Depredation by killer whale (*Orcinus orca*) and false killer whale (*Pseudorca crassidens*) on the catch of the Uruguayan pelagic longline fishery in Southwestern Atlantic Ocean

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This study analyses depredation by killer whales (*Orcinus orca*) and false killer whales (*Pseudorca crassidens*) on catches of the Uruguayan pelagic longline fishery in the Southwestern Atlantic Ocean between 1998 and 2007. Data were collected by scientific observers from the National Observer Program of the Tuna Fleet operating in the area between $19° - 40.5°$S and $20° - 54°$W. Depredation occurred in 67 of the 1029 sets and was restricted to the area from $25° - 40.5°$S to $27° - 53°$W, though larger proportions of depredation (DP: percentage of total fish caught damaged by cetaceans) were observed in the Brazil – Malvinas (Falkland) Confluence area ($34° - 37°$S and $51° - 53°$W) where most of the fishing effort was concentrated. Depredation occurred year-round though intra-annual variability in its intensity was recorded. The overall DP was 0.37% and was slightly higher in autumn. The spatial analysis showed that DP within grids of $1 \times 1°$ was homogeneous and generally <2.5%. Ten out of 57 fish species caught by the fishery were depredated by cetaceans. Swordfish (*Xiphias gladius*) showed the highest DP per species (1.17%). Using the frequency of resources selectivity index of Ivlev, it was determined that swordfish was selected as a preferred prey in 43.9% of the sets with depredation. Generalized linear models indicated that distance to coast, year, and vessel were significant variables in explaining the number of fish depredated per fishing event. The presence of killer whales in the fishing ground seems not to affect the catch per unit effort by the longline fishery. The losses caused by depredation of cetaceans on the catch are low with probably minor economic effects to the Uruguayan longline fishing industry.

Keywords: cetaceans, fishery interactions, longlining, pelagic fisheries, western South Atlantic.

Introduction

Depredation is one of several types of direct interaction between marine mammals and fisheries. It occurs when marine mammals remove or damage the fish caught in fishing gear (Alverson *et al.*, 1994; Donoghue *et al.*, 2003; Hamer *et al.*, 2012). Depredation may have negative consequences for both marine mammals and fisheries. For fishers, the damage to the catch or fishing gear results in economic losses, caused by having to invest in extra time, fuel, and food (for the crew) and in the search for alternative fishing areas to avoid depredation (Sivasubramanian, 1964; Yano and Dahlheim, 1995; Ashford *et al.*, 1996; Secchi and Vaske, 1998; Brum and Marín, 2000; Purves *et al.*, 2004; Clark and Agnew, 2010; Goetz *et al.*, 2011; Peterson *et al.*, 2013, 2014). Marine mammals may become incidentally hooked when removing the catch or bait (Read *et al.*, 2006; Dalla Rosa and Secchi, 2007; Garrison, 2007) or suffer the consequences of retaliation from

fishers, which include shooting them with firearms, harpoons, or the use of underwater explosives (Secchi and Vaske, 1998; Brum and Marín, 2000; Visser, 2000). Thus, depredation may represent a conservation issue for some marine mammal populations.

The first records of cetacean depredation on longline fisheries date back the 1950s (Sivasubramanian, 1964). The use of longlines in fisheries expanded in the late 1950s, when the Japanese fleet started operating in the Atlantic and Pacific Oceans and was successful in fishing for tuna with this gear (Suda, 1971; Honma, 1973). Since then, several species of marine mammals have learned to prey upon fish catch in longlines and depredation has been documented in all oceans (Donoghue et al., 2003; Secchi et al., 2005; Hamer et al., 2012). Killer whales (*Orcinus orca*), in particular, have been observed preying upon a variety of species caught in both pelagic and demersal longline fisheries around the world (e.g. Sivasubramanian, 1964; Visser, 2000; Hucke-Gaete et al., 2004; Roche et al., 2007; Yates and Brickle, 2007; Clark and Agnew, 2010; Passadore et al., 2012; Peterson et al., 2013). In the Southwestern Atlantic Ocean (SWAO), depredation by killer whales on pelagic longline fishery occurs frequently (e.g. Secchi and Vaske, 1998; Brum and Marín, 2000; Dalla Rosa and Secchi, 2007). Other cetaceans interacting with longlines in the SWAO are false killer whales (*Pseudorca crassidens*) that consume the fish caught and remove the bait, and Risso's dolphins (*Grampus griseus*) that feed on the bait, especially squids (Dalla Rosa and Secchi, 2007; Hernandez-Milian et al., 2008; Ramos-Cartelle and Mejuto, 2008).

Marine mammals could benefit from greater foraging success by feeding upon the catch of fisheries (Read, 2005, 2008). Some animals have learned to feed on particular prey species and seem to have a specialized diet, feeding only on some of the species caught in the longlines (Visser, 2000). Although some authors suggest killer whales in SWAO feed preferentially upon swordfish (*Xiphias gladius*; Secchi and Vaske, 1998; Dalla Rosa and Secchi, 2007), they do not consider the total catch, taking only the species consumed or the sets with depredation into account (Dalla Rosa and Secchi, 2007; Ramos-Cartelle and Mejuto, 2008). Thus, the total losses due to depredation and whether or not cetaceans perform a selective predation among fish caught in the longline in the SWAO remain unknown.

Fishers perceive cetaceans as competitors for the same resource and as the cause of losses to the industry. If the direct removal of fish by depredators is selective towards the highly valuable swordfish, the aversion of fishers towards these marine mammals could increase. Some fishers claim that killer whale presence frightens their target species away from the fishing area, thus reducing the catch (e.g. Sivasubramanian, 1964; Secchi and Vaske, 1998; Dalla Rosa and Secchi, 2007), though so far no study quantifying the impact of depredation on the overall catch has been conducted.

The nature and extent of interactions between marine mammals and fisheries varies among regions, species involved, target species, and fishing gear used (Donoghue et al., 2003; Read et al., 2006). All these components must be considered in any study aiming at understanding the determinants of the interaction between marine mammals and fisheries. The biological productivity of SWAO is strongly influenced by the Brazil–Malvinas (Falkland) Confluence, which varies its location throughout the year. This productive area supports high biomass throughout upper trophic levels and hence an important fishing industry (Brandini et al., 2000; Acha et al., 2004; Barré et al., 2006). In this area, the Uruguayan logline fishery operates using either the American monofilament or the Spanish

multifilament system to target tuna (bigeye—*Thunnus obesus*, yellowfin—*Thunnus albacares*, and albacore—*Thunnus alalunga*), swordfish, and pelagic sharks such as blue shark (*Prionace glauca*). They use squid (*Illex argentinus*), mackerel (*Scomber* spp., *Trachurus* spp.), and/or pieces of sharks as bait (Domingo et al., 2002; Mora and Domingo, 2006; Jiménez et al., 2009). A study conducted between 1994 and 1996, in the same fishing area where the Uruguayan fishery currently operates, reported that killer whales damaged 8.2% of swordfish caught in the longline (Brum and Marín, 2000). Previous reports from this region suggest that depredation varies spatially depending on fishing effort and the distribution of depredators (e.g. Brum and Marín, 2000; Ramos-Cartelle and Mejuto, 2008). Killer whales within the Uruguayan pelagic longline fishing ground are more frequently encountered during autumn and winter, particularly in SWAO waters 150–400 nm offshore near the shelf break and the continental slope (Passadore et al., 2012). Although Passadore et al. (2012) state that more than half of killer whale records were made when the species was depredating on fish caught, no further studies on the impact of depredation produced by this species (or other marine mammals) to this fishery has been carried out.

Thus, the objectives of this study are to: (i) analyse the spatio-temporal distribution of depredation, (ii) determine if marine mammals (killer and false killer whales) selectively depredate different fish species caught on the longline, (iii) analyse the influence of environmental variables, fishing practices, and capture composition on the amount of fish depredated from longlines, and (iv) determine the effect of the presence of depredators (particularly killer whales) on the catch of target species of the longline.

Material and methods
Study area
Uruguayan pelagic longline fishing vessels operate in the Uruguayan Economic Exclusive Zone and international waters, from 19° to 40.5°S and 20° to 54°W (Figure 1), including the shelf brake, continental slope, and deep waters of the SWAO. This region is characterized mainly by a northern subtropical zone, dominated by warm waters from the Brazil Current (average temperature of 22–23°C) and a southern zone, dominated by Subantarctic waters from the Malvinas (Falkland) Current (average temperature of 6°C) (Brandini et al., 2000). These two currents converge to form the Brazil–Malvinas (Falkland) Confluence, a mixture zone that moves seasonally between 30° and 50°S and 40° and 60°W. Temperature in the confluence decreases southward from ~20 to 8°C (Olson et al., 1988; Acha et al., 2004; Barré et al., 2006).

Data collection
Data were collected between 1998 and 2007 by scientific observers from the National Observer Program of the Tuna Fleet (PNOFA). For each fishing event, the following data were recorded: time at the start and end of the set, time at the start and end of hauling, geographic position (latitude and longitude) at the start and end of the set, sea surface temperature (SST; minimum and maximum) measured *in situ* at ~2–3 m of depth with the vessel's thermometer every time a radio-buoy was set or hauled, the number of hooks set, catch by species (number of individuals), and the number of individuals per species that were depredated by killer and/or false killer whales. In this paper, the term depredation is defined as the partial consumption of the fish from longline hooks performed by cetaceans (modified from Donoghue et al., 2003). Totally consumed fish from longline were not considered because the data collected in
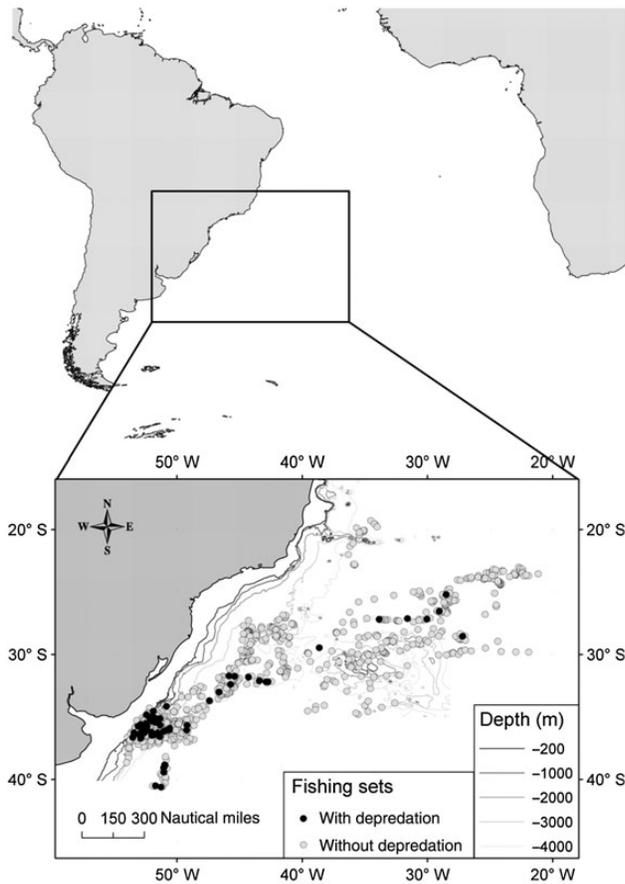
Figure 1. Spatial distribution of fishing events monitored by PNOFA observers between 1998 and 2007. Sets with (black dots) and without depredation (grey dots) by cetaceans.

this study did not allow for evaluating the causes of empty hooks. These two species (killer and false killer whales) are the only cetaceans that depredate on the capture of pelagic longline fisheries in the study area (Secchi and Vaske, 1998; Brum and Marín, 2000; Dalla Rosa and Secchi, 2007; Ramos-Cartelle and Mejuto, 2008). The description given by Secchi and Vaske (1998) was used to differentiate the bites of killer and false killer whales from those produced by sharks. According to these authors, cetaceans rip the body of the fish leaving irregular edges, preferably eating the flesh and avoiding the head and sometimes the spinal column and fins, while sharks' bites leave clear cuts and are relatively smaller.

For the analysis, other variables were also determined. The "ΔSST" per set was calculated from the difference between the maximum and minimum SST recorded *in situ*. The ΔSST could be used as an indicator of the presence of an SST front along the fishing haul. The "duration of the soak" was defined as the elapsed time between the end of the set and the end of the haul. The "effort per day" was determined as the number of hooks set multiplied by the duration of the soak (in hours) divided by 24. Each season was established according to the day of the setting as follows: winter (22 June–21 September); spring (22 September–21 December); summer (22 December–21 March); and autumn (22 March–21 June). For each set, the "distance to coast" was determined using coastline maps, while "depth" was obtained from global bathymetry databases (ETOPO-20; http://monsoondata.org). The variable

"depth variation of seabed" (DVS) along each set was then calculated as the difference between the depth of deepest and the shallowest points of the set.

Data analysis
Only fishing surveys for which observers performed a complete record of the catch, depredation and most of the variables (Table 1) were included in the analysis.

Spatial and temporal distribution of depredation
The depredation frequency (DF) by killer and false killer whales, herein referred as cetaceans, was calculated as the number of fishing events with depredation (DS) over the total number of fishing events monitored (TS) times 100. The DF was determined annually and seasonally, for the total catch and for each species (DF_i) that was damaged by cetaceans at least once.

The proportion of depredation (DP) was defined as the number of fish damaged by cetaceans (DC) over the total catch (TC) times 100. This proportion was calculated for both the total catch (all species together) and for each species (DP_i) that was depredated at least once. The DP was calculated for all the fishing events (DP_t) accumulated and also for each fishing event (DP_s), thus the effect of depredation per species per day can be evaluated.

The catch per unit effort (cpue) was calculated as the number of individuals caught (TC) per number of hooks set times 1000. The cpue was estimated for the total catch as well as per species for the entire study period, yearly and seasonally.

The distribution of DP and cpue for the total catch, as well DP for most depredated fish, was calculated for $1 \times 1°$ grid considering two time-scales (i.e. accumulated for the whole period and per season) to assess for spatial differences.

Prey preferences
To verify if cetaceans performed selective depredation among the fish species available in the longline, the resources selectivity index of Ivlev (Krebs, 1989) was determined for each fishing event with depredation. This index was calculated as:

$$E_i = \frac{r_i - p_i}{r_i + p_i},$$

where E_i is the Ivlev selectivity index for species "i", r_i the proportion of species "i" depredated by cetaceans in the fishing event, and p_i is the proportion of species "i" which was captured in the longline during that event. Therefore, in our study, these parameters were defined as:

$$r_i = \frac{DC_i}{DC_{total}}.$$

$$p_i = \frac{TC_i}{TC_{prey}}.$$

Ivlev's index values ranges between −1 and 1. Values from 0.6 to 1.0 were taken to indicate positive selectivity, while values from −0.6 to −1.0 were taken to indicate negative selectivity (i.e. avoidance). The remaining values between 0.6 and −0.6 represent neutral selectivity. Finally, the frequency distribution of positive, negative, and neutral selectivity was determined for each species.

Table 1. List of explanatory variables considered to be included in GLMs to assess the number of fish depredated by cetaceans in the Uruguayan longline fishery in the SWAO.

Name	Variable description	Type of variable	Levels of variables
Location			
LAT	Latitude of the starting position of the longline set	Continuous	
LONG	Longitude of the starting position of the longline set	Continuous	
COAST	Distance to coast: between the beginning of the set and the coastline (nautical miles)	Continuous	
DEPTH	Average depth: between the beginning and the end of the set (m)	Continuous	
DVS	Depth variation of seabed between the deepest and the shallowest points along the set (m)	Continuous	
Time			
YEAR	Year of fishing event	Categorical	1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007
SEAS	Season of fishing event	Categorical	Summer, autumn, winter, spring
Fishing operations			
VESSEL	Code assigned to each fishing vessel	Categorical	1, 3, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, and 21
EFFORT	Fishing effort per day (number of hooks × duration of the soak/24 h)	Continuous	
GEAR	Fishing strategy related to gear type	Categorical	1: American monofilament, 2: Spanish multifilament
Environment			
SST	Average sea surface temperature of the set (°C)	Continuous	
ΔSST	Sea surface temperature variation between the warmest and coldest values recorded along the set (°C)	Continuous	
Capture			
TC	Total no. of fish caught per set	Continuous	
SWO	No. of *X. gladius* caught per set	Continuous	
TUNA	No. of *T. alalunga*, *T. obesus*, and *T. albacares* caught per set	Continuous	
SHARKS	No. of *P. glauca* and *I. oxyrinchus* caught per set	Continuous	
BONY FISH	No. of *R. pretiosus*, *A. solandri*, billfish (Istiophoridae), and *Coryphaena* sp. caught per set	Continuous	
PREYS	Total no. of potential prey caught per set (includes BONY FISH, SHARKS, SWO, and TUNA)	Continuous	

The name of each variable, their description, type, and levels of the categorical variables are presented.

Influence of temporal, environmental, and operational variables on depredation

Generalized linear models (GLMs; McCullagh and Nelder, 1989) were used to evaluate the effect of spatial, temporal, environmental, and fishing operational variables on the number of fish depredated per fishing event. Before the models were built, collinearity between variables was checked using multipanel scatterpolts, Spearman's correlation coefficients (threshold ≥ 0.6) for categorical variables, Pearson's correlation coefficients (threshold ≥ 0.6), and variance inflation factors (threshold VIF ≥ 3) for continuous variables (Zuur *et al.*, 2010). To model depredation (Y_i = number of depredated fish in the fishing event i) as a function of the explanatory variables considered as relevant *a priori* (see Table 1 for description), two types of distributions were considered, the Poisson and negative binomial. According to the general equation of GLM [$\log(\mu_i) = \beta_0 + \beta_1\chi_{1i} + \beta_2\chi_{2i} + \dots \beta_n\chi_{ni}$), $\log(\mu_i)$ is the link function of the model, in this case, the logarithm of the number of depredated fish in the fishing event i; β_0 is the estimated coefficient of the number of depredated fish by cetaceans (intercept); β_1 is the estimated coefficient for variable 1; and χ_{1i} is the value of variable 1 in the fishing event i.

The models were first built with a Poisson distribution. After checking and confirming overdispersion, negative binomial distribution was used instead. Initial models containing only uncorrelated explanatory variables were simplified by a backward stepwise procedure using the tool *stepAIC* (library MASS), followed by manual simplification. The latter consisted of removing the least significant term in a model through the tool "*update*". Analysis of variance (ANOVA) was used to compare the resulting model with the previous model of the step procedure. When the removal of a term produced a significant increase in model's deviance, that term was considered statistically significant and, thus, returned and retained in the model. When the removal produced nonsignificant change in deviance, the term was left out of the model. Terms were sequentially removed until the model contained only significant terms; that model was considered as the minimum adequate model (Crawley, 2013). The explained deviance [$D^2 =$ (null deviance $-$ residual deviance)/null deviance $\times$ 100] of the minimal adequate model was determined, which corresponds to the percentage of data deviance explained by the model in relation to the null model.

Effect of killer whales presence on the catch of target species of the fishery

To evaluate if the presence of killer whales was "scaring" the target fish away from the longline fishery, hence reducing the catch, a comparison was performed between cpue values of consecutive days by the same vessel of the whales occurrence. The analysis was restricted to those sets that had both records of killer whales sighting and depredated catch, and for which there were no records of sightings

or depredation in the immediately previous or subsequent days. Therefore, each sample contains: cpue of the day with killer whale sighting associated with depredation and cpue of the days before and after that interaction. To reduce the chance of other factors affecting a possible variation in cpue, such as area (e.g. Pons and Domingo, 2008), only those fishing events that were performed on consecutive days with no changes in fishing area or fishing strategy (e.g. effort, time of setting, or hauling) were considered in this analysis. cpue values per set *before*, *during*, and *after* an event of depredation-sighting were compared using ANOVA (Sokal and Rohlf, 1979). Normality and homogeneity of variance of the data were tested with the Shapiro–Wilk and Bartlett's test, respectively. When homocedasticity was not met, the Wilcoxon test was used for comparing paired data. The cpue comparison was made for prey species that were caught in events of depredation-sighting, catch of potential preys all together (determined as the sum of the catch of all species depredated at least once), and total catch. Given that no sightings of false killer whales were recorded by on-board observers, the analysis on the effect of the predator's presence on the cpue was performed for killer whales only.

All statistical analysis was performed using the free software R (R Development Core Team, 2008).

Results

In all 50 trips performed on board, 16 fishing vessels with 1029 sets monitored by scientific observers from PNOFA between 1998 and 2007 (except for 1999 and 2000) were included in the present study. This represented observer coverage of 12% in relation to total sets reported by the Uruguayan fishing fleet. The coverage of on-board observers varied annually and seasonally. Annual variations ranged from 5.1% in 2001 to 31.7% in 2007 (Table 2). In summer, the number of sets by the fleet was minimum, while the coverage of observers was the highest (21.6%). The largest number of sets observed by PNOFA occurred in winter ($n = 340$), representing a coverage of 12.0%. In general, the beginning of the set of the longline took place at sunset or early evening and the average duration of the soak was 16.40 h (s.d. = 2.61 h).

Spatial and temporal distribution of depredation

The 1029 monitored fishing events comprised an area ranging from 19° to 40.5°S and 20° to 54°W. A total of 2 142 500 hooks were deployed, though effort distribution varied spatially. The highest fishing effort took place over the continental slope off southern Brazil and Uruguay (Figure 2a). Depredation by cetaceans occurred in 67 fishing events (DF = 6.2%) and was restricted to a smaller area, between 25° and 40.5°S [median = −35.6°S; percentile (25–75%) = −36.2 to −34.3] and 27°–53°W [median = −51.3; percentile (25–75%) = −52.2 to −49.0; Figure 1; Supplementary Figure S1). Depredation frequency was highest in southern Brazil and Uruguay, between the latitudes of 33° and 37° S (Figure 2b).

Of the 80 331 fish caught during the study period, 301 individuals had been depredated by cetaceans ($DP_t = 0.37\%$). The highest catch, catch per unit effort (cpue), and proportion of depredation (DP) were observed between 34° and 38° S and 47° and 53° W (Figure 2c–e). In general, DP was low (<2.5%), except in four 1 × 1° cells with higher values (Figure 2f).

The temporal analysis showed that the observed depredation varied over the years, with no records in 2001, when the coverage by on-board observers was very low (Table 2). The highest depredation frequency was observed in 2004, with slightly lower values in 1998 and 2002. The cpue and DP, however, were higher in 1998

Table 2. Annually and seasonally cumulated values of PNOFA percentage of coverage.

	Fishing events				Catch			
	% coverage	TS	DS	DF (%)	TC	cpue	DC	DP_t (%)
Year								
1998	8.63	59	6	10.2	6 428	111.009	67	1.04
2001	5.79	32	0	0.0	3 422	103.981	0	0.00
2002	9.93	69	7	10.1	4 413	81.151	50	1.13
2003	9.49	119	5	4.2	7 546	31.876	15	0.20
2004	15.28	206	24	11.7	18 417	38.442	79	0.43
2005	12.18	179	6	3.4	10 130	23.035	32	0.32
2006	19.19	179	4	2.2	12 084	26.478	20	0.17
2007	31.74	186	15	8.1	17 891	46.430	38	0.21
Season								
Autumn	9.4	233	22	9.44	19 649	49.595	86	0.44
Winter	12.0	340	23	6.76	32 978	48.558	126	0.38
Spring	9.6	195	13	6.67	12 674	38.998	31	0.24
Summer	21.6	260	9	3.46	15 004	20.251	58	0.39

Observed number of fishing events (TS), number of fishing events with depredation by cetaceans (DS), depredation frequency (DF), total number of individuals captured (TC), catch per unit effort (cpue), number of fish depredated (DC), and total proportion of depredation (DP_t).

and 2002, decreasing in the following years (Table 2). The geographical distribution of sets varied with season (Figure 3). In autumn, the fishing effort was concentrated to the south, between 26° and 41°S, while in winter, it was spread along the coast reaching areas further north up to 19° S. Although depredation occurred in all seasons, both DF and DP were higher in autumn (Table 2). Depredation occurred year-round between 34° and 37° S and 51° and 53° W, with DP values >5% in some areas (Figure 3).

Prey selection

Among the 57 species of fish that were caught by pelagic longline vessels monitored throughout the study period, only ten species were depredated upon by cetaceans at least once: swordfish, bigeye tuna, albacore, yellowfin tuna, wahoo (*Acanthocybium solandri*), pincel (*Ruvettus pretiosus*), blue shark, shortfin mako shark (*Isurus oxyrinchus*), dolphinfish (*Coryphaena* sp.), and billfish (Istiophoridae). The temporal analysis per species indicates that swordfish was depredated in every year except 2001, with a maximum DP recorded in 2002. Albacore tuna was also depredated in most of the years. However, the remaining species were only consumed in some years (Table 3). A seasonal variation was observed in both cpue and DP by species. The DP of swordfish was highest in autumn, when the cpue was the lowest of all seasons. The blue shark showed high and similar values of cpue in autumn and winter, but the DP was twice as high in autumn compared with winter. The highest DP of albacore and yellowfin tuna occurred in summer, while for bigeye tuna, it was recorded in autumn (Table 4). The number of individuals depredated per fishing event ranged from 1 to 25 (mean = 4.5; s.d. = 5.1; $n = 67$). The maximum DP_s for the total catch was 27.5% (mean = 0.37, s.d. = 2.22). For albacore, swordfish, and wahoo, the DP_s reached up to 100% in some fishing events (Table 5).

Among the four most frequently depredated species, swordfish presented the highest DP_t, followed by bigeye and albacore tuna, and blue shark. Although the cpue of blue shark was over eight times higher than that of albacore, DP on the later was more than seven times higher than that on blue sharks (Table 5). Depredation
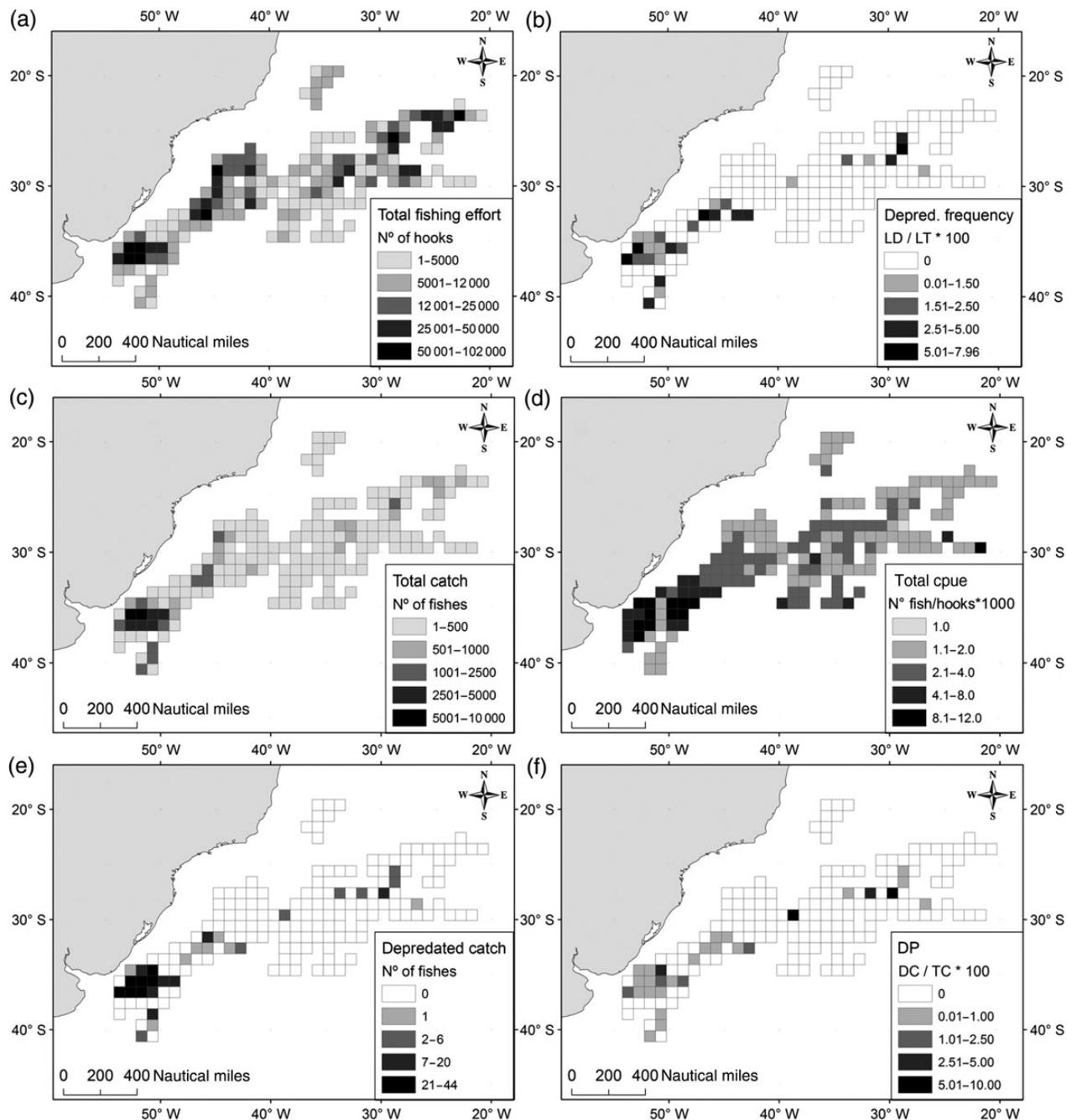
Figure 2. Spatial distribution of data collected by PNOFA for areas of 1 × 1° during the period 1998–2007: (a) Fishing effort (number of total hooks set); (b) depredation frequency (DF); (c) total catch (number of fish); (d) catch per unit effort (cpue = number of fish caught/1000 hooks); (e) total catch depredated by cetaceans; and (f) total proportion of depredation (DP).

of albacore occurred between 34°–37°S and 50°–54°W (Figure 4a). Although blue shark and swordfish also showed high levels of depredation in this area, they were depredated over a much wider area (Figure 4b and c).

The Ivlev index of selectivity shows that only the swordfish has a high relative frequency of positive values (43.9% of sets with Ivlev values > 0.6, Figure 5). This indicates a positive selectivity and thus a preference by cetaceans towards swordfish. For the remaining species, most index values per set indicate less than proportional depredation (Ivlev < −0.6, Figure 5).

Influence of environmental and operational variables on depredation

No information was available on SST for eight fishing events and one of the sets observed presented no fish capture, so they were excluded from model runs. A total of 1020 fishing events were selected to model the number of fish depredated as a function of explanatory variables (Table 1). Exploratory analysis indicated a strong correlation between the following pairs of variables: latitude and longitude ($R^2 = 0.88$), latitude and effort ($R^2 = 0.76$), longitude and effort ($R^2 = 0.81$), effort and depth ($R^2 = −0.60$), effort
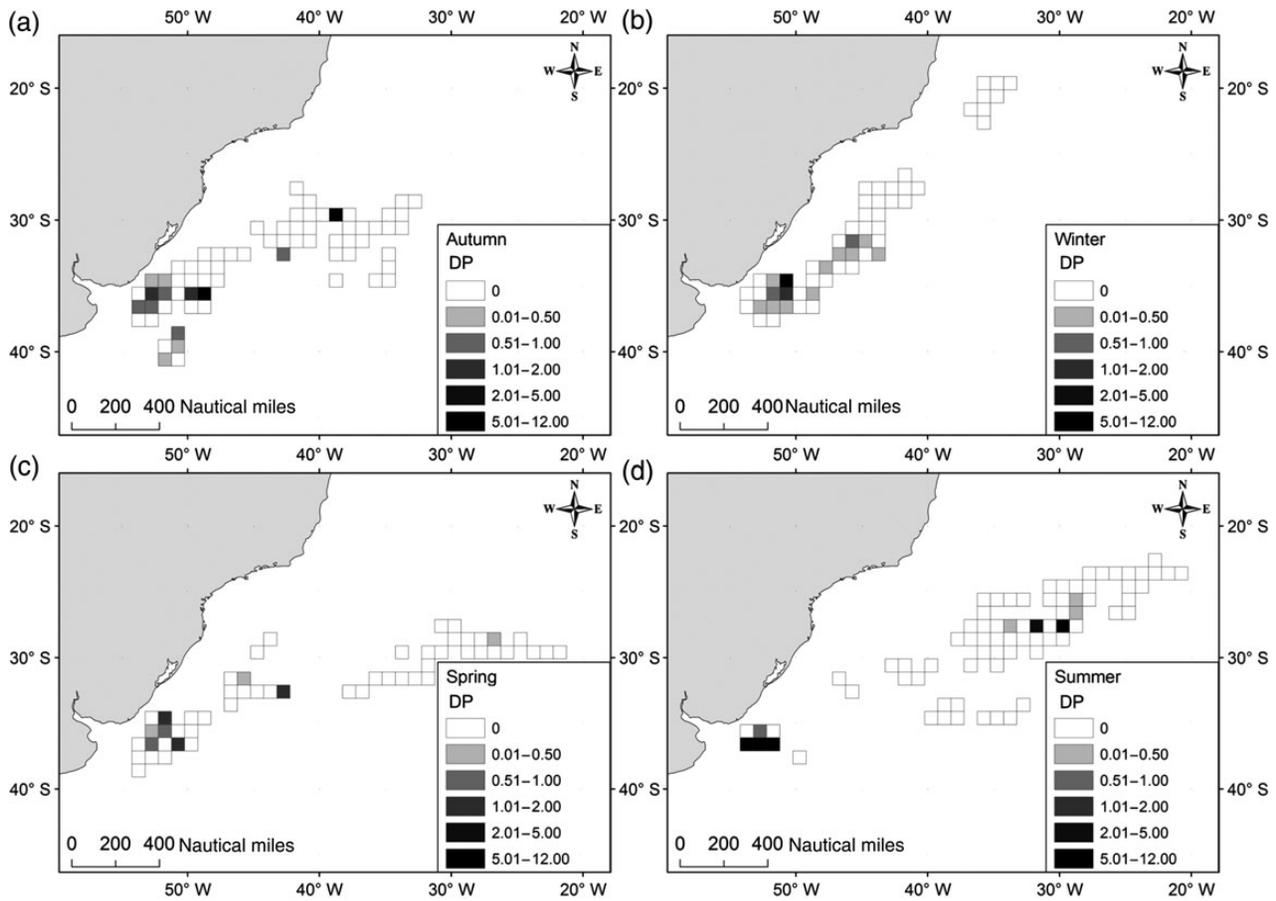
Figure 3. Total proportion of depredation (DP) accumulated seasonally in areas of $1 \times 1°$ for the period 1998–2007: (a) Autumn; (b) Winter; (c) Spring; and (d) Summer.

Table 3. Annual values of catch per unit effort (cpue) and proportion of depredation (DP) for each species depredated by cetaceans during the period 1998–2007.

	1998		2001		2002		2003		2004		2005		2006		2007	
	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP
Albacore (*T. alalunga*)	26.613	1.62	22.364	0	5.351	0.34	1.808	2.1	0.403	0	0.214	1.06	0.605	1.09	2.325	0
Yellowfin (*T. albacares*)	8.825	0	8.113	0	10.942	1.51	1.884	0	1.161	0.18	0.953	1.67	0.414	0	0.381	0
Bigeye tuna (*T. obesus*)	2.521	4.11	2.127	0	1.784	0	0.249	0	0.04	0	0.048	0	0.173	0	0.182	0
Swordfish (*X. gladius*)	22.105	2.66	13.4	0	8.385	8.77	6.049	0.35	6.974	1.47	5.439	1	7.601	0.49	7.656	0.51
Blue shark (*P. glauca*)	32.536	0	44.607	0	23.501	0	13.395	0	21.067	0.23	9.901	0	10.342	0	26.551	0.21
Shortfin mako shark (*I. oxyrinchus*)	1.33	0	1.124	0	2.611	0	2.137	0	1.634	0.26	1.335	0	0.857	0	0.695	0.37
Pincel (*R. pretiosus*)	2.452	1.41	1.702	0	0.846	0	0.334	0	0.954	0	0.45	0	1.078	0	1.048	0.25
Wahoo (*A. solandri*)	0.017	0	0.091	0	0		0.131	3.23	0.253	1.65	0.077	0	0.394	0	0.397	0
Dolphinfish (*Coryphaena* sp.)	1.157	0	0		1.214	0	1.103	0	0.488	0.43	0.02	0	0.07	0	0.353	0
Billfish (Istiophoridae)	0.19	0	0		0		0.363	0	0.077	2.7	0.011	0	0.044	0	0.016	0

and distance to coast ($R^2 = 0.70$), distance to coast and latitude ($R^2 = 0.61$), distance to coast and depth ($R^2 = -0.70$), latitude and SST ($R^2 = 0.76$), longitude and depth ($R^2 = -0.77$), longitude and distance to coast ($R^2 = 0.86$), longitude and SST ($R^2 = 0.70$), capture of sharks and total catch ($R^2 = 0.70$), capture of sharks and preys ($R^2 = 0.77$), total catch and capture of preys ($R^2 = 0.93$), longitude and capture of tuna ($R^2 = -0.62$), and distance to coast and capture of tuna ($R^2 = -0.66$).

The remaining explanatory variables included in the maximal model were: distance to coast, variation of depth along the set, SST, and its variation along the set, capture of preys, gear, year, season, and vessel. After running *stepAIC* and the manual simplification of all putative models, the minimal adequate model contained distance to coast, year, and vessel as explanatory variables (Table 6; Figure 6). This model explained 39.8% of the deviance of the data. According to the minimal adequate model, the

Table 4. Seasonal values of catch per unit effort (cpue) and total proportion of depredation (DP) for each species depredated by cetaceans between 1998 and 2007.

	Autumn		Winter		Spring		Summer	
	Cpue	DP	Cpue	DP	Cpue	DP	Cpue	DP
Albacore (*T. alalunga*)	2.463	0.31	4.130	1.14	1.658	0	0.182	2.96
Yellowfin (*T. albacares*)	3.016	0.67	0.711	0	3.123	0	0.589	2.06
Bigeye tuna (*T. obesus*)	0.318	2.38	0.480	0.92	0.271	0	0.028	0
Swordfish (*X. gladius*)	5.835	1.82	8.337	1.25	7.206	1.20	7.337	0.79
Blue shark (*P. glauca*)	26.606	0.25	25.900	0.10	13.653	0.02	6.240	0
Shortfin mako shark (*I. oxyrinchus*)	2.494	0.30	1.241	0	1.858	0	0.480	0
Pincel (*R. pretiosus*)	0.838	0	0.693	0.42	0.428	0.72	1.256	0
Wahoo (*A. solandri*)	0.111	0	0.056	0	0.132	2.33	0.539	0.50
Dolphinfish (*Coryphaena* sp.)	0.174	1.45	0.530	0	1.120	0	0.016	0
Billfish (Istiophoridae)	0.020	0	0.054	2.70	0.307	0	0.027	0

Table 5. For each species, depredated by cetaceans is presented: the number of fishing events with catch (TS), number of fishing events with depredation (DS), depredation frequency (FD), total number of individuals captured (TC), catch per unit effort (cpue), number of individuals depredated (DC), and total proportion of depredation (DP$_t$) cumulated for the period 1998–2007. The mean (X), standard deviation (s.d.), and maximum (Max.) proportion of depredation per fishing event (DP$_s$) is also shown.

	Fishing event			Capture				DP$_s$ (%)		
	TS	DS	DF (%)	TC	Cpue	DC	DP$_t$ (%)	X	s.d.	Max.
Albacore (*T. alalunga*)	521	9	1.73	4455	2.079	39	0.88	0.40	4.94	100
Yellowfin (*T. albacares*)	326	3	0.92	3130	1.461	17	0.54	0.20	2.84	50
Bigeye tuna (*T. obesus*)	251	3	1.20	561	0.262	6	1.07	0.42	4.47	50
Swordfish (*X. gladius*)	964	47	4.88	15 761	7.356	184	1.17	1.47	8.58	100
Blue shark (*P. glauca*)	995	12	1.21	37 199	17.362	44	0.12	0.15	2.47	66.7
Shortfin mako shark (*I. oxyrinchus*)	705	3	0.43	2791	1.303	3	0.11	0.12	2.10	50
Pincel (*R. pretiosus*)	475	2	0.42	1874	0.875	3	0.16	0.14	2.40	50
Wahoo (*A. solandri*)	237	2	0.84	525	0.245	3	0.57	0.84	9.17	100
Dolphinfish (*Coryphaena* sp.)	192	1	0.52	805	0.376	1	0.12	0.13	1.80	25
Billfish (Istiophoridae)	87	1	1.15	165	0.077	1	0.61	0.29	2.68	25
Total catch	1029	64	6.22	80 331	37.494	301	0.37	0.37	2.22	27.5

number of fish depredated increases with decreasing distance to coast. Depredation occurred between 155 and 819 nm offshore, at a median distance of 283 nm (Supplementary Figure S1). The categorical variables vessel and year were also significant in explaining the number of depredated fish. Depredation was not recorded or was low in some vessels and years, while it was very high in others (e.g. vessels 6, 7, 12, and 21; year 1998, 2002; Table 2; Figure 6).

Effect of killer whales on the catch of target species

In only 12 "cases" was there information from consecutive days (*before*, *during*, and *after*), when killer whale sightings occurred associated with an event of depredation with no subsequent change in the fishing location. Usually, the distribution of cpue met the assumption of normality but not of homocedasticity (except shortfin mako shark that met both assumptions). Therefore, cpue values were compared using non-parametric statistics. The results indicate no significant differences (p-value ≥ 0.05) in cpue values by comparing the sets before–during, during–after, or before–after depredation for any of the species studied, preys all together, or total catch (Table 7).

Discussion

This is the first study presenting a detailed analysis of several aspects of the depredation by cetaceans (i.e. killer and false killer whales) on the catch of the Uruguayan pelagic longline fishery over a relatively wide area and time span (1998–2007). The effect of environmental, temporal, spatial, and operational variables on the number of fish depredated was investigated. Furthermore, specific analyses were carried out to determine whether depredators select some preys or randomly depredate the catch and to assess the effect of the presence of depredators (killer whales) on the fishery's cpue. The fact that observers recorded depredation during the whole study period except in 2001, when observation coverage was minimal (5.7%), reflects the importance of on-board observer programmes and having a good coverage to evaluate several aspectos of interactions between marine mammals and the pelagic longline fishery.

Spatial and temporal distribution of depredation

The frequency and intensity of depredation varies spatially. It appears that a latitudinal trend exists, with the frequency of depredation increasing from lower to higher latitudes. The frequencies of depredation by false killer whales on catches of pelagic longline fisheries operating at lower latitudes off Brazil (DF = 3.3%) and the Azores (DF = 3.6%; Hernandez-Milian *et al.*, 2008) were lower than those observed in our study (DF = 6.5%) and the neighbouring fishing ground of southern Brazil (DF = 10%) (Danielle Monteiro, pers. comm.). Since in the present study, a significant proportion of observed sets were conducted during summer in northern waters (where the frequency of depredation is lower) and the
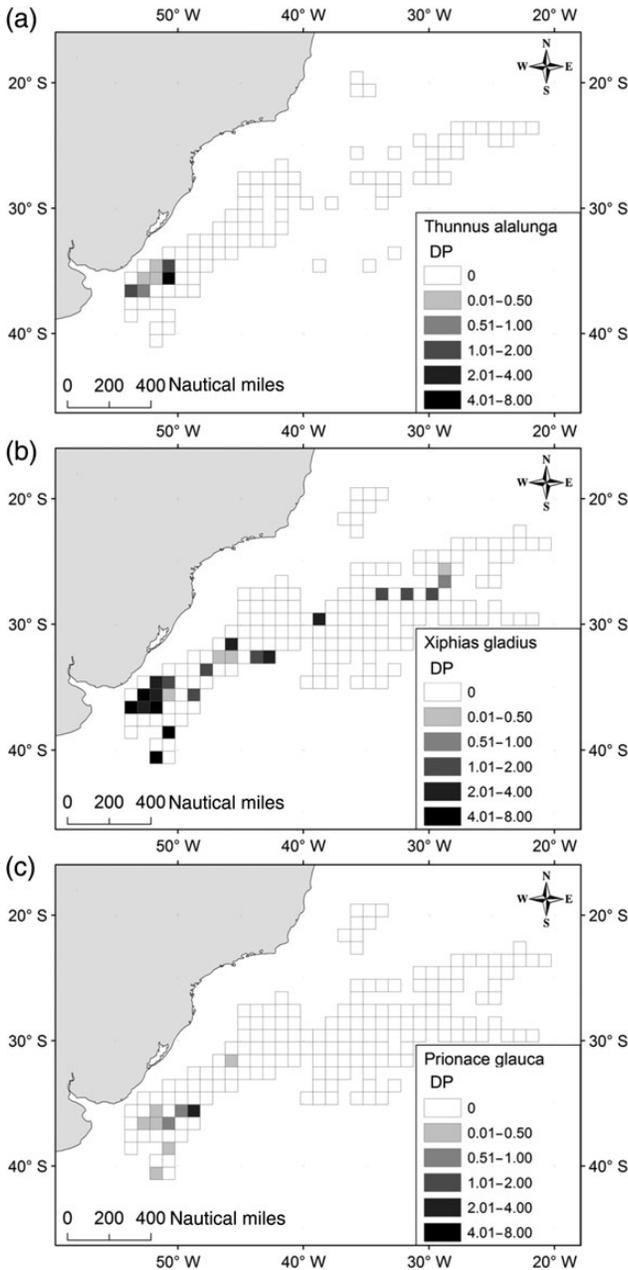
Figure 4. Proportion of depredation (DP) accumulated in quadrants of 1 × 1° during the period 1998–2007 for the following species depredated: (a) Albacore (*T. alalunga*); (b) Swordfish (*X. gladius*); and (c) blue shark (*P. glauca*). White squares indicate the areas where capture of the species occurred, but depredation was not observed.

Figure 5. Relative frequency of the values of Ivlev selectivity index of resources by species that indicate: positive selectivity (Ivlev = 1.0–0.6), neutral (Ivlev = 0.6 to −0.6), and negative selectivity (Ivlev = −0.6 to −1.0).

Table 6. Analysis of deviance table for the minimal adequate GLM: number of fish depredated per fishing event ∼COAST + factor(YEAR) + factor(VESSEL), init.theta = 0.0641, link = log, family = negative binomial.

	Degrees of freedom	Deviance	Residual degrees of freedom	Residual Deviance	Pr(>Chi)
NULL			1019	302.81	
COAST	1	41.491	1018	261.31	0.00000
YEAR	7	31.524	1011	229.79	0.00005
VESSEL	14	47.511	997	182.28	0.00002

Terms added sequentially (first to last).

activity of the fleet occurs mainly during winter and spring, the total values of depredation frequency reported here may be somewhat underestimated. The higher frequency of depredation towards colder waters may be related to the distribution of most frequently depredated target species and higher concentration of depredators in those locations. For instance, the highest cpue values of swordfish, the preferred prey by these cetaceans according to our results, occur southward of the study area (Domingo *et al.*, 2007). The frequency of depredation of Patagonian toothfish (*Dissostichus eleginoides*) by killer whales and sperm whales (*Physeter macrocephalus*) in the bottom longline fishery off southern Chile was 10 and 60%,
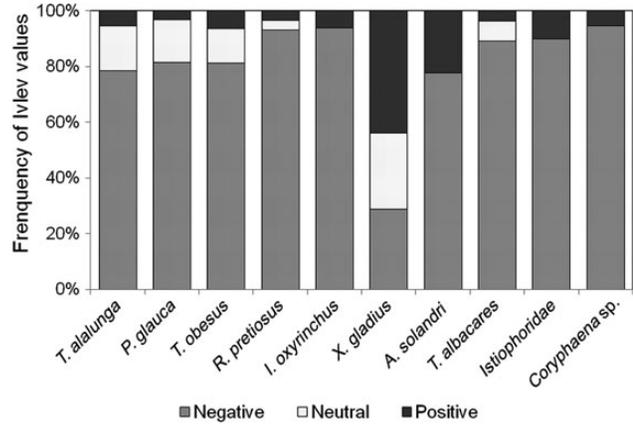
respectively (Hucke-Gaete *et al.*, 2004). Nevertheless, for a better assessment of the impact of depredation on the total catch of the fishery, the proportion of depredation has to be considered instead. By considering the fish damaged in relation to the total catch, better inferences on the relative economic losses caused by cetaceans to the industry can be made.

As in other pelagic longline fisheries, the total proportion of fish removed in the Uruguayan fleet was low ($DP_t = 0.37\%$) and within the range observed in the Azores (0.9%), tropical (0.2%), and subtropical (0.6%) Brazil (Hernandez-Milian *et al.*, 2008; D. Monteiro, pers. comm.). However, the spatial distribution of the intensity of depredation shows marked differences. The intensity of depredation increased southward as distances to the coast decreased, with high values (DP > 5%) within a few 1 × 1° cells. Specifically, total catch, cpue, and proportion of depredation were higher in latitudes between 34° and 38°S and longitudes from 47° to 53°W. The area of larger proportion of depredation coincides with the Brazil–Malvinas (Falkland) Confluence (Brandini *et al.*, 2000; Piola *et al.*, 2000; Acha *et al.*, 2004; Barré *et al.*, 2006). This area presents the highest cpue values of swordfish and blue shark (Mora, 1988; Mora *et al.*, 1991; Domingo *et al.*, 2007) and bycatch of marine mammals, birds, and turtles in pelagic longline fisheries in SWAO (e.g. López-Mendilaharsu *et al.*, 2007; Jiménez *et al.*, 2009; Passadore *et al.*, this volume), as well as high sighting rates of killer whales (Passadore *et al.*, 2012). This highlights the importance of such dynamic and productive oceanic area for both top predators and fisheries. Although a large proportion of depredation was also

observed in areas northward and far from the coast, this could be attributed to occasional depredation on sets with low catch in those areas (Figures 2 and 3).
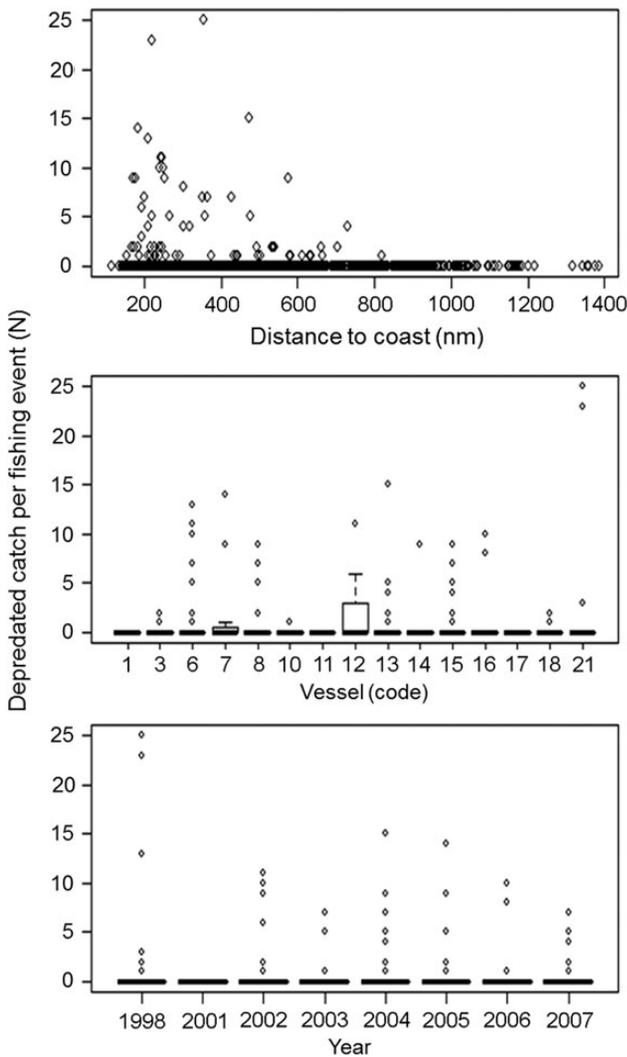

Figure 6. Number of fish depredated per fishing event in relation to the explanatory variables of the minimal adequate GLM: distance from the coast (nm), vessel (code), and year.

Depredation occurred year-round, though interannual variation was observed. Such variation could be associated with a combination of temporal changes in distribution of fishing effort and/or spatial variation in the intensity of depredation. During the period 1993–1995, the US fleet that operated in the SWAO reported higher values of swordfish total proportion of depredation (DP_t = 8.2%, Brum and Marín, 2000) than those observed between 1998 and 2007 by the Uruguayan fleet (DP_t = 1.17%, this study). This could be attributed to the fishing ground of the US fleet being concentrated mainly in Uruguayan and adjacent waters where the highest values of swordfish DP occur (from 2 to 8%, see Figure 4b). Furthermore, the decreasing proportion of depredation observed in our study since 2003 could be because some vessels of the Uruguayan fleet relocated their fishing effort to areas further north (Domingo *et al.*, 2008), where, according to our results, the proportion of depredation is lower.

Depredation occurred in all seasons, and while the highest cpue occurred in autumn and winter the highest frequency and proportion of depredation were recorded in autumn. This is probably due to an increase in the co-occurrence of fishing vessels and depredators within the fishing area during autumn, particularly an increase in killer whales (Passadore *et al.*, 2012). In the longline fleet operating off southern and southeastern Brazil, the interaction occurred mainly in winter (Secchi and Vaske, 1998; D. Monteiro, pers. comm.) or between late autumn and spring (Dalla Rosa and Secchi, 2007). These peaks on depredation in the SWAO coincide with the swordfish fishing season, which begins in autumn, has its peak in winter and ends in spring (Mora, 1988).

The general patterns of distribution of both species indicate that false killer whales occur mainly in tropical and offshore regions (Bastida *et al.*, 2007), while killer whales concentrate in both coastal and oceanic temperate and cold waters, especially in productive areas (Heyning and Dahlheim, 1988; Bastida *et al.*, 2007). While in our study, we analysed jointly the depredation of these two top predators, a contemporary study based on PNOFA observers sightings indicates that killer whales are found mainly between 34°–37°S and 48°–53°W at 150–400 nm from shore (Passadore *et al.*, 2012), thus this species is most likely to be responsible for the larger proportion of depredation recorded south of latitude 34°S and closer to the shelf break. False killer whales frequently depredate longline catches in the intertropical zone of the Atlantic Ocean (Hernandez-Milian *et al.*, 2008; Ramos-Cartelle and Mejuto, 2008).

Table 7. Wilcoxon test for paired data with significance level for two-tailed analysis for each species depredated, the total potential preys (as the sum of the catch of all species depredated at least once) and the total catch.

	Before–during				During–after				Before–after			
	W+	W−	N	$p \leq$	W+	W−	N	$p \leq$	W+	W−	N	$p \leq$
Albacore (*T. alalunga*)	14	22	8	0.640	19	26	9	0.734	26	10	8	0.312
Yellowfin (*T. albacares*)	16	20	8	0.843	17	19	8	0.945	23	22	9	1
Bigeye tuna (*T. obesus*)	4	6	4	0.875	12	3	5	0.312	9	6	5	0.812
Swordfish (*X. gladius*)	29	37	11	0.764	41	37	12	0.909	34	32	11	0.965
Blue shark (*P. glauca*)	31	35	11	0.898	42	24	11	0.464	32	34	11	0.965
Shortfin mako shark (*I. oxyrinchus*)	38	17	10	0.322	27	18	9	0.652	31	5	8	0.078
Pincel (*R. pretiosus*)	17	19	8	0.945	6	15	6	0.437	14	14	7	1
Potential preys	48	30	12	0.518	43	35	12	0.791	41.5	36.5	12	0.850
Total catch	46	32	12	0.622	53	25	12	0.301	48.5	29.5	12	0.469

Values of the sum of positive (W+) and negative (W−) ranges, number of paired data (N), and *p-value* of comparing the cpue of fishing events: before–during, during–after, and before–after depredation-sighting event of killer whale.

Prey selectivity

Cetaceans depredated upon only 10 species among the 57 captured in the longline, suggesting some selective depredation. Previous studies in the SWAO had reported depredation by killer whale and false killer whales mostly on bony fish that were also depredated in this study (Brum and Marín, 2000; Dalla Rosa and Secchi, 2007; Hernandez-Milian *et al.*, 2008; Ramos-Cartelle and Mejuto, 2008). Depredation on elasmobranchs such as shortfin mako and blue shark caught on longlines was also reported in the tropical Atlantic off Brazil and the Azores (Hernandez-Milian *et al.*, 2008) and in California, USA, and New Zealand (Fertl *et al.*, 1996), respectively. There are also occasional records of killer whales preying on free ranging specimens of shortfin mako shark in New Zealand (Visser *et al.*, 2000) and southern Africa (Williams *et al.*, 2009). Although the first records of depredation on blue shark were made only in 2004 in our study, this species is the second most damaged catch, after swordfish. This could be due to an increase in its relative catch rate. Before 2002, landings of blue sharks were kept below 200 t, in 2003, they peaked to 655 t landed and after that (until the end of the study period), it became one of the target species of Uruguayan pelagic longline fleet (Domingo *et al.*, 2008).

In general, the proportion of depredation was higher on swordfish and tuna (*T. alalunga*, *T. albacares*, and *T. obesus*) than the other species. This is consistent with other studies in the region (Secchi and Vaske, 1998; Brum and Marín, 2000; Dalla Rosa and Secchi, 2007; Hernandez-Milian *et al.*, 2008). The greatest intake of swordfish and tuna may be due to the high nutritional content of their meat. These oily fish (SACN and COT, 2004) contain high concentrations of polyunsaturated fatty acids (Vlieg *et al.*, 1993). Sharks, on the other hand, have white meat (SACN and COT, 2004) and oil content is mainly concentrated in their liver. In fact, our records and other studies show that bites of killer whales target almost exclusively the abdominal region of sharks (PNOFA, unpublished data), while they consume almost the entire body of tuna and swordfish except the head (Secchi and Vaske, 1998).

Nevertheless, according to the Ivlev selectivity index, swordfish was the only positively selected species during depredation. This preference for the swordfish had been suggested by previous work in the region (Secchi and Vaske, 1998; Dalla Rosa and Secchi, 2007). However, this selectivity was not effectively determined as those authors did not perform a formal assessment taking the availability and abundance of other potential preys caught in the longline into account. The preference towards swordfish may be because its meat has high nutritional value, high concentration of polyunsaturated fatty acids, and possibly higher overall caloric content compared with other pelagic fish (e.g. Vlieg *et al.*, 1993). The proportion of depredation per set in this region can be over 50% of the daily catch of swordfish, with occasional losses of up to 100% (e.g. our study; Secchi and Vaske, 1998; Dalla Rosa and Secchi, 2007). In our study, albacore and wahoo also had a maximum proportion of depredation per fishing event of 100%, but when this occurred the catch corresponded to only one or two individuals. Both species still showed low frequency of positive selectivity.

Influence of environmental and operational variables on depredation

GLMs demonstrated that besides the spatial (distance to coast) and temporal variation (year) in depredation, the number of fish depredated was also influenced by fishing operational variables (related to vessel identity). Depredation was low in very far offshore areas and increased towards the coast. Most of the depredation occurred over the lower continental slope with very few cases near the shelf break or over the outer continental shelf. As mentioned above, the areas with high depredation rates are influenced by the highly productive Brazil–Malvinas (Falkland) Confluence (Brandini *et al.*, 2000; Piola *et al.*, 2000; Acha *et al.*, 2004; Barré *et al.*, 2006), which might attract both prey (Mora, 1988; Mora *et al.*, 1991; Domingo *et al.*, 2007) and predators (Passadore *et al.*, 2012). In regard to the vessels, there were some with relatively high (e.g. vessels code 6, 7, 12, and 21) and others with low or without depredation. The proportion of depredation can vary considerably among vessels (Donoghue *et al.*, 2003; Tixier *et al.*, 2010). The reason for this variability is unknown but could be related to some physical characteristics (e.g. noise production) of some vessels that attract the depredators more than others. In a pelagic longline fishery that operated in the tropical Atlantic, for example, the estimated losses caused by cetaceans per vessel varied between 0.2 and 8.6% of the total catch (Hernandez-Milian *et al.*, 2008). Tixier *et al.* (2014) argue that differential interaction rates between vessel with killer whales in the Crozet Patagonian toothfish longline fleet may be related with the different ways that engine speed is used by skippers during hauling. Given the difference in depredation among vessels of the Uruguayan longline fleet, the potential influence of their physical properties (e.g. noise production by the engine or hydraulics of the fishing gear) should be further investigated. Similarly, no conclusive interpretation could be made towards the importance of the variable "year". Nevertheless, high depredation during the year 1998 might be related to particularly very high values reported by vessel 21 in that year. It is worthwhile noting that the overall mean cpue per set for the fleet was 53.4 fish/1000 hooks (s.d. = 51.4), while for the vessel 21, cpue was remarkably higher (mean = 148.4 fish/1000 hooks, s.d. = 47.0). In addition, the year 1998 marks the beginning of the observer programme for the Uruguayan longline fleet, therefore, perhaps the observed values were inflated because part of the depredation by sharks was attributed to odontocetes by some inexperienced observers.

Effect of killer whales presence on the catch of target species of the fishery

No differences were found in the cpue when comparing fishing events prior, during, and after the sightings of killer whales associated with depredation events. Despite the reduced number of observations, fishers' perception that the presence of depredators (particularly killer whale) in the fishing area frightens the target species away from the longline (reducing the catch) did not hold for the Uruguayan pelagic longline fleet during the study period. Our results are consistent with those from the demersal longline fishery targeting Patagonian toothfish around Malvinas (Falkland) Islands, where there was no difference between catches with and without the presence of killer and/or sperm whales (Yates and Brickle, 2007). However, in the toothfish fishery off South Georgia, catches declined to <50% when the killer whales were nearby fishing vessels, whereas losses due to sperm whales were less obvious (Kock *et al.*, 2006). This highlights the fact that patterns of interactions between marine mammals and fisheries varies regionally, according to target species and fishing gear used (Donoghue *et al.*, 2003; Read, 2005; Read *et al.*, 2006) and possibly temporally.

Besides killer and false killer, whales other depredators of the pelagic longline catches in the SWAO are some species of sharks (*Carcharhinus* spp., *P. glauca*, *Isurus oxyrhinchus* and *Sphyrna* spp.; Secchi and Vaske, 1998; Hamer *et al.*, this volume). All these shark species are also caught by the fishery, particularly the blue shark which became a target species a decade ago (Domingo *et al.*, 2008). While sharks depredate on the catch of longline vessels more often, when killer whales do so, the percentage of damaged fish is larger (Secchi and Vaske, 1998; Brum and Marín, 2000). This, as well as the fact that cetaceans are more conspicuous than sharks, generally makes the fishers to conclude that cetaceans are responsible for most of their catch lost to depredation (Hamer *et al.*, 2012).

Conclusions

The problem caused by marine mammal depredation on longline fisheries has been the focus of several studies (see Hamer *et al.*, 2012). Although some techniques have been tested to reduce cetacean depredation such as acoustic devices (e.g. to reduce false killer whales bycatch and depredation from longlines, Mooney *et al.*, 2009) and alteration of fishing gear (e.g. "umbrella-and-stones" system to reduce depredation of sperm whales from bottom longlines, Goetz *et al.*, 2011), none has proven to be sufficiently effective to justify the cost of implementation at an industrial scale. The strategies to reduce the negative impact (both for fisheries and for depredators) of these interactions must be specifically designed and their effectiveness would be determined by the characteristics of the species involved, type of fishing gear, fishing strategies, and the environmental conditions of the fishing area (e.g. Hamer *et al.*, 2012). Results presented here show that the intensity of depredation performed by cetaceans on the pelagic longline fishery in the SWAO is influenced by location (distance from shore), fishing operational variables (vessel) as well as by year. Thus, if the fisheries industry or management agencies consider that the reduction in this depredation is needed, these results should be considered at the time of designing management strategies. Historically, the most effective way of reducing the damage caused by marine mammals to fishing activities has been to change gear or fishing area (Northridge and Hofman, 1999). For the Uruguayan fleet, the outcomes of this study showed evident spatial differences on the distribution of depredation. Depredation takes place throughout the year in a broad area, but it mainly occurs within the Brazil–Malvinas (Falkland) Confluence zone where the major fishing effort and catches also occur. As the available data did not allow us to evaluate the causes of empty hooks, the number of fish depredated could be somewhat underestimated. This underestimation is probably small because it is more likely that empty hooks occur due to bait loss during setting/hauling of the gear or to bait removal by birds, turtles, sharks, or other species, rather than to depredation by killer or false killer whales. When these odontocetes depredate large swordfish and tuna, only part of the body is eaten (often the belly). Previous studies (e.g. Secchi and Vaske, 1998) have shown that the entire head of the fish often remains. This is different from the pattern observed when sperm whales depredate Patagonian toothfish from demersal longlining, leaving only lips or small parts of the head, thereby suggesting that some empty hooks may occur due to depredation (Hucke-Gaete *et al.*, 2004). Nevertheless, we consider that the total catch lost due to depredation is relatively low in the Uruguayan fleet. Even for swordfish, the preferred species by the depredators, the total proportion of depredation was as low as 1.17%. In addition, the presence of depredators (particularly killer whales) in the fishing area produced no significant decrease in the catch. Therefore, the losses caused by cetaceans to the longline fishery in the SWAO should be considered as low with probably minor economic effects to the fishing industry.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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