Tixier *et al.* 2021).

Depredation removals result in a mortality associated with the fishery being greater than the catch; fish that are caught in the gear are eaten before they can be brought on board the vessel to be counted or weighed. Not appropriately including these removals within fish stock assessments may introduce bias to both the stock and fishery metrics, as well as the sustainable management

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reference points (Gilman *et al.*, 2006; Roche *et al.*, 2007; Söffker *et al.*, 2015; Peterson and Hanselman, 2017; Hanselman *et al.*, 2018) due to the unrecorded mortality. Over a decade ago when the study of depredation was an emerging field, this mortality was often not considered (Purves *et al.*, 2004; Gilman *et al.*, 2006; Roche *et al.*, 2007). With increasing knowledge of depredation, modelling of removals has become a necessary component in stock assessments with a variety of approaches applied, including standardizing CPUE for whale depredation (Hanselman *et al.*, 2018; Earl, 2019) and including depredation within estimates of fishery catch (Peterson and Hanselman, 2017; Earl, 2019).

In some affected fisheries such as the tropical fisheries for tuna and swordfish, marine mammals can leave lips or heads on the hooks which can be counted (Rabearisoa *et al.*, 2012), however, in other fisheries such as the Southern Ocean fisheries the depredating odontocetes often leave no trace of removals, taking the whole fish off the hook (Gasco *et al.*, 2015). Direct observation is, therefore, impossible in these circumstances and depredation needs to be estimated through modelling.

Depredation models generally compare catch per unit effort (CPUE), with and without the presence of mammals, to estimate the catch removed over time and space, whilst standardizing with variables such as season, location, and vessel using for example generalized linear models (GLMs; e.g. Peterson *et al.*, 2013) or generalized additive models (GAMs; e.g. Peterson *et al.*, 2014; Tixier *et al.*, 2020) as well as generalized linear mixed models (GLMMs; e.g. Sigler *et al.*, 2008; Söffker *et al.*, 2015; Janc *et al.*, 2018) and generalized additive mixed models (GAMMs; e.g. Peterson and Hanselman, 2017). The performance of different modelling approaches has been compared by Hanselman *et al.* (2018), who evaluated fixed-effect GLMs and GLMMs (with random and mixed effects) and found that the mixed-effect models performed better than the fixed-effect models to describe sperm whale (*Physeter macrocephalus*) depredation of a sablefish (*Anoplopoma fimbria*) fishery in Alaska. An alternative method to estimate depredation is to compare catches with a species known to be less vulnerable to depredation; Gasco *et al.* (2015) developed an approach to corroborate the Tixier *et al.* (2010) estimates, which was based on killer whale (*Orcinus orca*) preference for toothfish compared to bycatch species and uses the change in ratio of bycatch species to toothfish catch as an indicator of depredation for a given fishing location.

The sub-Antarctic fisheries for Patagonian toothfish (*Dissostichus eleginoides,* hereafter toothfish) target a highly prized bottom dwelling deep water fish found in the Southern Ocean. Toothfish can grow in excess of 2.3 m, weigh up to 200 kg, and have been recorded living up to 50 years around South Georgia (Belchier, 2004). In these fisheries, marine mammals such as killer whales and sperm whales have been shown to interact with the demersal longline fishing gear (Kock *et al.*, 2006). The longlines are set on the seabed at depths ranging from 500–2000 m, but typically around 1000 m, and are, therefore within the diving and foraging range of sperm whales (Watwood *et al.*, 2006). This depth was thought to reduce killer whale depredation until lines are hauled and their catch becomes accessible in surface waters (Roche *et al.*, 2007; Tixier *et al.*, 2010; Söffker *et al.*, 2015). However, more recent studies have shown that killer whales can dive to 700–1000 m (Reisinger *et al.*, 2015; Towers *et al.*, 2019), and on occasion interact with longline sets at these depths (Richard *et al.*, 2020).

The level of depredation observed across the sub-Antarctic islands where the toothfish fishery occurs is heterogeneous, following different patterns and temporal trends (Tixier *et al.*, 2020). It ranges from relatively unaffected areas, such as Heard and McDonald Islands, where sperm whales are the only species involved and interact with <5% of the longline sets, to substantially depredated areas, such as Crozet Islands, where together, killer and sperm whales interact with >69% of the sets (Purves *et al.*, 2004; Kock *et al.*, 2006; Gasco *et al.*, 2015; Guinet *et al.*, 2015; Söffker *et al.*, 2015; Tixier *et al.*, 2020). Even within the same fishing ground there can be notable disparity with some areas clearly identifiable as depredation 'hot spots' (Clark and Agnew, 2010; Söffker *et al.*, 2015).

For the South Georgia fishery, depredation was first reported by scientific observers in 1994 (CCAMLR, 1994) and described in 1996 (Ashford *et al.*, 1996). The extent and patterns of depredation were first described in detail in 2004 (Purves *et al.*, 2004). The effect of depredation on CPUE was first modelled in 2010 (Clark and Agnew, 2010), and the results of the initial model were included in the toothfish stock assessment for this region in 2011 (Peatman *et al.*, 2011). The model was later extended to include additional species and spatial effects in 2015 (Söffker *et al.*, 2015). Estimation of depredation continues to be a routine element of the toothfish stock assessment around South Georgia to date (Earl, 2019).

In this paper, we examine five applications of common model structures (GLMs, GAMs, and GAMMs; Zuur, 2012; Zuur *et al.* 2013) to the dataset from the longline fishery around South Georgia. We then compare the estimates of depredation with those based on comparing local catch ratios between toothfish and grenadiers (*Macrourus* spp.), a family not targeted by killer whales (Gasco *et al.*, 2015). The models are compared with the aim of investigating whether an improved model compared to the existing approach can be identified, and whether the approaches estimate similar magnitude and trends in depredation.

Methods

To compare the performance of alternative models of depredation, a standard dataset was compiled that would be suitable for each of the models. All analysis was carried out in R versions 4.0.0 and 4.0.2 (R Core Team, 2020), using GAM fitting from packages mgcv (Wood, 2011), and surveyIndex (Berg, 2020). The notation for variables used in these modelling approaches are given in Table 1.

Data preparation

The toothfish fishery operates by setting longlines of around 10 km in length in one of three configurations (Spanish, trotline, or autoline) between buoys. After a typical soak period of 17 h, the line is recovered and hauled on board over several hours. Data collected during the setting and hauling of each longline (henceforth haul) deployed by vessels fishing in the South Georgia longline toothfish fishery provided catches of toothfish and grenadier by weight and number, as well as the associated fishing effort and corresponding scientific observer records of depredating killer and sperm whales, between 2003 and 2019 (Figure 1). Observation periods occur on an *ad hoc* basis for brief periods during hauling activity of around 50% of the hauls, with timing and duration dependent on the other tasks that the observer is required to complete. During each of these haul observation periods, the observer makes a visual estimation of the number of depredating whales in a 500 m radius around the vessel using a standardized protocol used across toothfish fisheries (Gasco *et al.*, 2016).

Data were removed when hauls occurred outside the regular bounds and timing of the fishery (retaining those deeper than

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Table 1 Notation used in the description of the models. Lines are indexed by i and cells by j.

Continuous variables	Discrete factors
$CPUE_i$ – The CPUE observed from line i	$year_i$ – year when line i was set
$\widehat{CPUE}_{A,j}$ – The average CPUE observed from lines in cell $j$where depredating odontocetes were not observed	$month_i$ – month when line i was set
$\widehat{CPUE}_{P,j}$ – The average CPUE observed from lines in cell $j$where depredating odontocetes were observed.	$area_i$ – one of four areas for fishing: Shag Rocks, South, North West or East South Georgia
$CPUE_{loss,j}$– CPUE lost from a line in cell j.	$depthband_i$– average depth (m) of the endpoints of line i in 500m bands
lon_i, lat_i – longitude and latitude of midpoint line i	
$depth_i$ – average depth (m) of the endpoints of line i	
$N_{spw\,i}$ – number of depredating sperm whales observed for line i	$vessel_i$ – code randomly allocated to the vessel setting line i
$N_{kiw\,i}$ – number of killer whales observed for line i	$nationality_i$ – code randomly allocated to the nationality of the vessel setting line i
$soak_i$ – time that line i was left to soak	$cetacean_i$ – presence of killer whale, depredating sperm whale or both
$speed_i$ – haul speed of line i	$P_{kiw\,i}$ – presence of killer whales when hauling line i
day_i – day of year that line i was set	$P_{spw\,i}$ – presence of depredating sperm whales when hauling line i
$T_{loss,j}$ – number of toothfish lost to depredation in cell j.	$gear_i$ – fishing gear autoliner, Spanish or trotline used on line i
$T_{P,j}$ – number of toothfish caught in cell $j$when killer whales were observed	$cell_i$ – the cell in which the midpoint of line i occurs
$T_{A,j}$ – number of toothfish caught in cell $j$when killer whales were not observed	
$G_{P,j}$ – number of grenadiers caught in cell $j$when killer whales were observed	
$G_{A,j}$ – number of grenadiers caught in cell $j$when killer whales were not observed	

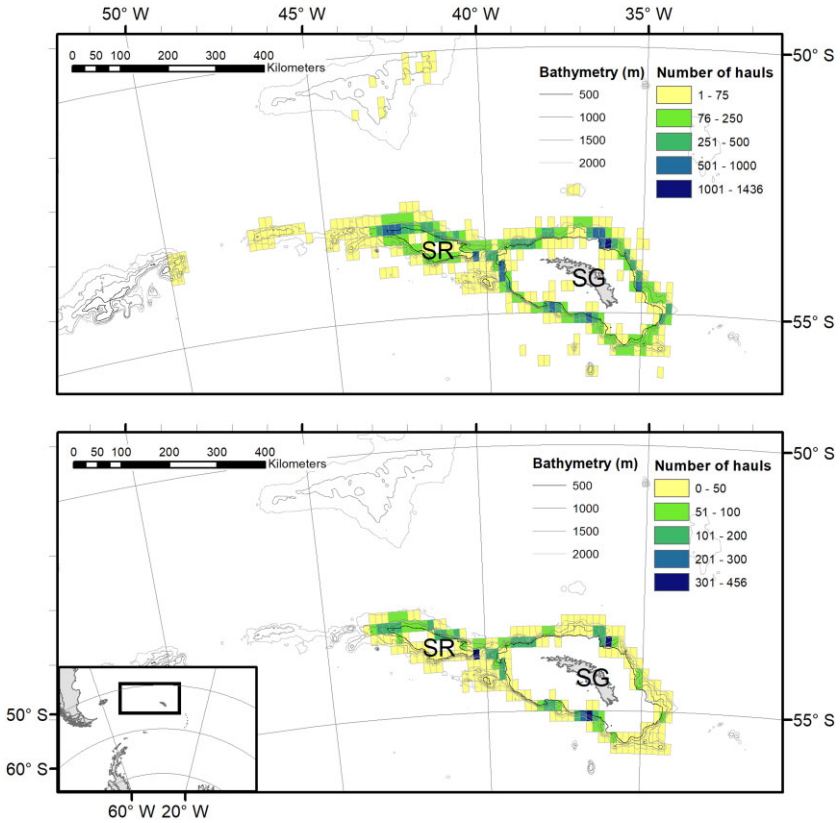


Figure 1. Study area around the island of South Georgia (SG) and Shag Rocks (SR) in the Southern Ocean shown in relation to 500–2000 m depth contours derived from GEBCO Compilation Group (2021) data. Top: fishing effort (number of hauls 2003–2019 by 0.2° × 0.2° cells) . Bottom: the subset of hauls included in this study, where observations for mammals occurred and data met the requirements outlined in the data preparation section.

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500 m, South of 52°S, East of 45°W, and between 1st April and 31st August) to exclude data entry errors. Data points that were outliers regarding line length, soak time and haul duration were excluded. Hauls in isolated locations where fewer than 20 hauls occurred within 10 statute miles were also removed as fisheries on isolated seamounts may exhibit different patterns to fishing along the shelf edge. In addition, only data from vessels that either participated in the fishery for more than 3 years or participated in 2019 were included (14 vessels met these criteria). The final dataset (Figure 1, bottom) contained 8710 hauls with observation periods during hauling, of which mammals were present in 2643 cases. The final dataset represented 30% of the total hauls in the fishery, with the number of hauls in each year included in the data varying between 217 and 1220. In some years and on some vessels, the abundance of depredating sperm whales or killer whales near the vessel were recorded as a range rather than a single figure, or multiple observation periods took place during the hauling of one longline set. In those instances, the mean between the minimum and the maximum was used for each observation period, and the median of the observation periods was associated with the line.

Sperm whale and killer whale longline interactions

The depredation patterns around South Georgia are described in Söffker *et al.* (2015), which showed that in this region catch rates with killer whales near the vessel, whether feeding was observed or not, were significantly lower than catch rates in the absence of killer whales. In contrast, catch rates were typically lower when the sperm whales were recorded by observers as "feeding" near the vessel and "interacting" with the vessel (dives near the longline and vessel) during hauling activity than when they were recorded as present, but not interacting during hauling activity (Söffker *et al.*, 2015). Therefore, in this paper depredation by sperm whales is considered to have occurred when they have been observed as 'interacting' with the longlines during hauling, while for killer whales depredation is considered to have occurred whenever they were present during hauling.

Depredation estimation approaches

Current stock assessment GLM

The current stock assessment GLM is the method used to estimate depredation and CPUE trends for the stock assessment for toothfish around South Georgia (Earl, 2019). The approach fits a linear model predicting CPUE based on the factors: year, month, nationality, area, depth class, and presence of killer whales or depredating sperm whales. The nationality of the ship's registration acts as a proxy for a variety of factors such as gear type and configuration, and the fishing experience of the captain and fishing master, rather than as a factor directly affecting the catch rate. An alternative model, replacing nationality with individual vessels was overparameterized because of a high degree of dependence between year and vessel. This model fits a General Linear Model (GLM) with a normal distribution and square root link function to the CPUE of the form of Equation), where i is an index that identifies data specific to a haul.

$$\sqrt{CPUE_i} = \alpha + \beta_1 year_i + \beta_2 month_i + \beta_3 nationality_i + \beta_4 cetacean_i + \beta_4 area_i + \beta_5 depthband_i + \epsilon_i \quad (1)$$

CPUE comparison

The CPUE comparison method developed by Tixier *et al.* (2010) compares the CPUE locally ($0.2^\circ \times 0.2^\circ$ cells) in the presence of depredating mammals to that observed in their absence to estimate a change in CPUE implied by the presence of mammals. The effect of depredation on CPUE ($CPUE_{loss,j}$) is calculated as the difference between the average for each cell j in the absence of mammals (independently for occurrences of sperm whales, killer whales, and both species) and the average in cell j when mammals are present, according to Equation (2).

$$CPUE_{loss,j} = \widehat{CPUE}_{A,j} - \widehat{CPUE}_{P,j}. \quad (2)$$

Data for all years are combined to maximize the number of cells where CPUE loss can be calculated. In order to compare the estimates of depredation, and their uncertainty with the other models, the model was reformulated as a GLM with a normal distribution, according to Equation (3) where the CPUE loss from each haul is estimated by the β_2 and β_3 terms.

$$CPUE_i = \alpha + \beta_1 Cell_i + \beta_2 Cetacean_i + \beta_3 (Cell_i \times Cetacean_i) + \epsilon_i \quad (3)$$

Circumpolar GAM

The Circumpolar GAM model is based on the GAM derived by Tixier *et al.* (2020) for several sub-Antarctic fisheries fitting an additive model to observed CPUE to standardize for factors that include marine mammal abundance. We take the general form of the GAM and keep the same specifications of the smoothers as in Tixier *et al.* (2020), while estimating parameters to provide the best fit to our dataset. This model fits a GAM with a normal distribution and log link function to the CPUE of the form of Equation (4), where the $f_{1,2,4,5,6}$ are thin plate splines with four knots, and f_3 is the thin plate spline with estimated degrees of freedom.

$$\log(CPUE_i) = \alpha + \beta_1 (year_i) + f_1 (day_i) + \beta_2 (vessel_i) + f_2 (depth_i) + f_3 (lat_i, lon_i) + f_4 (soak_i) + f_5(N_{kiw\,i}) : gear_i + f_6(N_{spw\,i}) : gear_i) + \epsilon_i \quad (4)$$

South Georgia specific GAM

The South Georgia specific GAM was developed from the circumpolar GAM by selecting the parameters most appropriate for estimating CPUE in the current study. Initially, the explanatory variables for sperm whale and killer whale presence were added in addition to the dependence on the abundance of depredating whales used in the circumpolar GAM. This was added to reflect the large difference in observed CPUE between no individuals observed and one individual observed, which was not well-modelled by fitting a smoother to the abundance. The thin plate spline was replaced by a full product tensor smooth to allow for an anisotropic relationship. Parameters in the model were reduced by backward stepwise selection using the Akaike Information Criterion (AIC; Akaike, 1974) value and residuals as a guide to achieve a best fitting GAM for South Georgia data. The dimension of the basis for the chosen smooth terms (k) was adjusted using the residuals as a guide. This resulted in a removal of the interaction between gear type and mammal abundance for both sperm whales and killer whales, but gear remained in the model as a factor. This model fits a GAM

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with a normal distribution and log link function to the CPUE of the form of Equation (5), where the $f_{1,2,4,5,6,7}$ are thin plate splines with eight, ten, four, six, four, and four knots, respectively, and f_3 is the full product tensor smooth, using cubic regression spline with estimated degrees of freedom.

$$\begin{aligned}\log(CPUE_i) = {} & \alpha + \beta_1 year_i + f_1(day_i) + \beta_2 vessel_i \\ & + f_2(depth_i) + f_3(lon_i, lat_i) + f_4(soak_i) \\ & + f_5(speed_i) + \beta_3 P_{kiw\,i} + \beta_4 P_{spw\,i} \\ & + f_6(N_{kiw\,i}) + f_7(N_{spw\,i}) + \beta_5 gear_i + \epsilon_i \end{aligned} \quad (5)$$

Survey standardization GAMM

Survey standardization GAMM, a standardization technique based on the approach of Berg *et al.* (2014), was applied to the CPUE from the commercial vessels, adding mammal abundance as a factor for both sperm whales and killer whales. This method was initially developed to combine survey indices from multiple vessels by allowing for standardization where the vessel, gear, timing, or spatial extent of the survey has varied over time. The model allows for zero-inflation but this is not required for our data, because only a small number of hauls (less than 1.5%) have zero toothfish catch. The model applied fits a GAMM with a Tweedie distribution and log link function to the CPUE of the form given in Equation (6), where f_1 is the default full product tensor smooth, using Duchon splines with 12 knots, $f_{2,3,4,5}$ are Duchon splines with five knots and the vessels are treated as random effects.

$$\begin{aligned}\log(CPUE_i) = {} & \alpha + \beta_1 year_i + f_1(lon_i, lat_i) + f_2(depth_i) \\ & + f_3(N_{kiw_i}) + f_4(N_{SPW_i}) + \beta_2(vessel_{f_i}) \\ & + f_5(day_i) + \epsilon_i \end{aligned} \quad (6)$$

Bycatch as an indicator of depredation

The bycatch as an indicator of depredation method takes advantage of catch species selectivity of killer whales (Tixier *et al.*, 2016). Gasco *et al.* (2015) estimated the number of depredated toothfish using the proportion of grenadiers caught in relation to toothfish on each haul (Equation (7)) aggregated in $0.2^\circ \times 0.2^\circ$ cells to account for spatial variations in grenadier bycatch rates. As with the CPUE comparison method, data from all years were combined into a time-invariant model. Around South Georgia, grenadier are caught in lower proportions (typically a ratio of 0.2 grenadiers to toothfish by number) than in the original study area used by Gasco *et al.* (2015), which might affect the accuracy of the approach. Therefore, we excluded all cells that had four or fewer hauls within them (as in Gasco *et al.*, 2015) but made no further data exclusions (the original method only included areas with ratios between 0.35 and 0.65). The number of toothfish lost in each cell was estimated using Equation (7). As with the statistical models, the notation for variables used in these modelling approaches are given in Table 1.

$$T_{loss,\,j} = G_{P,\,j}\left(\frac{T_{A,\,j}}{G_{A,\,j}}\right) - T_{P,\,j}. \quad (7)$$

Building on the method used in Gasco *et al.* (2015), the total depredation in the area was determined by calculating the estimated depredation rate for each cell and applying this to the reported catch in each haul. To apply the method to as much of the available data as possible, the hauls in cells with insufficient hauls to estimate

Table 2 Summary of the fit of alternative models and estimated depredation. Ranges indicate one standard error around the mean estimate.

Model	% deviance explained	AIC	Effective parameters	Average annual catch removals (tonnes of toothfish) from fishery				Average total depredation rate (%)
				Killer whales	Sperm whales	Both	Total	
Current stock assessment GLM	25.7	−6496	34	94.7 (89.5–100.0)	28.0 (21.0–35.0)	10.9 (9.5–12.3)	133.6 (123.8–143.5)	5.2
CPUE comparison	23.5	−5211	549	93.5 (87.3–99.7	22.4 (1.54–29.4)	13.5 (11.9–15.2)	129.5 (118.9–140.0)	5.0
Circumpolar GAM	33.3	−7351	76.5	80.7 (76.0–85.3)	44.7 (39.2–50.1)	9.8 (9.2–10.3)	135.1 (126.8–143.4)	5.3
South Georgia specific GAM	34.6	−7512	81.5	86.5 (81.2–91.7)	28.5 (21.6–35.4)	9.7 (9.1–10.3)	124.7 (114.8–134.6)	4.8
Survey standardization GAMM	30.2	−8410	87.3	77.8 (74.6–80.9)	44.3 (38.9–49.6)	9.7 (9.3–10.0)	131.7 (124.7–138.8)	5.2
Bycatch as an indicator of depredation	–	–	–	195.8	–	–	–	7.4

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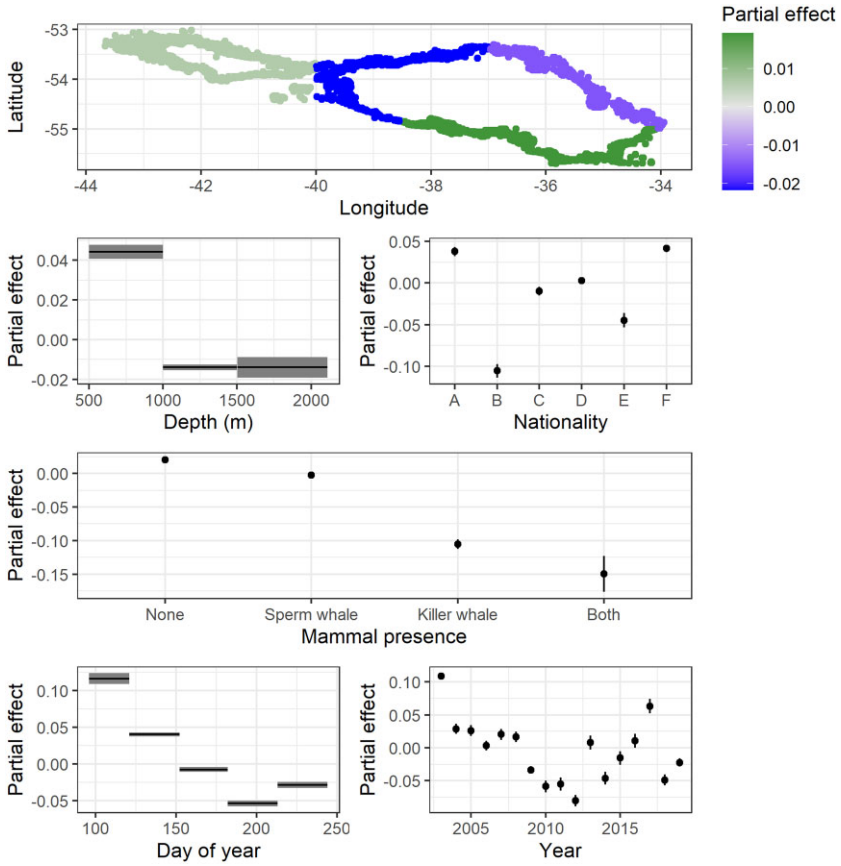


Figure 2. Partial effects on CPUE of longitude/latitude, depth (m), vessel nationality, killer whale or depredating sperm whale presence/abundance, time of year (days), and year from the current stock assessment GLM. Shaded areas and whiskers indicate two standard errors. Positive partial effects indicate higher estimated CPUE.

depredation from the bycatch were instead estimated using average depredation rate in that year weighted by the proportion of total catch in that year. Number of fish depredated was converted into catch weight lost using the average weight of toothfish on each line.

A re-formulation of this method into a statistical model (GAM) to allow comparison with the other models, and to provide a method of estimating uncertainty was considered. However, due to the approach estimating catch loss rather than CPUE loss, and the separate treatment of data from cells with few hauls it was not possible to construct such a model in a way that would allow meaningful comparison with the other approaches that estimate the impact on CPUE of mammal presence and abundance.

Model comparison

Estimates of depredation within the CPUE models for the hauls included in the final dataset were calculated by predicting the total weighted catch from a dataset, where each haul was included twice, first with the observed abundance of depredating whales, weighted by −1 times the number of hooks on the line, and second with no depredating whale present, weighted by the number of hooks on the line. This allows for calculation of the total depredation, including confidence intervals, taking into account the variance–covariance structure of the models. Despite the CPUE comparison method estimating parameters that do not depend on time, the estimated depredation does vary by year because of the different spatial distribution of the fishery in each year. Total depredation attributable to the entire fishery (including hauls where observations to determine the presence of depredating whales were not made) was calculated by dividing the estimates of depredation by the proportion of the total hauls fished in each year that were included in our final dataset. The estimates of depredation from the bycatch as an indicator of depredation method were also divided by this proportion to provide comparable estimates from the whole fishery.

Model diagnostics were produced for the statistical models to assess their suitability, and the AIC, degrees of freedom, deviance explained, and estimates of annual depredation are presented in Table 2.

Results

Statistical models of CPUE

Current stock assessment GLM

The current stock assessment GLM estimated partial effects for each of the factors used to estimate CPUE (Figure 2). To reflect the non-linear impact of depth, time of year, and fishing location on CPUE, each of these data were aggregated into blocks (Table 1), which is visible in the step-like estimation of partial effects (Figure 2). Overall, the parameters in this model explained 25.7% of the deviance, with an AIC of −6496. This model estimates similar effects of fishing depth, vessel effect, and annual variability on CPUE as the South Georgia specific GAM. The spatial variability within the defined data blocks shows the difference in CPUE between Shag Rocks and south of South Georgia ($p = 0.02$), northwest

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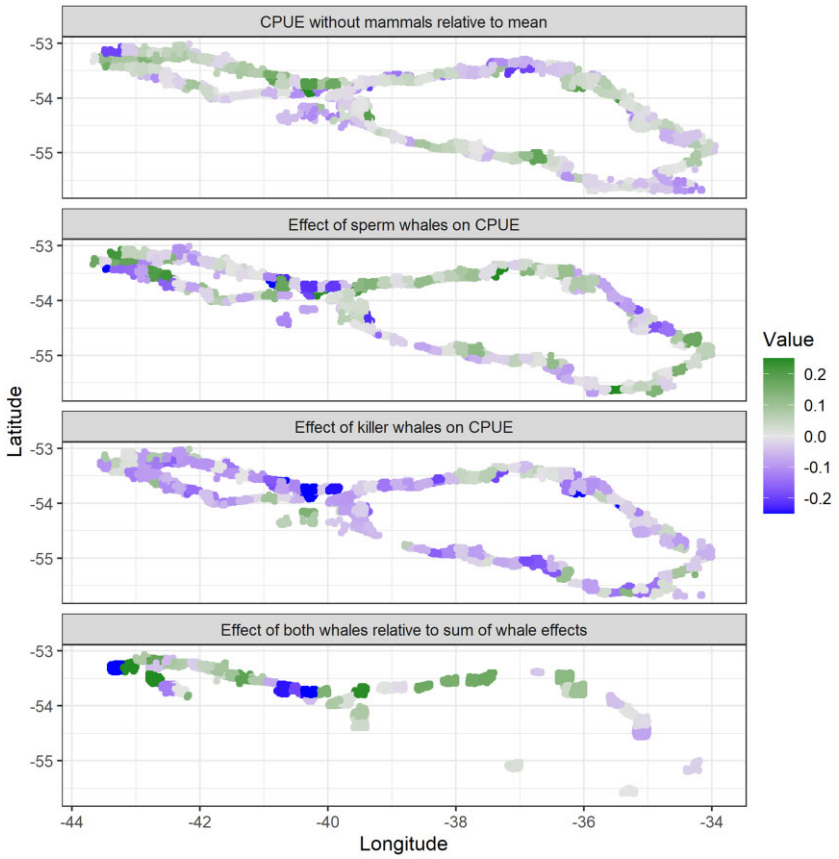


Figure 3. Average CPUE (kg/1000 hooks) by 0.2° × 0.2° cells (relative to the overall average) in the presence of neither interacting sperm whales nor killer whales (top), change due to sperm whales (top middle), change due to killer whales (bottom middle), and change due to both sperm whales and killer whales additional to the sum of the change due to both mammals (bottom right).

of South Georgia ($p < 0.0001$), and east of South Georgia ($p = 0.0007$; Figure 2). This model does not include the abundance of killer whales or sperm whales, but instead estimates the effect of presence or absence. The presence of killer whales, interacting sperm whales, or both, resulted in significantly lower CPUE than when neither were present (all $p < 0.0001$). Similar to the South Georgia specific GAM, the time of year describes a similar pattern of initial decrease in CPUE over the season followed by an increase towards the end of the season.

CPUE comparison

Average CPUE estimates by grid square showed the reduction in CPUE associated with presence of depredating killer whales and sperm whales compared to the average without depredating whales (Figure 3). Due to the small scale of the grid squares relative to the extent of the fishery, the model estimated a large number of parameters (549) but still explained relatively little of the variance in the CPUE (23.5%) and an AIC of −5211. Depredating sperm whales and killer whales were observed to reduce CPUE across most of the spatial extent of the fishery, although the hauls where both were observed occurred more commonly in the north of the fishery.

Circumpolar GAM

The GAM developed for a circumpolar dataset highlighted the effects of hauling speed, fishing depth, location, and abundance of killer whales and depredating sperm whales on CPUE. The best fitting model explained 33.3% of the South Georgia data deviance, with an AIC of −7351. There were significant differences between years ($p < 0.0001$, $F_{16} = 28.1$) as well as between vessels ($p < 0.0001$, $F_{13} = 18.54$). The model estimated a decrease in CPUE with fishing depth (edf = 2.30, $F = 35.3$) and throughout the season (edf = 2.70, $F = 316$). There was a linear decrease in CPUE with increasing depredating sperm whale abundance for autoline and Spanish gear types (edf = 1.00, $F = 43.8$; edf = 1.00, $F = 15.1$) but not for trotlines (edf = 1.00, $F = 2.84$). Killer whale presence also affected CPUE negatively with increasing number of individuals. However, after an initial reduction, that effect was then less pronounced with larger numbers of killer whales for autoline and Spanish gear types (edf = 2.29, $F = 28.15$; edf = 2.71, $F = 44.6$). Large numbers of killer whales were not observed when trotlines were used and only the initial reduction in CPUE was observed (edf = 1.04, $F = 2.99$). The relationship of CPUE with location was highly non-linear and showed substantial spatial variability (edf = 27.88, $F = 17.2$; Figure 4).

South Georgia specific GAM

The South Georgia specific GAM included adjustments in the variables used to formulate the circumpolar GAM to better fit the variation of CPUE through the fishing season, and to allow a discontinuity in the dependence on killer whale and depredating sperm whale abundance. This model described the data slightly better and

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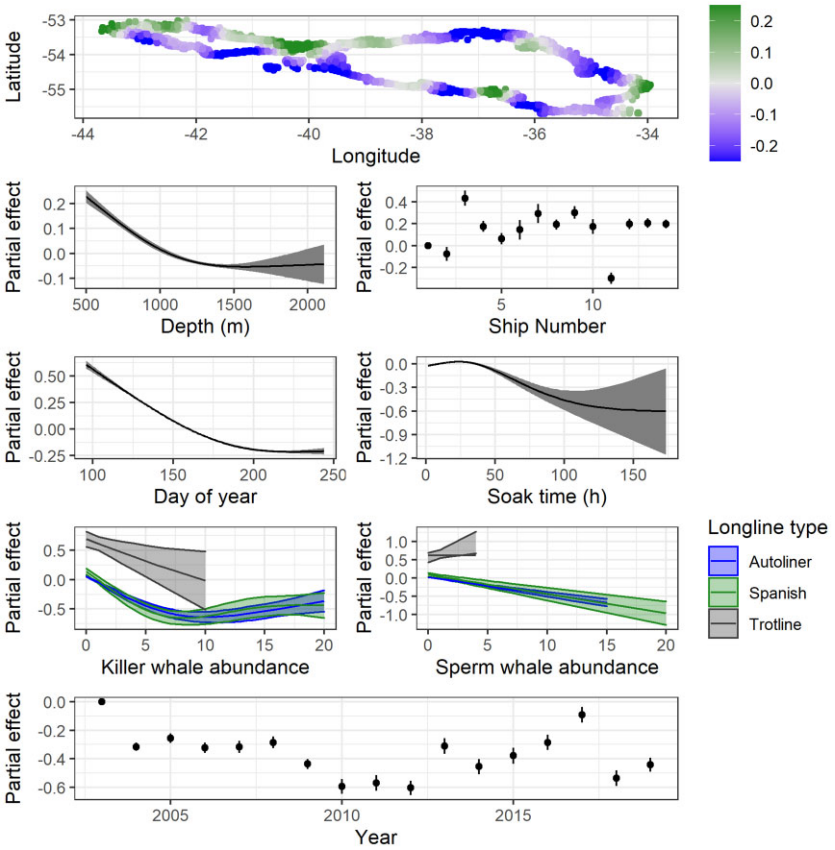


Figure 4. Partial effects on CPUE from the circumpolar GAM of longitude/latitude, depth (m), vessel, time of year (days), soak time (hours), killer whale and interacting sperm whale abundance (by gear type), and year based on the GAM derived by Tixier *et al.* (2020). Shaded areas and whiskers indicate two standard errors. Positive partial effects indicate higher estimated CPUE.

explained 34.6% of the deviance, with an AIC of −7,512. As for the circumpolar GAM, there were significant differences in CPUE between years ($p < 0.001$, $F_{16} = 24.3$), as well as between vessels ($p < 0.001$, $F_{13} = 18.4$). Presence of killer whales ($p = 0.006$, $F_1 = 7.42$) and feeding sperm whales ($p < 0.001$, $F_1 = 15.2$) significantly reduced CPUE, and there was no significant difference between the current gear types used in the fishery ($p = 0.59$), but CPUE was higher on trotline sets ($p = <0.001$). Overall, results were broadly similar to the circumpolar GAM from which it was developed, although there were notable differences in the partial effects for sperm whale abundance and fishing depth. Unlike the circumpolar GAM the relationship between sperm whale abundance and CPUE was not directly linear, with CPUE initially declining with increasing sperm whale abundance but remaining relatively stable after that (edf = 1.97, $F = 24.0$). The fishing depth relation with CPUE was non-linear, decreasing at deeper depths but remaining relatively similar across the depth range of the fishery (edf = 8.13, $F = 23.4$). The smoother for day of the year in this model described the seasonal effect with CPUE dropping to a minimum part way through the season (edf = 6.71, $F = 114$). There was a clear spatial relationship identified by this model (edf = 27.8, $F = 15.1$; Figure 5), which closely resembles the estimates from the circumpolar GAM.

Survey standardization GAMM

The GAMM based on the method by Berg *et al.* (2014) described the data slightly less well than the South Georgia specific GAM and explained 30% of the deviance, but with a lower AIC of −8410. As with the previous statistical models, there were significant differences in CPUE between years ($F_{16} = 25.8$, $p < 0.0001$) and vessels (edf = 11.6, $F = 20.7$). The abundance of killer whales (edf = 3.72, $F = 114$) and interacting sperm whales (edf = 2.80, $F = 32.8$) was related to reduced CPUE on affected hauls. This model did not describe the relationship between sperm whale abundance and CPUE as linear, but followed a pattern of an initial reduction of CPUE with increasing abundance and then remained relatively stable (edf = 2.74, $F = 30.6$). The partial effect of the abundance of killer whales was more non-linear than for sperm whales, with CPUE overall declining with increasing abundance but with some variability and a slight increase towards larger pods (edf = 3.71, $F = 105$, Figure 6).

Estimation of depredation through bycatch

A total of 166 spatial grid cells met the criteria set out in the methods, by having at least five hauls. The estimation of depredation through bycatch highlighted several regions with higher depredation removals for all years combined (Figure 7). Areas with higher rates of depredation were to the northwest of South Georgia, and in the north-eastern region at Shag Rocks, where this method estimated a total removal of over 65 tonnes from observed hauls in two areas. Overall depredation removals were estimated higher along the northern side of South Georgia, while the south-eastern side of South Georgia was less affected (Figure 7). The average estimated

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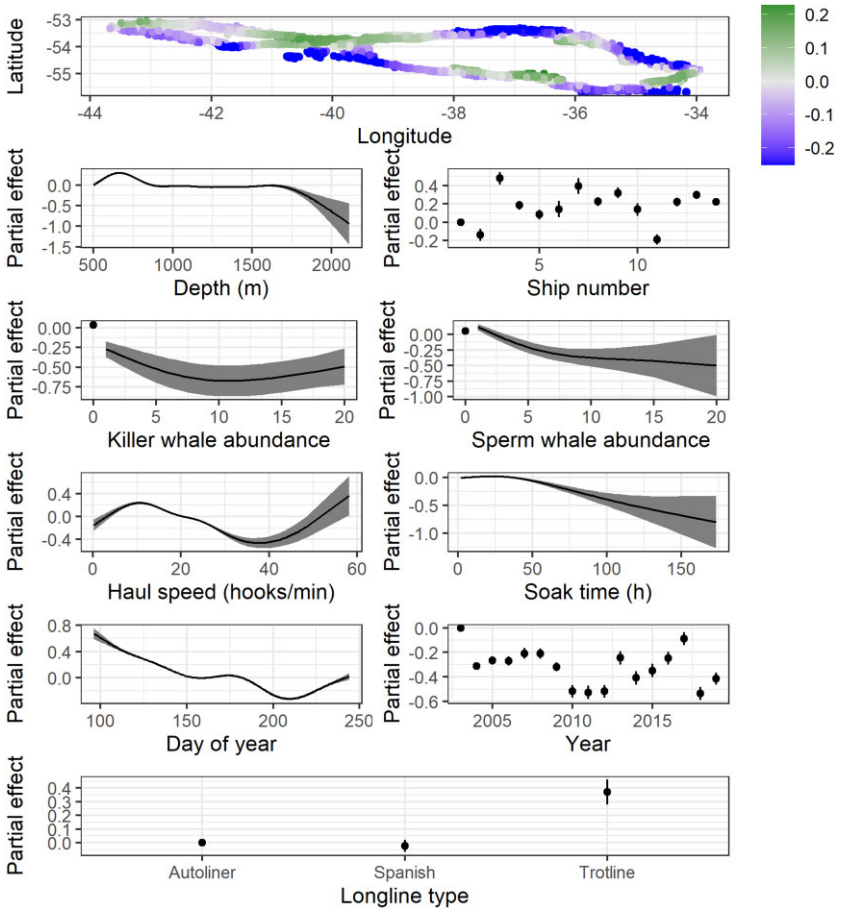


Figure 5. Partial effects on CPUE of longitude/latitude, depth (m), vessel, killer whale or depredating sperm whale presence and abundance, haul speed, soak time, time of year (days), year, and longline code from the South Georgia specific GAM. Shaded areas and whiskers indicate two standard errors. Positive partial effects indicate higher estimated CPUE.

catch removals per year from killer whales are 196 tonnes using the bycatch approach and is higher than that estimated by the statistical models (Figure 8).

Comparison of model estimates

Each of the statistical models accounted for spatial variability in CPUE, either through splines or through dividing the study area into independent regions and estimating local CPUE. Each of the GAMs (including the GAMM) used similar smoothers and estimated areas of higher CPUE in the North West, at the Easternmost extremity of the fishery and around 37°W in the Southern part of the fishery (Figures 3, 4, and 6). Similar areas were highlighted as having high CPUE by the CPUE comparison method, with the addition of an area in the North East of the fishery (Figure 2). The current stock assessment GLM estimated the spatial variability on a coarser scale, with only four regions, and highlights higher CPUE to the West and to the South of the fishery (Figure 5).

The GAM methods and the current stock assessment GLM included depth as an explanatory variable. Although the exact form of the relationship differed between models, they each showed CPUE dropping between 500 and 100 m, before stabilizing, with increased variability above 1500 m (Figures 3–6).

The GAM methods and the current stock assessment GLM included year as an explanatory variable, generally estimating the years 2003 and 2017 to have high CPUE, and the years 2010–2012 to have lower CPUE. The models differ slightly in their estimates for 2018, which is estimated to be among the lowest years by the South Georgia GAM, while the other models estimate it to be higher than 2010–2012 (Figures 3–6). Within each year, a similar trend of decreasing CPUE until around day 200 (mid-July), followed by an increase was estimated by each of these models, although the increase at the end of the season was lowest in the circumpolar GAM.

The effects of depredating mammals were included in four different ways within the models. The stock assessment GLM and the CPUE comparison considered only the presence of sperm whale, killer whale or both, rather than their abundance. In the CPUE comparison, this effect interacted with the spatial distribution of CPUE. In both of these estimates, killer whales implied a larger reduction than sperm whale, and the effect of both depredating mammals occurring together resulted in a slightly greater CPUE drop than the sum of their effects (Figures 1 and 2). The GAMs included depredating mammal abundance rather than presence, but did not estimate an effect of the interaction between sperm whale and killer whale. For sperm whales, the South Georgia specific GAM, and the survey standardization GAMM estimated a roughly linear

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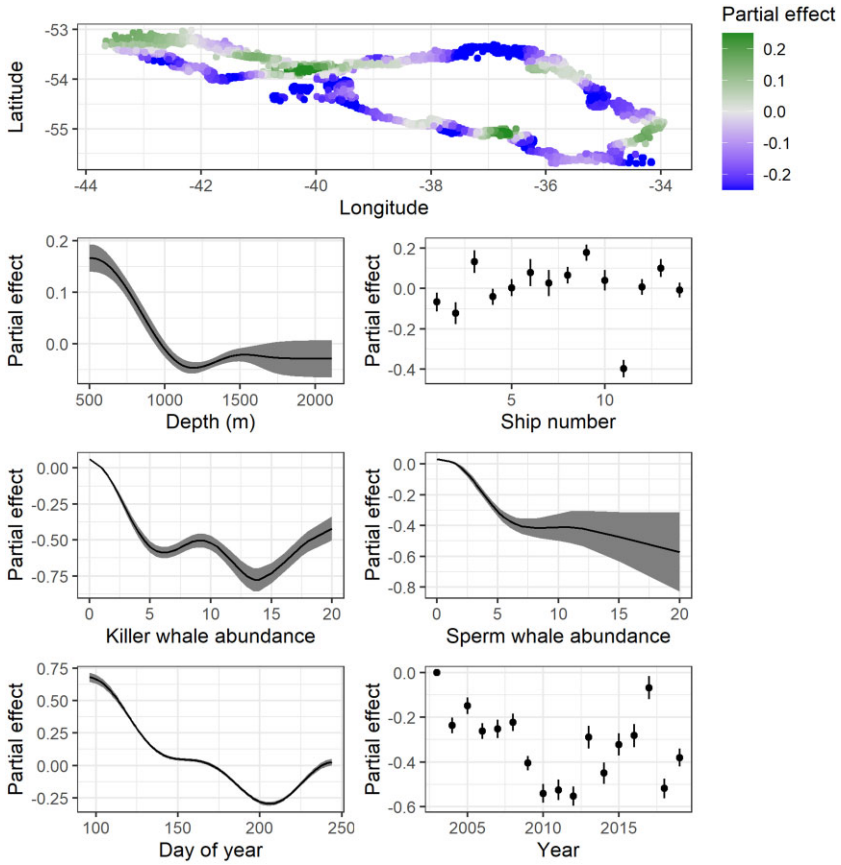


Figure 6. Partial effects on CPUE of longitude/latitude, depth, vessel, killer whale or depredating sperm whale abundance, time of year, and year from the survey standardization GAMM. Shaded areas and whiskers indicate two standard errors. Positive partial effects indicate higher estimated CPUE.

reduction in CPUE between one and five individuals, with less effect for subsequent mammals (Figures 3, 4, and 6). The South Georgia specific GAM estimated little difference between the effect of one mammal and none. The circumpolar GAM estimated a linear reduction in CPUE with abundance for the two most common gear types, with only limited data available for trotlines. For killer whales, a steep reduction in CPUE was seen between 0 and 5 individuals, while the effect of further individuals was small (Figures 3, 4, and 6).

Comparison of model diagnostics

Among the models considered, the current stock assessment performs relatively poorly with the second-highest AIC, and second-lowest percentage of deviance explained (Table 2). Each of the GAMs explain more of the variability than the current stock assessment GLM due to the improved modelling in two key assumptions; the GAMs show much greater spatial variability than the structure of the current GLM allows, and the GAMs include killer whale and depredating sperm whale abundance, whereas the GLM only includes presence or absence. The South Georgia specific GAM explains the highest proportion of the variance, at 35%, but each of the GAMs, explains a proportion of variance greater than 30%. The performance of the models judged by the AIC indicates that the survey standardization GAMM is superior to the other models according to this metric. The South Georgia specific GAM represents a small improvement on the circumpolar GAM as measured by both the deviation explained and the AIC, as might be expected for a model optimized for a specific area.

The survey standardization GAMM showed that among the models considered it has the lowest AIC, and additionally, the residuals shown in Figure 9 showed no concerning patterns of autocorrelation or evidence of poor fits, except in the case of depth, where CPUE at depths greater than 1800 m (the extreme depth of the fishery) is poorly estimated. The partial effects estimated from this model are consistent with fishers' knowledge regarding optimal depths for fishing, and a period of lower CPUE during the fishing season, as well as the expected decreasing relationship in CPUE in the presence of mammals. The use of continuous relationships dependencies of CPUE on location, depth, and time of year is a more defensible hypothesis than assuming fixed break points as is done in the current stock assessment GLM.

Comparison of depredation estimates

Despite the differences in performance according to statistical measures, the total depredation estimates from each of the statistical models were very similar to the current stock assessment GLM (Table 2). Average annual estimates of total depredated catch range between 78 and 95 tonnes where only killer whales were observed, 22–45 tonnes where only sperm whales were observed, and 10–14 tonnes on hauls where both occurred, compared to a total fishery

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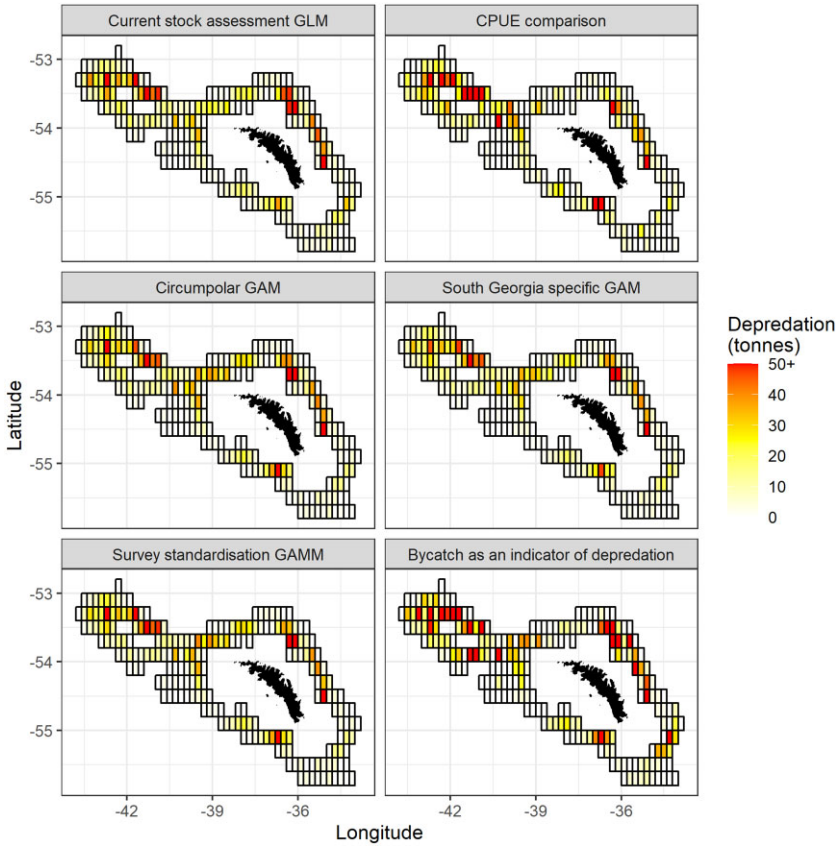


Figure 7. Estimated total depredated catch in tonnes by 0.2° × 0.2°cells across all years derived from the stock assessment GLM, CPUE comparison, circumpolar GAM, South Georgia specific GAM, survey standardization GAMM, and from using bycatch as an indicator of depredation. Shag rocks are the shallow area to the west of the main island around 42°W 53.5°S.

catch (i.e. that brought onboard the vessel) averaging 2,850 tonnes. Therefore, the total mortality implied by a catch of 2850 tonnes would be around 2980 tonnes.

Depredation estimates from all six models showed an overall increasing trend between 2003 and 2019 with larger amounts depredated in 2009, 2010, 2014, and most recently around 2018 (Table 3 and Figure 8). The GAMs were consistent with the current stock assessment GLM. The estimates from the three GAM approaches were closest with average depredation rates of 5.0–5.3%, only differing by the magnitude of the high depredation years. The CPUE comparison was similar to the current stock assessment GLM until around 2015, and then estimated lower depredation. Estimates of depredated catch removal using the bycatch as an indicator of depredation were overall slightly higher, and although the highest years are the same as the other models, the annual estimates since 2015 show a different pattern to the current stock assessment GLM, and were more similar to the CPUE comparison.

There was a good level of consistency in the spatial distribution of the depredation estimates (Figure 7), showing areas of higher depredation to the northwest of South Georgia and in the northeast. In addition, the bycatch comparison approach identified two areas subject to notably higher depredation that were not seen in the statistical modelling approaches, to the north of Shag Rocks and in the Gully between Shag Rocks and South Georgia (Figure 7).

Discussion

Comparison of model applicability

We examined the application of a range of approaches to modelling depredation by killer whales and sperm whales from the longline toothfish fishery around South Georgia to compare and evaluate the performance of these models, and understand whether there are substantial differences in the predicted removals compared to the current stock assessment GLM. There was close agreement between the different model structures in estimating the scale of the annual removal of toothfish by depredation from the fishery and the trends in the effects of the main parametric drivers of toothfish CPUE.

The CPUE comparison method (Tixier *et al.*, 2010) provides a simple way to estimate depredation, taking into account its spatial variability. However, it does not take into account the behaviour of different fishers, and so the model could be refined by including these factors. Despite being developed for different purposes, the circumpolar GAM and the survey standardization GAMM estimated similar magnitudes for the main parameter effects and trends as the models developed specifically for the South Georgia fishery. Although, estimating similar patterns in the main partial effects, the GAMs have the advantage over this application of the current stock assessment GLM in that the flexibility of the GAM approach means non-linear relationships can be modelled without detailed assumptions and knowledge on shape and non-linearity of those underlying relationships. The choice of link function and error

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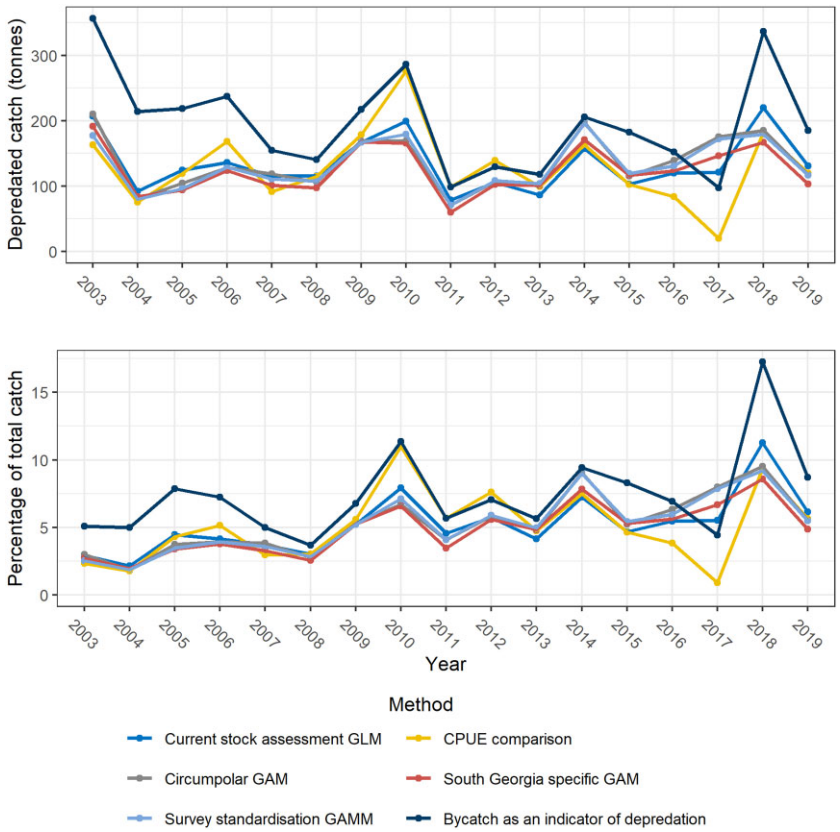


Figure 8. Estimated total depredated catch in tonnes by year (top) and as a percentage of total catch (bottom) derived from the stock assessment GLM, CPUE comparison, circumpolar GAM, South Georgia specific GAM, survey standardization GAMM, and bycatch as an indicator of depredation.

distribution assumed by the statistical models resulted in only small differences in the fit and the error distribution. The South Georgia specific GAM had a better fit to the CPUE than any of the other methods due to the combination of a smoother for abundance and a factor for presence. This was a key component to improving the estimation of the scale of depredation and could be used in future depredation estimates, along with a GAM model structure as it better captures variability in the number of depredating killer whales.

While all the models predicted similar annual depredation removals and encapsulated the trends in the main effects determining CPUE variability, such as depth and season, they only explained around 35% of the CPUE variance; there is still much about the fishery and toothfish population dynamics that remains to be described. The spatial distribution of toothfish is likely to vary at a much finer scale than the spatial smoothers in the depredation models can estimate, due to local bathymetric features such as slope angle and direction (Péron *et al.*, 2016; Yates *et al.*, 2018). In addition, the changing spatial and temporal distribution of interaction between the fishers and whales is complex, as both learn and adapt. The small number of vessels fishing, captains' preference for favoured fishing grounds and different approaches to avoid whales, leads to a degree of complexity, and noise that can be difficult to disentangle (Richard *et al.*, 2018). Some differences result from changes in mammal observation protocols through time and to the frequency and quality of observations, due to the workload of other scientific observation tasks. In particular, there is no record of when the observations took place during hauling, which makes it impossible to evaluate whether the whale abundance increases during the haul, or remains constant.

In our comparative study, we showed that the bycatch as an indicator of depredation method is successful in identifying the same patterns as the models that standardize CPUE across a range of variables. This method has proved to be a practical approach for areas that do not have sufficiently detailed data collection for model-based estimation, if sufficient bycatch data are available (Gasco *et al.*, 2015). With only relative catch data available, a first estimate of whether depredation occurs, and a scale of its extent can be made. This method is a very useful first step in estimating the relative magnitude of depredation once detected, before a time series of sufficient data is available for more complex analysis. A further potential development is to investigate pairwise matching of adjacent hauls within each season for areas where catch is not as homogeneously distributed, as at South Georgia, and where a gridded solution may be too coarse for the resolution required.

Depredation impacts on the fishery

The estimated depredation from the South Georgia catches is relatively low compared to fishery catches, averaging around 5%, although showing a slightly increasing trend. While depredation is a locally important contributing factor for the catch of each vessel, and is important in the stock assessment, it is not likely to be a major contributor to the dynamics of the estimates of total fishery associated mortality rates estimated within the stock assessment.

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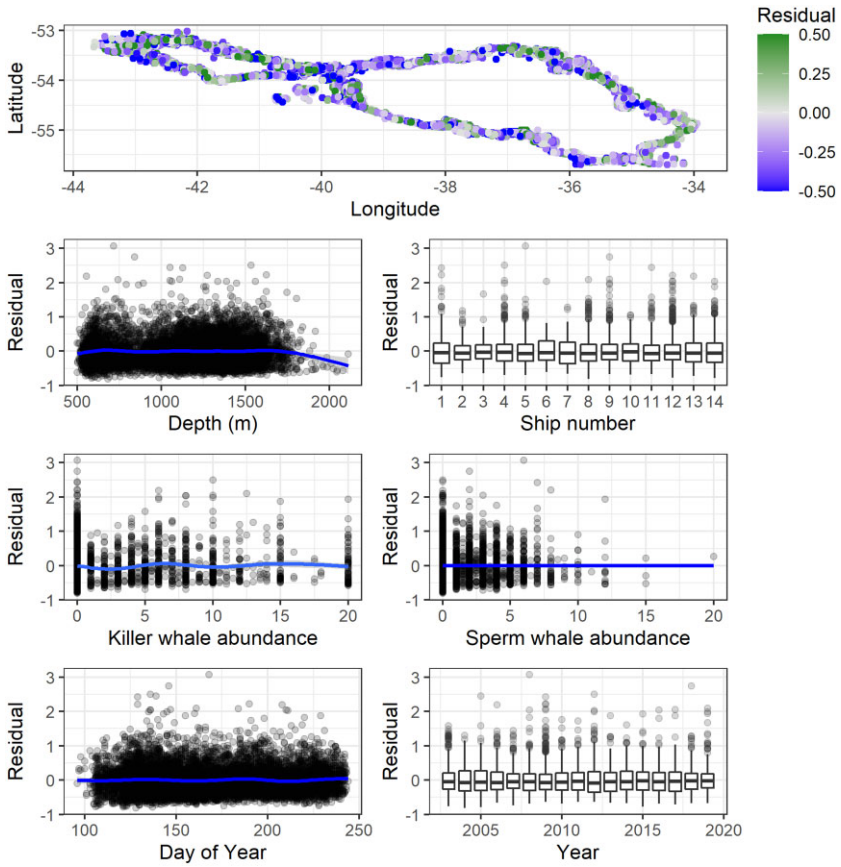


Figure 9. Residuals for CPUE of longitude/latitude, depth, vessel, killer whale or depredating sperm whale abundance, time of year, and year from the survey standardization GAMM. Smoothers (blue line) are fitted to continuous explanatory variables to aid determination of any trends. Note that killer whale and sperm whale abundance are not always integers due to taking the midpoint of a range of observed abundances on some lines.

Table 3 . Estimated total depredated catch in tonnes and as a percentage of total catch by year derived from the stock assessment GLM, CPUE comparison, circumpolar GAM, South Georgia specific GAM, survey standardization GAMM, and bycatch as an indicator of depredation.

Year	Current stock assessment GLM	CPUE comparison	Circumpolar GAM	South Georgia specific GAM	Survey standardization GAMM	Bycatch as an indicator of depredation
2003	207 (2.9%)	163 (2.3%)	210 (3%)	192 (2.7%)	177 (2.5%)	357 (5.1%)
2004	92 (2.2%)	76 (1.8%)	81 (1.9%)	84 (2%)	80 (1.9%)	214 (5%)
2005	124 (4.5%)	120 (4.3%)	104 (3.8%)	94 (3.4%)	96 (3.5%)	218 (7.9%)
2006	136 (4.1%)	168 (5.1%)	128 (3.9%)	124 (3.8%)	129 (3.9%)	237 (7.2%)
2007	115 (3.7%)	91 (3.0%)	119 (3.8%)	101 (3.3%)	111 (3.6%)	154 (5%)
2008	115 (3%)	115 (3.0%)	106 (2.8%)	97 (2.6%)	107 (2.8%)	141 (3.7%)
2009	167 (5.2%)	179 (5.6%)	169 (5.3%)	168 (5.2%)	167 (5.2%)	217 (6.8%)
2010	199 (7.9%)	276 (11%)	169 (6.7%)	166 (6.6%)	179 (7.1%)	286 (11.4%)
2011	79 (4.5%)	98 (5.7%)	71 (4.1%)	60 (3.5%)	71 (4.1%)	98 (5.7%)
2012	105 (5.7%)	140 (7.6%)	107 (5.8%)	103 (5.6%)	108 (5.9%)	130 (7.1%)
2013	87 (4.1%)	99 (4.7%)	101 (4.8%)	101 (4.8%)	104 (5%)	118 (5.6%)
2014	158 (7.2%)	163 (7.5%)	197 (9%)	171 (7.8%)	196 (9%)	205 (9.4%)
2015	103 (4.7%)	102 (4.7%)	115 (5.2%)	117 (5.3%)	119 (5.4%)	182 (8.3%)
2016	120 (5.5%)	84 (3.8%)	139 (6.3%)	123 (5.6%)	131 (6%)	152 (6.9%)
2017	121 (5.5%)	20 (0.9%)	175 (8%)	146 (6.7%)	172 (7.9%)	97 (4.4%)
2018	220 (11.3%)	182 (9.4%)	185 (9.5%)	167 (8.6%)	179 (9.2%)	336 (17.3%)
2019	131 (6.1%)	120 (5.7%)	118 (5.5%)	103 (4.9%)	116 (5.5%)	185 (8.7%)

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Spatial estimates of depredation were consistent between approaches and identified similar regions to those previously described as depredation 'hot spots' based on whale abundance observations in this region (Söffker *et al.*, 2015). The additional areas identified by the bycatch as an indicator of depredation method corresponded to locations where high grenadier catch has occurred in a cluster of benthic trawl survey stations (Morley *et al.*, 2004), as well as higher longline grenadier CPUE (Laptikhovsky *et al.*, 2014).

Model selection and comparison to other regions

Having considered the relative performance of the approaches for estimating depredation, the survey standardization GAMM has been identified as having an improved fit to the data, and reduced dependence on the arbitrary areas and depth bands compared to the current depredation estimates used in the assessment of this stock. As a result, the survey standardization GAMM is suggested as a basis for making depredation estimates for future assessments. All modelling approaches in this paper fitted the data similarly to the models in Tixier *et al.* (2020), and within the lower range of the models developed to describe depredation off the coast of Alaska (Peterson *et al.*, 2013, 2014; Peterson and Hanselman, 2017). The approaches presented here are not specific to the South Georgia toothfish fishery, in principle the requirements for estimating depredation are simply that observations of the presence or abundance of predators can be made, and that there is a measure of CPUE (potentially standardized) which is impacted by the predators. These models could therefore be applied to the depredation on Alaskan sablefish, Australian recreational and commercial fisheries, western Atlantic tuna, and swordfish fishery, as well as other Southern Ocean toothfish fisheries (Hanselman *et al.*, 2018; Ryan *et al.*, 2019; Charles *et al.*, 2020; Tixier *et al.* 2020).

The Alaskan fisheries have substantial variability in depredation between different locations and fisheries (Peterson *et al.*, 2013; Peterson and Hanselman, 2017), similar to that observed in the Southern Ocean. Depredation models in both regions fit similar variables, including standardizing for location, year, season, and depth. In all cases, models for fisheries with higher depredation rates fitted better than those with low rates, highlighting that only when depredation becomes substantial, and the signal to noise ratio is also substantial, do the models provide robust estimates. The main drivers for the extent of depredation of fisheries is the spatial overlap and / or the duration of fishing activities (Tixier *et al.*, 2019a). The extent of depredation is also affected by measures that specifically impact interactions such as vessels setting shorter lines, increasing hauling speed, and tying off lines when killer whales approach, returning only once they have left the area; all of which have been shown to reduce depredation (Tixier *et al.*, 2015a). The use of some or all of these practices by vessels around South Georgia will have contributed to the current comparatively low interaction rate.

Future developments

A future research question is the effectiveness these changes have had to fishing practices over time, both in the context of reducing depredation and of the economic and social cost to fishers. As new technologies and approaches in longline fisheries develop, it will become increasingly necessary to understand how these affect the response of depredating whales and changes in CPUE. Another dynamic not yet considered in the models is the potential for unrecorded removal of toothfish at depth during fishing rather than observed near the surface during hauling. The relative importance, or magnitude of this cryptic depredation is at present poorly understood. Our results showed that the presence of killer whales, whether observed depredating or not, resulted in a decrease in CPUE which was consistent with previous findings in this region (Söffker *et al.*, 2015); while observations of sperm whales that were present but not identified feeding around the vessel was not associated with a similar reduction. The observers record these interactions during hauling activity only, and distinguish between individuals deep-diving or surfacing during hauling activities around the vessel as feeding or interacting. Outside hauling activities or away from the vessel, feeding behaviour of sperm whales is not recorded. Sperm whales regularly dive and forage at similar depths as those where toothfish lines are set, and a recent study demonstrated through use of the vessel Automatic Identification System (AIS) and data loggers on the longlines that depredation can occur at depth on the seabed (Richard *et al.*, 2020). Evidence of sperm whale depredation derived from line movement showed that sperm whales were more likely than killer whales to feed on soaking longlines (Richard *et al.*, 2020). Killer whales on the other hand were more frequently seen to start deep dives along the line with the start of hauling rather than on soaking lines, which is consistent with a previous observation around South Georgia where deeper dives by a tagged killer whale were also associated with the start of hauling activities (Towers *et al.*, 2019; Richard *et al.*, 2020).

Given that killer whale depredation is more prevalent on hauling than sporadically on soaking longlines, and that in some regions toothfish are part of the natural diet of killer whales (Reisinger *et al.*, 2015; Tixier *et al.*, 2019b), the estimates based on hauling should be sufficient to capture the majority of their depredation. Understanding the natural diet composition of killer whales around South Georgia would be a valuable area of research to determine whether toothfish form a natural part of the killer whale diet around South Georgia, and depredation mostly focuses this mortality spatially or if depredation results in an increased intake of toothfish by killer whales specifically associated with the longline fishery. Estimation of cryptic sperm whale depredation, and whether it has a critical impact on depredation mortality, may be more difficult. Sperm whales are thought to feed largely on squid species in the Southern hemisphere (Clarke, 1980; Gaskin and Cawthorn, 1967; Pascoe *et al.*, 1990; Evans and Hindell, 2004) and toothfish have not been recorded as a primary prey species to date but can form a small part of their diet (Yukhov, 1971).

Compared to the global extent of depredation, interactions with the longline fishery around South Georgia are relatively well-understood. Observations by the scientific observers indicate that depredation is not a static situation but continues to evolve as whales adapt to changed fishing practices and fishers try to reduce losses (e.g. Peterson and Carothers, 2013; Tixier *et al.*, 2015b). Following initial descriptions over two decades ago (Ashford *et al.*, 1996), first estimations of removals over a decade ago (Purves *et al.*, 2004; Clark and Agnew, 2010) and more recent updated models highlighting the highly localized effects as well as seasonal patterns around South Georgia (Söffker *et al.*, 2015), revisiting these models periodically has allowed changes to be monitored over time and continuing to do so will allow the ongoing dynamics of depredation to be captured.

The waters around South Georgia were commercial whaling grounds until the mid-20th century. Sperm whales were not among the main targeted species around South Georgia in the earlier years (Shackleton, 1919), but were taken more frequently during the

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modern whaling period in the early 20th century. Killer whales were not directly harvested during the whaling period but were subject to considerable culling by whalers as they were scavenging on harvested whale carcasses (Bonner, 1980; Moore *et al.*, 1999). Data on cetacean sightings and abundances after this period are relatively limited and for a large part come from opportunistic sightings such as cruise ships, fishing vessels, or from research stations (Moore *et al.*, 1999; Richardson *et al.*, 2012). Fishers from longline vessels anecdotally report that the groups interacting with their vessels are increasing and changing behaviour. While it is likely that both populations of sperm whales and populations of killer whales are stable or recovering around South Georgia, it is difficult to provide certainty as to whether these perceived changes in interaction are signs of their recovery, or adaptation of behaviour. Periodic dedicated transect surveys combined with standardized opportunistic sighting protocols on vessels of opportunity that regularly visit the waters around South Georgia such as cruise ships (Williams *et al.*, 2006; Johnston *et al.*, 2012; Viquerat and Herr, 2017) would provide much-needed data in this regard.

Data availability statement

Data access is governed by the Rules for the Access and Use of CCAMLR Data https://www.ccamlr.org/en/document/publications/rules-access-and-use-ccamlr-data

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