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Contribution to the Theme Section 'Drivers of dynamics of small pelagic fish resources: biology, management and human factors'

Portuguese purse seine fishery spatial and resource overlap with top predators

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ABSTRACT: The Portuguese purse seine fishery, with average annual catches of 70000 tonnes, operates mainly in coastal areas and targets small pelagic fish (SPF). Potential competition for resources may occur between the fishery and some species of marine mammals and seabirds, as suggested by observed incidental catches. For those species directly affected by the fishery, the spatial distribution of marine taxa and the fishing fleet are key pieces of information for spatial planning and management. We analysed the spatial and resource overlap between the fishery's distribution and effort, and the distribution and abundance of 6 species of top predators—seabirds (n = 4) and marine mammals (n = 2) between 2010 and 2014. Estimates of annual consumption by top predators and the fishery catch within the distributional range of one of their main prey species (sardine Sardina pilchardus) were also determined. Spatial overlap between all considered species and the fishery was low (< 0.221), and only 2 species (common dolphins Delphinus delphis and Cory's shearwaters Calonectris borealis) showed high resource overlap with the fishery (>0.7). Overall, values of consumption of SPF by the top predators were of the same order of magnitude as mean annual purse seine landings for the studied area. Our results can be used for marine spatial planning, including designation of Marine Protected Areas and the development of an ecosystem-based model for the effective management of the Portuguese purse seine fishery that takes into account the consumption of natural predators.

KEY WORDS: Spatial overlap · Resource overlap · Competition · Marine mammal · Seabird · Fisheries · Pelagic fish · Prey availability

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1. INTRODUCTION

Fisheries interactions with marine mammals and seabirds have long been described in the literature and are highly diverse (e.g. Northridge 1991, Furness

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2003, Read 2008). From both perspectives (humans and top predators), interactions can range from negative (e.g. damage/loss of fishing nets or death in fishing nets) to positive (e.g. guide to prey or removal of competitors). Fisheries can impact top predators

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directly by unintentionally injuring or killing them, or indirectly by competing for prey. Historically, the indirect effects of fishing have received less attention by scientists and fisheries managers, although their consequences on the populations of top predators could be significant. Kaschner & Pauly (2005) highlighted the political pressure of international fora to account for competition between top predators and fisheries in management strategies. This is mainly due to the economic value of involved resources (Thirgood et al. 2000, Yodzis 2001, Graham et al. 2005), the conservation status of an increasing number of top predators, the increasing frequency of conflicts due to the expansion of human activities (Woodroffe 2000, Graham et al. 2005) and the increase in populations of some top predator species (Wickens & York 1997).

Competition between fisheries and top predators is a situation where the presence of the 2 competitors is mutually disadvantageous and can occur when the 2 groups share a common prey species or when one of the top predators may prey on a species that is also an important component of the diet of a commercial fish species (Plagányi & Butterworth 2009). This source of conflict between humans and top predators has been an issue in many fisheries (Harwood & Croxall 1988, Trites et al. 1997, Yodzis 2001) and many approaches, ranging from the most simple and static to the more complex and dynamic, have been applied to address the problem (Matthiopoulos et al. 2008, Bearzi et al. 2010, Bertrand et al. 2012). Several studies have already associated seabird and marine mammal population declines with prey decreases due to fishing (Duffy 1983, Loughlin & Merrick 1989, Trites et al. 1997, Furness 2002, 2003, Grémillet et al. 2016). Few studies have shown inconclusive (Hui et al. 2015) or negative results—Ratcliffe et al. (2015) found very low impact of Antarctic krill Euphausia superba Dana fisheries on macaroni penguins Eudyptes chrysolophus, while Ocampo Reinaldo et al. (2016) showed that the increase in sea lion Otaria flavescens biomass has not led to a significant increase in predation mortality of Argentine hake Merluccius hubbsi. One of the effects of competition with fisheries is the potential for local depletion of prey species, which will force top predators to change their feeding grounds. This might be an issue for species with very restricted ranges or in particular seasons such as the breeding season. Other effects are adult mortality caused by lack of food, insufficient food to raise the young or poor reproductive success.

Other studies have introduced new concepts of competition, such as indirect competition for primary

production. Trites et al. (1997) studied competition from an ecosystem perspective, undermining the simplistic view of the surplus-yield model by shedding light on the other roles that top predators play (Roman et al. 2014). These roles are considered to be crucial for the sustenance of fisheries, such as stimulating primary production (Lavery et al. 2014). Harwood & Croxall (1988) pointed out that a realistic evaluation of the direct competition between fisheries and top predators requires information on the distribution in space and time of all the ecosystem components involved. Matthiopoulos et al. (2008) made the same point, identifying 4 sources of ecological complexity: spatial heterogeneity, individual variation, multi-species interactions and long-term dynamics. They stressed the importance of incorporating spatial and temporal variation in management and decision making. Sydeman et al. (2017) reached similar conclusions, and added that such studies should make sure that collected data on fisheries, prey and seabirds are in the same spatiotemporal scale. In agreement with the above suggestions, Catry et al. (2013) developed maps of albatross Thalassarche melanophris and fisheries to assess the spatiotemporal variability of their overlap and possible competition in order to make predictions that could be incorporated into management plans.

In Portugal, the purse seine fishery for small pelagic fish (SPF) has a history of about a century, and contributes approximately 50% of mainland Portugal's annual catches (INE 2016). This fishery currently consists of around 180 vessels and annual landings of up to 70 000 tonnes (t) of SPF (INE 2016). The main target species is sardine *Sardina pilchardus*, with annual landings that have oscillated between 13000 and 55000 t in the last decade (INE public database). Chub mackerel *Scomber colias*, horse mackerel *Trachurus trachurus*, European anchovy *Engraulis encrasicolus* and Atlantic mackerel *Scomber scombrus* make up the rest of the SPF catch.

In this work, we followed the same rationale and methodological guidelines as Catry et al. (2013) to evaluate competition between the Portuguese purse seine fishery, seabirds and marine mammals for SPF along the Portuguese coast. Specifically, we evaluated the spatial and resource overlap between the fishery and 6 species of top predators found off mainland Portugal: common dolphins *Delphinus delphis*, minke whales *Balaenoptera acutorostrata*, northern gannets *Morus bassanus*, Balearic shearwaters *Puffinus mauretanicus*, Cory's shearwaters *Calonectris borealis* and sandwich terns *Thalasseus sandvicensis*. All of these top predator species are expected to have a substantial resource overlap with the fleet, since the SPF caught by the fishery are also known to form part of their diets (Silva 1999, Alonso et al. 2012, Fróis 2014). In addition, operational interactions with purse seiners off mainland Portugal are registered for several of these species (Wise et al. 2007, Marçalo et al. 2015, Oliveira et al. 2015), suggesting that spatial overlap also occurs to some degree. We also describe the contribution of SPF in the diet of top predators and in the catches of purse seiners, and estimate the annual consumption of SPF by top predators, comparing them with quantities landed annually in Portugal. This information can be used in management measures in the area, including Marine Protected Areas designation for threatened, endangered or protected species conservation and related fishery regulations.

2. MATERIALS AND METHODS

2.1. Study area

The Portuguese mainland coast is 860 km long, ranging from Caminha (41° 50' N, 8° 50' W) to Vila Real St. António (37° 12' N, 7° 25' W). We considered 3 main areas along the coast based on topography and oceanographic differences (Fiúza 1983, Relvas et al. 2007, Oliveira et al. 2009). The North-Central coast (NC) is a 310 km stretch between Caminha and Peniche (Cape Carvoeiro). This section represents a wider continental shelf (40 to 70 km), characterized by a strong, homogeneous seasonal upwelling, with northern wind regimes resulting in colder waters with high productivity. The Central-South coast (CS), located between Peniche and the western tip of Cape S. Vicente, is 380 km long and represents a narrower continental shelf (10 to 20 km wide) and weaker upwelling associated with the nearshore deep features of the Lisbon and Setúbal canyons, resulting in warmer waters with less productivity. The southern coast (S) is 170 km long, spreading from the southern tip of Cape S. Vicente to Vila Real St. António. This zone represents a very narrow continental shelf (5 to 20 km wide), warmer waters and prevailing southern winds.

2.2. Marine mammal abundance and distribution data

Data on the distribution of marine mammals were obtained from aerial surveys carried out during the following time periods: September and October 2010, September 2011, September 2012, October 2013 and September 2014. The surveys covered the entire Portuguese Continental shelf up to 50 nautical miles (nmi). The methodology applied followed standard line transect distance sampling techniques (Buckland et al. 2001, Panigada et al. 2011, Scheidat et al. 2012).

All in-flight procedures and optimal flight conditions were based on internationally tested methodologies for line transect campaigns (Hammond et al. 2013). Flights were carried out along a systematic set of parallel 50 nmi long transects separated by a distance of 10 nmi and oriented either in east-west (along the west coast) or north-south directions (along the south coast), with 2 observers and 1 data recorder. Flight surveys were performed at an average speed of 100 knots (185 km h^{-1}), and an altitude of 500 ft (150 m). All surveys were carried out in twinengine, high-wing aircrafts equipped with 2 bubble windows (Partenavia P-68 modified with 'bubble windows'), which allowed scanning directly underneath the plane. For each observation, we measure the perpendicular angle from the track line to the animals observed, using a hand-held inclinometer. Surveys were conducted with visibilities >5 km and with Beaufort Sea state <3. The abundance values presented were estimated using conventional distance sampling (CDS) with 5% standard truncation for sightings detected at the largest distances (Buckland et al. 2001). They were computed by multiplying density of individuals by the surface area of the study region. The coefficients of variation (CVs) and the 95% confidence intervals (CIs) were estimated by bootstrapping (999 replicates) within strata, using transects as sampling units (Buckland et al. 2001, Thomas et al. 2010).

A density surface modelling (DSM) approach (Thomas et al. 2010, Miller et al. 2013) was used to predict the spatial distribution of estimated abundance (Hammond et al. 2013, Winiarski et al. 2014, Roberts et al. 2016) of common dolphins and minke whales over the study area. It was based on the 'count method' developed by Hedley & Buckland (2004), which involves fitting a spatially referenced density surface to cetacean counts in areas covered by search effort. The density surface estimator is a model-based estimator that relies on the correct model being fitted to the data. In distance sampling methodology, stratum-specific density estimates are obtained, whereas the DSM allows density to be a function of location and environmental variables.

This method was applied using the 'dsm' package in R (Miller et al. 2013, 2014). The analysis takes into consideration animal sightings, so it demands their allocation into segments of effort line transects disposed into a grid with the same resolution as the segment length (in this case approximately 4 km) and adjusts the counts based on detectability using a supplied detection function. A generalized additive model (GAM) is then used to model the adjusted counts based on a formula that includes environmental covariates — in this case latitude, longitude, bathymetry, distance to shore, sea surface temperature (SST) and chl a (all tested for collinearity) as smooth terms. Mean SST and mean chl a concentration of the respective surveyed month were obtained from 2 Aqua-MODIS satellite imageries (spatial resolution = 4 km; NASA 2014). In 2010, an average was calculated for September and October SST and chl a data. Once the DSM has been built, density or abundance can be estimated over an area of interest within the study area by predicting over a grid of points to which the same covariates/predictors are attached (Thomas et al. 2010, Miller et al. 2013). All the produced models were corrected for availability bias. We considered 0.106 for minke whale (Witting 2005) and 0.676 for the common dolphin (Gómez de Segura et al. 2006) as in previous aerial survey reference studies (Hammond et al. 2013). The best models were selected based on the minimum Akaike's information criterion (AIC) values.

2.3. Seabird abundance and distribution data

Data on seabird species distribution were available from shipboard surveys conducted from 2011 to 2014 off the coast of Portugal and Cádiz (Spain). Data were selected for the area limited to the <200 m bathymetric line to match fishing data since purse seine fishing grounds are located within this area. Most of the survey effort was carried out between March and November each year, with fewer surveys from December through February (2011 and 2013). The standard European Seabirds at Sea protocols for data collection (Tasker et al. 1984, Camphuysen & Garthe 2004) was followed onboard 4 similar research vessels. One observer and one data recorder were present in each survey. Birds observed sitting on the water were continuously counted when inside the 300 m width transect on one side of the vessel. Flying birds were counted using the snapshot methodology. Only counts of birds that were observed inside transects were included in the analysis. Seabird observations were summed up into 5 min survey units. Although several studies have suggested that the detectability of seabirds when conducting at sea

surveys varies as a function of species, weather conditions and observer (e.g. Spear et al. 2004), we assumed a negligible bias in the abundance estimates due to the relatively large size of the species considered in this study and the use of a 300 m wide transect.

Hurdle and zero-inflated models (Mullahy 1986, Lambert 1992, Cameron & Trivedi 2005, 2013), assuming a binomial distribution for presence-absence data and either a Poisson or a negative binomial distribution for count data, were explored to describe the distribution and abundance of the seabird species. The full model included the following variables as predictors: latitude, longitude, year, season, bathymetry, SST and chl a. Since dynamic oceanographic data (SST and chl a) were extracted as monthly averages from Aqua-MODIS satellite imagery, they were integrated over a period of 3 mo prior to each season (winter, spring, summer, autumn; Louzao et al. 2009) to account for time lags of oceanic effects on the ecosystems, and were also used as predictor variables ('SST_prev' and 'chla_prev'). The response variable was the total number of birds observed in each survey. To account for varying monitoring effort, the number of km² surveyed was included in the model as an offset variable. In a second step, variables with p > 0.05 were excluded and new models were generated. To evaluate the model's overdispersion, rootograms available in the 'countreg' R package were used (Zeileis & Kleiber 2017). The plots visualize where the model is over- or under-fitting. The AIC criterion was then used to select the best model (between full and reduced models) for each species. All model evaluation statistics and optimal thresholds were calculated using the R package 'pscl' (Zeileis et al. 2008). Species density was estimated on a common regular prediction grid with 4 km (0.0417°) spaced nodes to match the spatial resolution of remotely sensed environmental data.

2.4. Purse seine fishery data

Vessel monitoring system (VMS) and logbook data from purse seine vessels (>12 m) for the years 2010 to 2014 were integrated to produce maps of fishing activity. Fishing effort distribution maps were developed according to Katara & Silva (2017) by analysing vessel speed patterns from VMS data and linking them to logbook data to identify fishing activity. We report fishing effort as the number of fishing sets per grid cell in a common regular prediction grid with 4 km spaced nodes. Official landing data from the purse seine fleet were analysed to determine total landings per year. For comparison purposes in terms of SPF species consumed by the marine mammal/seabird species, we only considered the top 5 landed species, i.e. species that constitute at least 90% of the official landings over the period of 2010 to 2014, namely sardine, chub mackerel, horse mackerel, European anchovy and Atlantic mackerel.

2.5. Annual consumption

Quantities of prey consumed annually (I_t , in tonnes) by marine mammal/seabird species were estimated using the following equation:

$$I_t = N_t \times \frac{\text{IB}}{1000} \times P_i \times \text{T}$$
(1)

where N_t is the population abundance estimation (see 'Marine mammal' and 'Seabird abundance and distribution data' sections above) for the study area at time *t*; IB is the average daily food intake of an individual (in kg), P_i is the adjusted proportion by weight of prey species *i* in the diet taking into account all prey remains, and *T* is the number of days that prey and predator are in contact; assumed here to be constant and equal to 365 d. This approach ignores seasonal and regional variation in diet and sizerelated dietary variation. The values used for the P_i were based on % of weight obtained from stomach content analysis of stranded animals (Pierce et al. 2004, Santos et al. 2004, 2013, 2014, Tollit et al. 2010). Diet was quantified using 3 standard indices: (1) the frequency of occurrence of each prey type, which corresponds to the number of stomachs in which a prey type was present (% occurrence); (2) the proportion of number of individuals of each prey type versus the total number of all prey individuals (% number); and (3) the proportion of the reconstructed total prey biomass represented by each prey type (% weight). The reconstructed prey biomass (W) of each species was calculated as the product of the number of individuals and the average reconstituted body mass, in each stomach, summed throughout the sample set.

Following the methodology used in Bearzi et al. (2010), average daily food consumption of common dolphins (IB) was estimated using 4 different published relationships: (1) IB = $0.123M^{0.8}$ (Innes et al. 1987); (2) IB = $0.482M^{0.524}$ (Leaper & Lavigne 2002, Kaschner 2004); (3) IB = 0.035M (Tamura 2003, Kaschner 2004); and (4) IB = $0.1M^{0.8}$ (Trites et al. 1997), where *M* is the mean body mass (kg). The

results of these 4 estimates were averaged. Adult body mass (60.97 kg) was estimated from measures of maximum body length (L_i in cm) of each individual (Bearzi et al. 2010) as follows:

$$M = 7.5814 \times (L - 140)^{0.5345} \tag{2}$$

For the minke whale, IB was estimated using body mass M = 3548 kg and the following relationship (Sigurjónsson & Víkingsson 1997): (1) IB = $0.420M^{0.670}$. Adult body mass for the minke whale was determined as the mean value of different relationships described for this species (Lockyer 1976).

Diet composition for each of the seabird species was derived from a literature review of published accounts of stomach contents and other information (Stienen et al. 2000, Arcos & Oro 2002, Hamer et al. 2007, Dias 2011). Diet composition was aggregated at the family level because (1) diet information for individuals in Portuguese colonies is only available for Cory's shearwater (e.g. Alonso et al. 2012) and (2) some prey species described for the seabird species are not found in Portuguese continental waters.

The IB of seabirds was estimated following Croxall's (1987) approach:

$$\log IB = -0.293 + 0.850 \log M$$
(3)

Seabird species' annual food consumption was estimated using the mean values of abundance per season.

Estimates of annual consumption by the top predator species were then compared with annual landings of the purse seine fleet to obtain a first indication of the potential scale of competition among the target species and the purse seine fishery.

2.6. Spatial and resource overlap

The degree of spatial and resource overlap between the purse seine fishery and the top predator species (Fig. 1) in the study was calculated using the simplified Morisita index (\widehat{C}_H) (Horn 1966):

$$\widehat{C_H} = \frac{2\sum_i^n \widehat{p_{ij}} \ \widehat{p_{ik}}}{\sum_i^n \widehat{p_{ij}^2} + \sum_i^n \widehat{p_{ik}^2}}$$
(4)

where $\widehat{p_{ij}}$ and $\widehat{p_{ik}}$ are percentage of the prey species i in the diet of the predator j and k, respectively, if we are calculating resource overlap. If we are calculating spatial overlap, $\widehat{p_{ij}}$ and $\widehat{p_{ik}}$ are the percentage of individuals in grid cell i of the species j and the fishery k. This index ranges from 0 (no overlap) to 1 (total overlap).

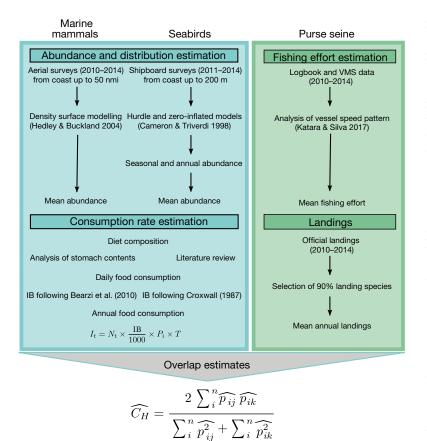


Fig. 1. Schematic representation of the overlap estimation. To estimate the Morisita index $(\widehat{C_H})$, it was necessary to estimate the abundance of top predators, fishing effort, the diet and consumption rates of top predators as well as fishery landings

Spatial overlap was determined using a 4×4 km grid. Each grid cell was associated with a measure of fishing effort (if any) and the abundance of the species in question (mean annual abundance for marine mammals, mean seasonal abundance for seabirds). For resource overlap estimation, the mean value of total landings of the fleet was used.

3. RESULTS

3.1. Marine mammal abundance and distribution

The abundance values (density) obtained by DSM relate to the estimated average number of animals (ind. $\rm km^{-2}$) observed in the study area during the study period (2010 to 2014), rather than the abundance estimates (ind.) of the common dolphins or minke whale population in the entire Portuguese continental coast.

The common dolphin was the most commonly encountered and widely distributed marine mammal

in our study, and the best abundance estimate was derived from the DSM model including latitude, longitude, chl *a*, distance to shore and bathymetry as explanatory variables with an adjustment to a negative binomial distribution. The mean density map shows that the common dolphin is distributed over the Portuguese continental shelf with higher levels of abundance in the north and centre of the study area (Fig. 2).

For the minke whale, the best model had latitude, longitude and chl a as explanatory variables with an adjustment to a quasi-Poisson distribution. This species was characterized by a sparser distribution, having a higher concentration of sightings near the coast and south of 38° N (Fig. 2). The mean value of abundance across all years shows a more scattered distribution compared to the common dolphin, with the most important nuclei associated with the 200 m depth contour, close to the continental slope. The only exceptions are near Aveiro, a region with the largest continental platform, where the species is present in shallower waters, and in the region of Sagres in the south, where the continental slope is very close to shore.

3.2. Seabird abundance and distribution

The mean density maps for seabird species are shown in Fig. 3. All studied species are broadly distributed along the Portuguese Continental shelf all year-round, with some variation in terms of distribution and density over the different seasons (data not shown). Hurdle models showed smaller overdispersion (data not shown) and lower AIC values when compared to the zero-inflated models except in the case of the sandwich tern. The highest densities of Cory's shearwater were found to the south of Figueira da Foz, with important concentration areas located in the centre and south during the winter and spring seasons (data not shown). The best model included year, season, latitude, longitude, chl a and chla_prev as explanatory variables. Northern gannet had higher density values, with concentration areas located in centre and south during winter and south during autumn (data not shown). The best model included year, season, bathymetry, latitude, longi-

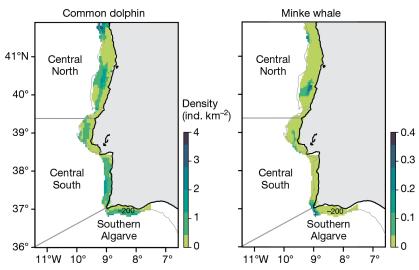
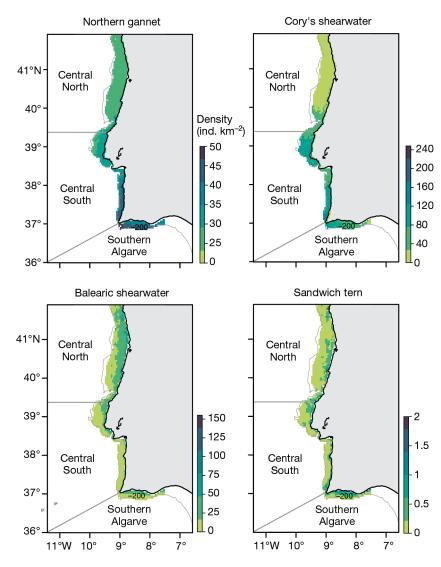


Fig. 2. Mean density maps (number of ind. $\rm km^{-2}$) of the common dolphin (left panel) and the minke whale (right panel) (2010 to 2014). The grey line corresponds to the -200 m isobath



tude, chl *a*, chla_prev, SST and SST_prev as explanatory variables.

For Balearic shearwaters, the best model included year, season, bathymetry, latitude, longitude, chl *a*, chla_ prev, SST and SST_prev as explanatory variables. This species tends to use more coastal areas and highest densities were found in the north area all year except spring (data not shown). Sandwich terns' best model included year, season, bathymetry, latitude, chl *a*, chla_prev and SST as explanatory variables. The species tends to concentrate in the central coastal area mainly during spring (data not shown).

3.3 Purse seine fishery catches

Around 16% of the 72364 raw logbook records were removed after basic cleaning and checking of overlapping trips. 33126 logbook records (45.8% of the raw data) were associated with VMS records but only 12967 (39.1% from the remaining logbook records) had fishing sets identified by the speed pattern algorithm.

Of the total VMS records considered, around 9% were excluded from further analysis as being either duplicate points or locations close to the port, and a further 72% were excluded because no link to logbook data could be established. Using the speed algorithm to signify fishing, 16028 (of the remaining 293331) records were classified as fishing.

Spatial patterns of the purse seine fishery were very similar among years (Fig. 4), as the fishery usually uses the same fishing grounds over the years.

Fig. 3. Mean density map (No. of ind. km⁻²) of the northern gannet (top left panel), Cory's shearwater (top right panel), Balearic shearwater (bottom left panel) and Sandwich tern (bottom right panel) (2011 to 2014) The grey line corresponds to the -200 m isobath

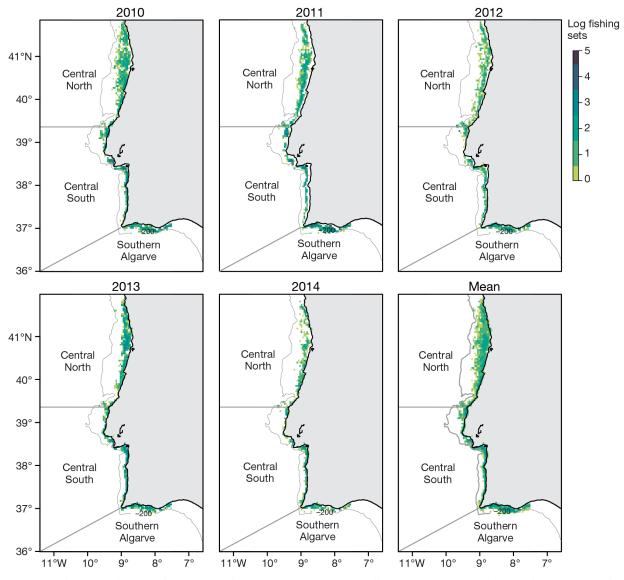


Fig. 4. Logarithmic number of fishing sets of the Portuguese purse seine fleet (2010 to 2014). The grey line corresponds to the -200 m isobath

Official landing data from the Portuguese purse seine fleet showed that the top 5 landed species in weight were sardine, chub mackerel, horse mackerel, Atlantic mackerel and European anchovy (Fig. 5). Landings (mean \pm SD) fluctuated over years (66447 \pm 10250 t). However, sardine and chub mackerel formed the bulk of the landings, representing on average 53.7 \pm 19% and 37.3 \pm 19.3% of total landings, respectively.

3.4. Annual consumption

SPF represented more than 75% of the diet composition of the 2 marine mammal species analysed in the present study (Table 1), similar to the percentage that these species represent in the fishery landings (90%). For seabirds, the representation of SPF in their diet composition ranged from 33 to 48% (Table 1).

In terms of median annual consumption rates, the 6 studied species combined consumed 88×10^3 t while the fishery itself took out 66×10^3 t (Table 2).

3.5. Spatial and resource overlap

The greatest resource overlap with the purse seine fishery occured with the common dolphin (0.932) and the least resource overlap with the Balearic shearwater (0.350) (Table 3).

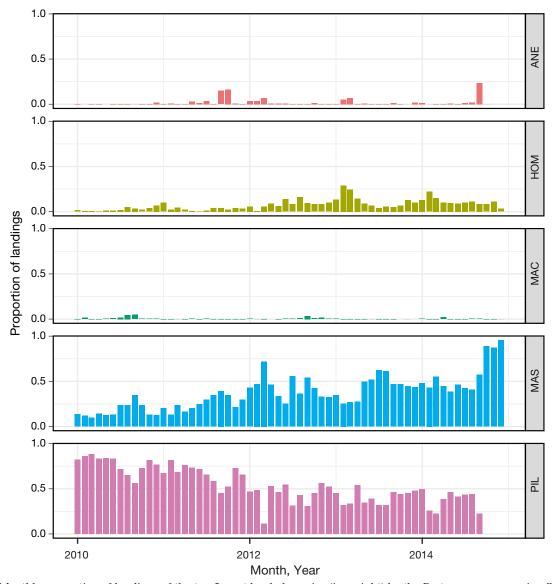


Fig. 5. Monthly proportion of landings of the top 5 most landed species (in weight) by the Portuguese purse seine fleet. ANE: European anchovy *Engralius engrasicolus*; HOM: horse mackerel *Trachurus trachurus*; MAC: Atlantic mackerel *Scomber scombrus*; MAS: chub mackerel *Scomber colias*; PIL: sardine *Sardine pilchardus*

Compared with the common dolphin there was a smaller overlap of this fishery with the minke whale, both spatially (Fig. 6) and in terms of resources (Table 3). Common dolphins showed a high resource overlap with the fishery, mainly due to their preference for sardine and chub mackerel. However, their spatial overlap was relatively small.

Spatial overlap of the purse seine fishery with the seabird species was relatively low, especially in the first semester of the year when seabird abundances are lower (Table 3). The 2 species that showed higher values of spatial overlap with the fishery are Cory's shearwater and sandwich tern (Table 3).

4. DISCUSSION

Our results indicate that the potential for competition between 6 top predator species and the Portuguese purse seine fishery in the period 2010 to 2014 was low. Spatial overlap between all species considered and the fishery was also low (<0.221) and only 2 species (common dolphins and Cory's shearwaters) showed a high resource overlap with the fishery (>0.7). Results showed that the group of top predators consumed similar quantities of pelagic fish species as the purse seine fishery. These findings have also been reported in other studies in different

	Common dolphin	Minke whale	Cory's shearwater	Northern gannet	Balearic shearwater	Sandwich tern	Purse seine
Clupeidae	37.1	23.6	19.1	18.7	18.3	59.5	53.5
Engraulidae	0.7	0	0	0	29	0	1.8
Scombridae	28	0.5	23.7	14.6	0	0	37.5
Carangidae	15.4	59.5	4.8	0	0	0	7.2
Ammodytidae	0	0	0	51.5	0	39.8	0
Sparidae	2.6	8.2	0	0	1.6	0	0
Gobiidae	0.2	0	0	0	18.8	0	0
Caproidae	0	2	0	0	0	0	0
Belonidae	0.1	0	11.9	0	0	0	0
Scomberesocidae	0	0	16.7	0	0	0	0
Gadidae	4.5	0.1	0	10.4	17.5	0	0
Merluciidae	4.2	0	0	0	0	0	0
Atherinidae	1.1	0	0	0	0	0	0
Soleidae	0.2	0	0	0	8	0	0
Mugilidae	0.4	6.1	0	0	0	0	0
Other fish	0	0	0	4.8	6.8	0.7	0
Crustacea	0	0	2.4	0	0	0	0
Sepiolidae	0.8	0	0	0	0	0	0
Loliginidae	4.5	0	0	0	0	0	0
Ommastrephidae	0.2	0	0	0	0	0	0
Unidentified	0	0	21.4	0	0	0	0
Source	Marçalo et al.		Dias	Hamer et al.	Arcos & Oro	Stienen et al.	DGRM
	(2018)	unpubl. data	(2011)	(2007)	(2002)	(2000)	(2010–2014)

Table 1. Proportion (%) of prey weight in the diet of the different species and catch weight of the purse seine fishery

Table 2. Estimated mean annual consumption by the 2 species of cetaceans and 4 species of seabirds, and mean total landings by the purse seine fleet. In parentheses percentages within the respective prey families are presented

Species	————Mean annual consumption and landings ——— [10 ³ t (% within prey family)]					
	Clupei-	Scombri-	Carangi-	Engrauli-	Other	
	dae	dae	dae	dae		
Common dolphin	4.6 (6.1)	3.5 (6.2)	1.9 (11.3)	0.1 (2.1)	2.3 (2.1)	
Minke whale	3.2 (4.3)	0.1 (0.2)	8.0 (47.6)	0 (0)	2.2 (2.0)	
Cory's shearwater	10.4 (13.9)	12.9 (22.8)	2.6 (15.5)	0 (0)	28.5 (25.7)	
Northern gannet	19.5 (26.1)	15.2 (26.8)	0 (0)	0 (0)	69.1 (62.3)	
Balearic shearwater	r 2.5 (3.3)	0 (0)	0 (0)	3.9 (81.3)	7.1 (6.4)	
Sandwich tern	0.1(0.1)	0 (0)	0 (0)	0 (0)	0 (0)	
Purse seine	34.5 (46.1)	25.0 (44.1)	4.3 (25.6)	0.8 (16.7)	1.8 (1.6)	
Total	74.8	56.7	16.8	4.8	111.0	

Table 3. Resource and spatial overlap (Morisita-Horn index) between top predator species and the purse seine fishery

Resc	Resource overlap			Spatial overlap		
Common dolphin Minke whale	0.932 0.404	$0.221 \\ 0.064$				
		Winter	Spring	Summer	Autumn	
Cory's shearwater	0.717	0.040	0.048	0.084	0.073	
Northern gannet	0.406	0.046	0.059	0.105	0.069	
Balearic shearwater	0.350	0.072	0.090	0.169	0.112	
Sandwich tern	0.673	0.087	0.129	0.179	0.128	

parts of the world, where top predators have diets that overlap with fishery resources and their biomass consumption is similar to landings (e.g. Bax 1989, Trites et al. 1997, Brooke 2004). In the Bay of Biscay, the diet of common dolphins overlapped significantly with small pelagic fisheries landings, and their consumption was of the same order of magnitude as the fisheries due to the large population size of the common dolphin (Pusineri et al. 2004, Lassalle et al. 2012).

4.1. Resource overlap

Resource overlap was found to be high for the common dolphin and Cory's shearwater. Sandwich terns also had a relatively high resource overlap with the fishery, which is unexpected since we know from onboard observations that this species is not the one that interacts the most with the fishery (Oliveira et al. 2015). In addition, anecdotal records of

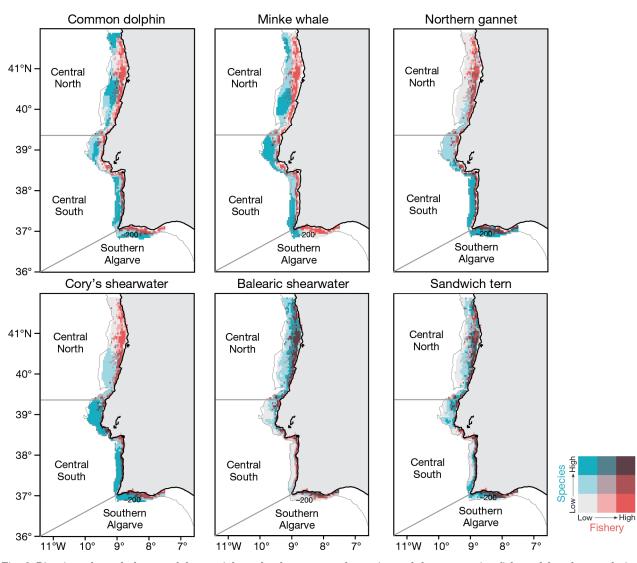


Fig. 6. Bivariate choropleth map of the spatial overlap between each species and the purse seine fishery. Map shows relation between the abundance of each species and the fishing effort (number of sets) of the fleet. The grey line corresponds to the -200 m isobath

their diets in the study area report them to feed mainly on sand eel and *Atherina* spp. at sea, or on small fish and invertebrates in estuarine areas (J. Vingada unpubl. data). Moreover, their sibling species little tern *Sternula albifrons*, that breeds in Portuguese estuarine areas, are known to feed extensively on *Atherina* spp. (Catry et al. 2006, Ramos et al. 2013).

By itself, resource overlap is not direct evidence of competition, given the fact that resources can be adequate to support these predator species and the fishery. Competitive effects could, however, be inferred when key prey species become scarce and are subject to heavy fishing pressure (Kaschner 2004, Pusineri et al. 2004, Bearzi et al. 2010). In this case, only the stock of sardine is currently at a very low biomass level. However, competition may have been avoided because the fishery has been reducing effort and catches (ICES 2017). Moreover, common dolphins fulfil their energy needs with abundant SPF species, such as chub mackerel and horse mackerel, although sardines are still important in their diet (Marçalo et al. 2018).

4.2. Spatial overlap

Spatial overlap with the fishery was found to be low for all species considered. A possible explanation for this is that the Portuguese purse seine fishery, although actively targeting SPF and large aggregations of fish, is known to operate mainly in relatively shallow waters (<50 m). Therefore, when an area up to 200 m is considered and when species explore a wider area of distribution compared with the fishery, the degree of estimated spatial overlap is expected to be relatively low. Differences among the seabird species can be attributed to their habitat use. Cory's shearwaters have a wider and more pelagic distribution than the other seabird species considered in this study (Meirinho et al. 2014). The individuals found in the Portuguese mainland waters probably belong to the breeding colony located on the Berlengas Archipelago. These individuals are known to forage around the colony with some annual variations due to resource availability (Paiva et al. 2017). This might explain the concentration of Cory's shearwaters observed around the Berlengas and towards the south. The other seabird species often use Portuguese coastal waters during migration or non-breeding periods, which explains the higher spatial overlap values observed here. Balearic shearwaters are commonly observed following purse seiners (N. Oliveira unpubl. data) and are involved in bycatch events (Oliveira et al. 2015). Low levels of spatial overlap might also be attributed to using an inadequate scale to measure this index (Reid et al. 2004), or underestimating fishing effort.

4.3. Study limitations

The uncertainty in the analysis arises from different sources of data, data-processing methodologies and applied models. Results should be seen through the prism of data limitations and revisited as better data becomes available and methodologies improve.

Uncertainty regarding the diet of the different species stems from different sources of data. For some seabird species, information was collected from studies conducted in different areas and on different populations (resident versus migratory populations), and therefore the diet of a species was assumed to be homogeneous and similar to those areas where information was available. For marine mammals, diet information came from stomach content analysis of stranded animals. Caution is recommended when inferring the diet of populations based on stomach contents because diet may be biased towards unhealthy animals and adults, or there may be an underestimation of prey importance due to different digestive rates of prey items (e.g. Tollit et al. 2010). Interannual and seasonal changes in the diet and sizerelated resource variation were not taken into account. Some studies on the diet of common dolphins have indicated that cetaceans tend to feed on similar prey sizes as the fishery (Marçalo et al.

2018), but we lack information for the other top predator species.

Relative consumptions calculations are sensitive to population size estimates. For marine mammal species these estimates were considered accurate, but for the seabird species, special attention is needed and estimates must be treated as 'order of magnitude' estimates rather than real, accurate estimates. Studies have successfully modelled seabird distribution based on at sea count data (Oppel et al. 2012, Studwell et al. 2017). Due to the high spatiotemporal mobility of birds and their foraging behaviour, modelling count data in order to produce accurate density or abundance estimates is a great challenge. A solution may include the combination of several modelling techniques (i.e. an ensemble modelling strategy; Oppel et al. 2012). Fishing effort might be underestimated due to the fact that the 2 h time interval of the VMS data is known to affect the accuracy of the identification of fishing trips and fishing sets (Katara & Silva 2017). However, general spatial patterns of fishing operations are not significantly altered, and VMS data seem to give a reasonable indication of the main areas where the fleet operates and where higher levels of overlap with the top predator species exist.

Goldsworthy et al. (2001) found that indices of resource overlap are sensitive to the taxonomic resolution of prey species groups. In this study, the sensitivity of these indices was not tested, but considering that resource overlap was determined at the family level, this grouping is expected to affect the results. When detailed information is available at the species level, these indices should be recalculated to evaluate their sensitivity to taxonomic resolution.

4.4. Conservation and management issues

Despite the above-mentioned limitations, due to the lack of fundamental knowledge regarding marine top predators and detailed data on fishing effort, our results provide crucial insights to support conservation and management strategies for the Portuguese marine ecosystem. Similar studies should be repeated regularly to evaluate changes in overlap indicators in time. The abundance of SPF fluctuates greatly in time, and any protection measure that might be implemented for any of the top predator species is expected to increase their total population size. Ongoing monitoring programs should continue, and new schemes should be developed to track population parameters and provide insights into the effects of competition with the fishery. The reproductive success of top predators needs to be monitored since this is one of the first parameters to affect population size (Crawford 2007). The aspect of marine habitat utilization should also be taken into account. Spatially explicit estimates of species density can inform species distribution and local abundance, but they lack information on what they are doing in those areas. Differences in levels of spatial and resource overlap can also arise from these patterns of utilization of the marine habitat.

The outputs of this study can be useful in the development of an ecosystem-based model for the effective management of the Portuguese purse seine fishery by taking into account the consumption of natural predators. Although still uncommon, one way to account for this type of information would be to integrate predation into the fish population assessment model. Studies (e.g. ICES 1997, Hollowed et al. 2000) suggest that predation mortality values assumed as part of the total natural mortality were underestimated prior to the calculation of consumption of a particular forage species. To facilitate implementation of an ecosystem-based model, one could calculate biological reference points (BRPs) that reflect and account for important ecological interactions such as predation (Tyrrell et al. 2011). The methods to incorporate predation mortality into quantitative determinations of BRPs exist across a wide range of applications (Tyrrell et al. 2011). However, with the generally insufficient data available (e.g. food habits, predators, abundance, food chains) one could at least use indirect approaches to estimate predation, that might suggest revisions to the natural mortality (where predation is included) or total mortality components of the assessment model.

In Portugal, several marine protected areas were recently proposed within the Natura 2000 network (e.g. Banco Gorringe marine site; EU 2018) according to the Habitats Directive and Birds Directive guidelines. With respect to the Habitats Directive and in the case of cetaceans, Natura 2000 sites must consider the species' population proportion of the member state population, the degree of conservation of habitat features important for that species, the isolation of the species population and a global assessment. With respect to the Birds Directive, the new Natura 2000 sites (Ministério do Ambiente, Ordenamento do Território e Energia 2015) were based on species which belong to Annex 1 of the Birds Directive or that are regular migrators, that have a high threat status and that represent more than 1% of the European population in the designated area. The Natura 2000 network does not exclude human activities and therefore management mechanisms are necessary. Management mechanisms within the Natura 2000 network can benefit from studies on fisheries overlap with predators, such as the present one, to advise on potential fishing effort regulations in particular areas (e.g. breeding colonies, high concentration areas, high bycatch areas) or periods of time (e.g. during reproduction periods). Fisheries overlap with predators could be integrated in a spatial planning analysis such as the Zonation software (Moilanen et al. 2009).

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