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Favorites and leftovers on the menu of scavenging seabirds: modelling spatio-temporal variation in discard consumption

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Abstract :

Fishery discards subsidise the food supply of a large community of scavenging seabirds, thus significantly influencing seabird ecology. Seabird preference for certain types of discards determines the number and composition of discards available for non-avian marine scavengers. To quantify both portions of discards temporally as well as spatially, we have used a modelling framework that integrates the spatial and temporal variation in seabird distribution, seabird attraction to fishing vessels and discard distribution. The framework was applied to a case study in the Bay of Biscay, where a wide variation in discard consumption was observed across seabird foraging guilds, discard types, periods and locations. Seabirds removed about one-quarter of the Bay of Biscay discards. The remaining sinking discards have limited potential to subsidize scavenging benthic communities on a large scale, but they may contribute substantially to scavenger diets on a local scale. Changes in food subsidies caused by discard mitigation measures, such as the 'landing obligation' in the European Common Fisheries Policy, are likely to have ecosystem effects on both scavenging seabirds and non-avian marine scavengers.

Keywords : predation, discard consumption, food subsidies, scavengers, seabirds

Résumé :

Les rejets de la pêche profitent aux populations d'oiseaux marins, et modifient leur écologie. Le prélèvement sélectif des rejets par les oiseaux affecte aussi la disponibilité de ces rejets pour les autres animaux marins nécrophages, comme les organismes mésopélagiques et benthiques. Cet article propose une approche pour estimer la consommation des rejets par les oiseaux marins en tenant compte des variations spatio-temporelles de la distribution des rejets et de celle des oiseaux, ainsi que celles de leur attraction par les navires de pêche. Cette approche, appliquée au golfe de Gascogne, montre de grandes variations de la consommation des rejets par les oiseaux marins, que ce soit entre guildes d'oiseaux, types de rejets, semestres, ou régions. A l'échelle du golfe les oiseaux prélèvent environ un quart des rejets totaux; ce qu'ils laissent et qui retourne à l'eau ne semble pas constituer un apport significatif aux communautés benthiques à cette échelle. A des échelles plus locales cependant, les rejets, s'ils parviennent au fond, pourraient fournir une contribution substantielle aux ressources de certains nécrophages benthiques. L'évolution de ces ressources sous l'effet de mesures de gestion des rejets, comme l'Obligation à Débarquer de la Politique Commune des Pêches de l'Union Européenne, pourrait avoir des conséquences écosystémiques concernant les oiseaux.

Mots-clés : predation, consommation des rejets, apport alimentaire, necrophages, oiseaux marins

1. Introduction

Fishery discards, a major food source for seabirds, significantly affect seabird ecology (Bicknell et al., 2013). Marine mammals such as dolphins and killer whales have also been observed scavenging from discards that float on the surface (Hill and Wassenberg, 2000; Luque et al., 2006) and scavengers in lower trophic positions consume sinking discards, with the greatest proportion of discards being consumed close to the seabed (Erzini et al., 2003). Although discards potentially represent a large portion of the diet of some fish species such as lesser spotted dogfish (*Scyliorhinus canicula*) and common hake (*Merluccius hubbsi*) (Laptikhovsky and Letisov, 1999; Olaso et al., 2002), studies of scavenging and predation upon discards are scarce (Raby et al., 2014). Little is known about the degree to which discards supplement the diet of scavengers in the water column or on the seabed (Olaso et al., 1998; Luque et al., 2006). Because discarded roundfish and cephalopods tend to float, they remain available to scavenging seabirds and scavengers in the water column, while less-buoyant flatfish and benthic invertebrates quickly sink to the seabed (Garthe and Hüppop, 1998; Hill and Wassenberg, 2000).

Once discards have reached the seabed, they may also be consumed by benthic invertebrates. One study of discard consumption in the North Sea estimates that they deliver only 1-3% of the annual secondary production of the macrobenthic community, thus limiting their potential to cause direct population effects (Groenewold and Fonds, 2000). Contrasting data from another North Sea study indicate that discards represent up to 21% of the energy needs of benthic scavengers, resulting in a substantial influence on their population dynamics (Catchpole et al., 2006). The different findings of both studies stress the need to better understand the underlying causes and the role of discards in benthic food webs. Meanwhile, new legislation aiming to reduce discarded biomass is being introduced in many jurisdictions, most notably the phased-in ‘landing obligation’ in Europe (EU, 2013). Such large-scale cutbacks in discarding practices may reduce the seabirds' food supply and may exhibit knock-on effects at several trophic levels (Heath et al., 2014*a*, 2014*b*; Fondo et al., 2015). To better understand these often-overlooked effects, a framework is needed that can account for the role of discards as a food source in the marine ecosystem (Sardà et al., 2015).

Scavenging seabirds have easy access to the water surface, giving them the first opportunity to consume fishery discards. Their selective discard consumption determines the composition and amount of food remaining for other scavengers. In general, seabirds take a large share but this varies according to region, season and scale (Garthe et al., 1996; Furness et al., 2007). The objective of this study was to partition all discards into two portions: those removed by seabirds versus those available to non-avian marine scavengers. Although this approach has been evaluated for vast areas such as the entire North Sea, local effects have either been ignored completely or have not been placed within a larger perspective (Catchpole et al., 2006; Furness et al., 2007; Fondo et al., 2015). Discarding patterns and bird abundance exhibit a wide variability in time and space at various scales (Uhlmann et al., 2014; Certain et al., 2007). Birds' relationship to fisheries also varies according to scale (Louzao et al., 2011; Cama et al., 2012), making the number of seabirds and the species composition of the flock scavenging around fishing vessels highly variable in space and time (Bartumeus et al., 2010). Furthermore, the abundance and heterospecific interactions of scavenging seabirds around fishing vessels invoke intra and inter-specific competition, which results in wide differences in discard consumption (Camphuysen and Garthe, 1997). In this study, a framework was developed to explicitly account for the spatial and temporal variability in bird presence and composition, and to examine whether this variation results in spatial and temporal differences in discard consumption. The spatial and temporal variability in discard consumption is then combined with spatial and temporal variation in fishery discards to calculate the number and composition of discards that become available to either seabirds or sea-dwelling scavengers.

This approach was applied to the Bay of Biscay, an area characterised by a high diversity in benthic and pelagic fish assemblages, fishing fleets and scavenging seabirds (Lorance et al., 2009). The focus was on the French fisheries which are comprised of bottom trawlers, *Nephrops* trawlers, gill netters, longliners and pelagic fisheries. This variety of fishing gears is mirrored in the variety of species targeted (from crustaceans to cephalopods to demersal and pelagic fish). The landings of the French fleet account for approximately 60% of the landings from this area (STECF, 2013) and are well documented via year-round monitoring of all discarded species (Fauconnet et al., 2011; Dubé et al., 2012; Cornou et al., 2013). Seabird distributions were documented using biannual ship-based and aerial surveys covering the French continental shelf of the Bay of Biscay (Certain et al., 2007; Pettex et al., 2014).

2. Materials and methods

The number of fishery discards consumed by scavenging seabirds depends intrinsically on a range of seabird and fishery related processes (Bartumeus et al., 2010; Furness et al., 2007; Bodey et al., 2014*a*). To quantify these processes, we first introduce the Bay of Biscay case study data in relation to seabird and fishery processes. Then we discuss the modelling framework that combines those processes. To end, we apply the framework to the case study data in order to estimate discard consumption in the Bay of Biscay and analyse the emerging spatial patterns.

2.1 The Bay of Biscay case study data

2.1.1 Scavenging seabirds and ship followers

Aerial and ship-based surveys have covered the French continental shelf of the Bay of Biscay (ICES Divisions VIIIa and VIIIb). Aerial monitoring was conducted in May – July 2012 (period 1) and December – February 2012 (period 2). Observations were performed by two observers during daylight hours only. Flight height was about 180 m above sea level at a speed of 90 knots. Visual census was accomplished under conditions of limited wave heights and wind speed $\leq$ 4 Beaufort. The resolution of taxon identification was at least between species and genus level, as detailed in Pettex et al. (2014: 18). Ship-based surveys were performed biannually (period 1: April – June; period 2: October – November) aboard the research vessel (RV) ‘Thalassa’ in 2009, 2010 and 2011 following the protocol outlined in Certain et al. (2011). Bottom trawl surveys took place in October – November (period 2) deploying a 36⁄47 GOV bottom trawl during 30 min hauls at 4 knots (see ICES (2010*a*) for further details). Trawling during pelagic surveys was conducted in April – June (period 1) with a pelagic trawl of 40 m (horizontal) by 20 m (vertical). Pelagic hauls were conducted at a speed of 4 knots and varied between 30 and 60 min with a duration of 45 min (Petitgas et al.,2011).

Number and identification of 'ship followers' (seabirds following fishing vessels with the main purpose of consuming discards) were recorded during ship-based surveys. Ship followers were registered during daylight and only when they occurred within a radius of 200 m around the RV. Numbers of seabirds were recorded at species level within five hours after hauling. During period 1 a total of 88 observations of ship followers were made and 212 during period 2. The number of hauls preceding registration of the number of ship followers by species was 1 or 2 (period 1) or 1 to 4 (period 2).

2.1.2 Experimental discard consumption by ship followers

Discard consumption by scavenging ship followers was examined during the bottom trawl survey aboard the RV 'Thalassa' (EVHOE, 4-17 November 2013). Fishing took place between 46° and 50° N and 4° and 11° W, according to the ICES protocol (ICES, 2010*a*). From 41 hauls, 69 standardised discard samples were prepared. Each sample contained a mixture of 75 roundfish (total length, TL: 9 - 31 cm) and 50 individuals of another discard type: cephalopods (N=22, mantle length: 3 - 18 cm), *Nephrops norvegicus* (hereafter called *Nephrops*) (N=22, carapace length: 1.8 - 4.4 cm) or boarfish (*Capros aper*) (N=25, TL: 9 - 17 cm) (see species list for the discard types in Table S1 in Supp. Mat. [1]). *Nephrops* was used as a proxy for benthic invertebrates, given the socio-economic importance of *Nephrops* trawling and the high discard levels in this fishery. Experiments took place immediately after hauling the gear, and consisted of randomly throwing a discarded individual into the sea during 5-min intervals. Bird species and plumage stage (juvenile to adult) and the type of discard (roundfish, cephalopod, *Nephrops* or boarfish) that the bird successfully captured were

[1] Supplementary material is available with the article through the journal website.

recorded. Species composition of the flock of ship followers was voice-recorded prior to and immediately after throwing each discard sample into the water.

2.1.3 Discard sampling

Fishery-dependent data from the French fishing fleet have been collected in the Ifremer onboard observer programme ‘Obsmer’ to fulfil the data requirements of the European Commission Data Collection Framework (EC, 2008*a*; 2008*b*). Catch sampling was stratified by metier and quarter. Metiers were defined by the European level 5 definition (EC, 2008*a*: 57-59), based on gear type, fishing area and target species assemblage. Landed and discarded numbers of each taxon were sampled by fishing operation. Subsamples were raised to the level of fishing operation, and then raised to trip level on the basis of sampled fractions (Fauconnet et al., 2011; Dubé et al., 2012; Cornou et al., 2013).

This study relies on discard and landing data from 2009, 2010 and 2011 in ICES Divisions VIIIa and VIIIb. The six metiers with the most discards were selected: (i) bottom trawlers targeting demersal fish and cephalopods (hereafter called ‘demersal trawlers’), (ii) bottom trawlers targeting crustaceans (‘*Nephrops* trawlers’), (iii) midwater trawlers targeting small pelagic fish (‘pelagic trawlers’), (iv) midwater trawlers targeting demersal fish and cephalopods (‘midwater trawlers’), (v) gill netters and (vi) longliners.

2.2 Modelling framework to estimate discard consumption by seabirds

In this modelling framework, estimates were made of (1) the densities of scavenging seabirds and the number of ship followers, (2) the Experimental Discard Consumption (EDC) by the ship followers and (3) the fishery discards (Figure 1). Subsequently, the discard consumption by seabirds was estimated from the fishery discards and the EDC for a discarded taxon l by a ship-following bird of taxon k. Estimates were calculated at experimental level (small letters) or fleet level (capital letters) for each location *i* and period *j*, as is explained in the following sections and equations.

2.2.1 Scavenging seabirds and ship followers

First, the density of scavenging seabirds was estimated for each bird taxon *k* in location *i* and period *j*. Scavenging seabirds were defined as seabird taxa that are frequently associated with fishing vessels and are known to consume discards. Then, the number of ship followers ($F_{i,j,k}$) was estimated for each location *i*, period *j* and bird taxon *k* from the bird densities ($B_{i,j,k}$), the number of fishing vessels ($V_{i,j}$) and the scavenging index ($S_{j,k}$) (equation 1).

$$F_{i,j,k} = \frac{S_{j,k} * B_{i,j,k}}{V_{i,j}} \quad [1]$$

The scavenging index is a time-specific measure that expresses the area over which a seabird searches for food discarded from fishing vessels rather than naturally-occurring sources (Furness et al., 2007) (equation 2).

$$S_{j,k} = \frac{\bar{F}_{j,k}}{\bar{B}_{j,k}} \quad [2]$$

where $\bar{F}_{j,k}$ is the mean number of ship followers and $\bar{B}_{j,k}$ the mean density of bird taxon *k* in period *j*. Assuming that birds are equally attracted to the vessel from all directions, the attraction radius of a bird to a vessel can be calculated as $\sqrt{(S_{j,k}/\pi)}$ (Skov and Durinck, 2001).

2.2.2 Experimental discard consumption by ship followers

Discard consumption of the ship followers was estimated for each discarded taxon *l* and bird taxon *k* as the ratio of the number of discards *c* that are consumed by seabird taxon *k* to the total number of discarded individuals *d* (Hudson and Furness, 1989; Camphuysen et al., 1995). This Experimental Discard Consumption (EDC) is given in equation 3.

$$EDC_{k,l} = \frac{c_{k,l}}{d_l} \quad [3]$$

2.2.3 Fishery discards at fleet level

Total trip discards of discarded taxon *l* were raised to total fleet discards using a ratio estimator with fishing effort as auxiliary variable. The discard raising procedure was applied in each location *i* and period *j* (equation 4).

$$D_{i,j,l} = \frac{E_{i,j}}{e_{i,j}} * o_{i,j,l} \quad [4]$$

where *D* is the total number of discards at fleet level and *o* is the number of discards observed during the on-board observer programme. Fishing effort (*E*, *e*) was estimated in days at sea.

2.2.4 Spatio-temporal variation in discard consumption by seabirds

To obtain an estimate of discard consumption at fleet level, the total number of discards was combined with EDC. Discard consumption is estimated for each seabird taxon *k* and discarded taxon *l* in units defined by location *i* and period *j* (Equation 5).

$$C_{i,j,k,l} = \frac{D_{i,j,l}}{d_l} * c_{k,l} \quad [5]$$

where *C* and *c* refer to the discard consumption, and *D* and *d* are the total number of discards. The total number of discarded individuals available to marine scavengers other than seabirds is subsequently calculated from equation 6.

$$R_{i,j,l} = \sum_l D_{i,j,l} - \sum_k \sum_l C_{i,j,k,l} \quad [6]$$

where R is the remaining fraction of discards of discarded taxon *l*, available to marine scavengers in the water at location *i* during period *j*.

2.3 The modelling framework applied to the Bay of Biscay case study

2.3.1 Defining the resolution of the case study application

To incorporate spatial and temporal differences in the modelling framework, the lowest resolution of the distributions of discards and seabirds had to be determined. The resolution of discard data limited inferences in space, while seabird data were temporally defined (i.e. biannual surveys). To standardise discard data, taxa were pooled into five discard types based on morphological similarities (Camphuysen et al., 1995): benthic invertebrates, cephalopods, depressiform fishes, flatfish and roundfish (Table S1 in Supp. Mat.[1], Nikolsky, 1963). Scavenger taxa were pooled into eight foraging guilds based upon similar morphology and discard foraging behaviour (Bicknell et al., 2013; Bodey et al., 2014*a*), i.e. gannets (Sulidae), large gulls, small gulls and terns (henceforth called small gulls), unidentified gulls, kittiwakes (*Rissa* sp.), procellariids (Procellariidae), storm petrels (Hydrobatidae) and skuas (Stercorariidae) (see species list in Table S2 in Supp. Mat.[1]). These guilds included all scavenging seabird species in the Bay of Biscay, except auks (Alcidae) and cormorants (Phalacrocoracidae) that do follow fishing vessels but only rarely consume fishery discards (Valeiras, 2003; Bicknell et al., 2013). Unidentified gulls in a spatio-temporal entity were attributed to either small or large gulls following the ratio of local densities of small to large gulls.

2.3.2 Scavenging seabirds and ship followers

Both aerial and ship-based data (pooled across all experimental years) were processed following the strip transect methodology, assuming that all species were recorded within a strip width of 200 m (aerial, Certain et al., 2008) or 300m (ship-based, Tasker et al., 1984). The densities of foraging guilds were estimated by ICES Statistical Rectangle (0.5° latitude by 1° longitude) to match the spatial distribution of discards. Density calculations were iterated 999 times using random resampling with replacement of bird observations to obtain the coefficient of variation (CV). Density estimates of the aerial and ship-based surveys were compared by calculating the log ratio of the densities in each rectangle and subsequently smoothing the log ratios with a two-dimensional spline, assuming normal errors and identity link. The fitted values were used to test whether the log ratio in each rectangle differed from zero (Fraser et al., 2008). Although both methodologies are common for bird census (Katsanevakis et al., 2012), significant differences between methodologies occurred for all foraging guilds. The limitations in taxon identification in aerial surveys did not hamper our guild-specific analysis (Pettex et al., 2014: 18), but the disturbance from and attraction to the ship-based platform may have created bias in the density estimates from ship-based surveys (Cama et al., 2012). Because the advantages of aerial surveys outweighed ship-based surveys for the purpose of this study, seabird distribution was based on the aerial surveys only.

The ship-based surveys were used to determine the biannual scavenging index and the number of ship followers. Each seabird taxon was assumed to be equally attracted to fishing vessels at all locations in the Bay of Biscay and across all fishing metiers, because there were not enough registrations of the number of ship followers to estimate rectangle and metier-specific scavenging indexes. To calculate the number of ship followers, the spatial distribution of fishing vessels was assumed to be homogenous within each rectangle.

2.3.3 Experimental Discard Consumption by ship followers

Experimental Discard Consumption (EDC) was calculated from the Bay of Biscay experiments. EDC estimates from the North Sea were used when Bay of Biscay estimates were absent (i.e. EDC of small gulls, flatfish and depressiform fishes: Table 1). When EDC and its variability were low for a particular foraging guild and discard type, we assumed that discard consumption in a spatio-temporal entity was only limited by whether the bird was determined to be a ship follower. In contrast, when EDC and its variability were high (EDC > 0.15; CV (EDC) > 0.5), the intra and inter-guild competition between ship followers was examined (see 'Model variability' in Figure 1). The thresholds for EDC and its CV were arbitrarily chosen. Inter-guild competition was divided into exploitation and interference competition. Exploitation competition does not reduce access to the resources (in this case, discards), whereas interference competition does reduce such access (Case and Gilpin, 1974). Gannets were considered to be interference competitors due to their socially dominant behaviour (Hudson and Furness, 1989). EDC was re-estimated by fitting a logistic regression curve to the predictor variables 'overall flock size', 'the natural logarithm of the number of birds of each foraging guild', the 'proportion of the scavenging birds in the flock of interference competitors' and 'proportion of the scavenging birds in the flock of exploitation competitors' (Lloyd et al., 1967) (Equation 7).

$$EDC_{k,l} = \log_e\left(\frac{p}{1-p}\right) = \beta_0 + \beta_n X_n \qquad [7]$$

where EDC is modelled as the probability of consuming a discarded individual of taxon *l* by seabird taxon *k* (*p* = 1 if consumed and 0 if not consumed), and β_0 is the intercept and β_n the coefficients for the predictor variables X_n. Logistic regression was based on a Generalised Linear Model (GLM) with logit-link function and quasi-binomial error distribution to account for over-dispersion. Collinearity between explanatory variables was examined using a variance inflating factor of two, while influential observations were removed using the Cook's distance. Models with a lower quasi-Akaike Information Criterion (QAIC) were selected if the ΔQAIC was >3. Models with ΔQAIC of <3 were deemed equal, and the most parsimonious model was selected.

For guilds that had low EDC variability during the Bay of Biscay experiments, but occurred in large flocks in the Bay of Biscay, we used parallel investigations from two data sources in the North Sea. The first series of experiments were conducted aboard the RV 'Belgica' in the southern North Sea (between 52° and 51°N; 1° and 2° E) in December 2011, February, April and December 2012, and April 2013. Gear and fishing specifications followed the outline described in Depestele et al. (2014). The experimental protocol largely followed the procedure of the Bay of Biscay experiments, except for the discard samples. Samples contained either 105 (December 2011) or 150 discarded individuals, composed by two-thirds sole (*Solea solea*; TL: 6-28cm) and one-third roundfish (*Merlangius merlangius* or *Trisopterus* sp.; TL: 9-31cm). A total of 150 experiments were performed. Consumption of depressiform fishes was also tested (Rajidae, N=52, TL: 30-163cm) by throwing an individual fish into the water (six experiments performed in December 2011). An additional data source from the North Sea was obtained from Camphuysen et al. (1995). Pooling the experiments from the North Sea and the Bay of Biscay allowed assessment of roundfish consumption by large gulls following the regression procedure outlined above (equation 7).

2.3.4 Fishery discards from the French fishing fleet

Total trip discards by discard type were raised to total fleet discards for each of the six metiers in the spatio-temporal entities defined below. Temporal strata were pooled into two periods to match seabird distribution data: April to September (period 1) and October to March (period 2). Spatial resolution was defined by merging rectangles to enable sufficient discard samples per spatial entity. Neighbouring rectangles were merged if reported landings were similar (based on visual inspection of histograms). Each entity was required to include a minimum of ten fishing operations from at least three trips because between-trip variability is generally larger than within-trip variability (Rochet et al., 2002). Mean sampling coverage of the fishing days in the spatial entities was 1.1% in period 1 and 0.5% in autumn for all metiers (Table S3 in Supp. Mat.[1]). This was comparable to the mean sampling coverage of the study area without the spatial segregation (period 1: 0.7%, period 2: 0.4%) and to other discard observer programmes (Rochet et al., 2002; Depestele et al., 2011).

2.3.5 Spatio-temporal variation in discard consumption by seabirds

Discard consumption by seabirds was applied to the fleet-based discard estimates in each period and rectangle. Discard consumption was not applied in rectangles beyond the limits of the experimental conditions, i.e. in four rectangles during period 2, comprising >150 ship following gannets or >220 large gulls. To identify which input variables contributed most to the variability in the output variable, the contribution of each input variable to the overall CV was approximated with the Taylor expansion, as described in the Delta method (Stratoudakis, 1999). The CVs of the number of ship followers and EDC were calculated as the ratio of the standard deviation to the mean of the experimental observations. The CVs of the bird density estimates were calculated from the resampling the observations (see above). The CVs of the discard estimates were calculated using the COST software (Vigneau, 2009, ICES, 2010*b*).

Conventional statistical parameters (mean, CV) were used to quantify the variability of seabird densities, ship followers, EDC and fishery discards. However, these statistics provide little detail on the resulting spatial pattern in discard consumption. The Moran's I index was used for spatial pattern analysis (Fortin and Dale, 2005). This index measures the correlation of univariate quantitative variables between spatial units such as the spatial correlation of foraging guilds or discards between rectangles. Moran's I indices range from clustered to dispersed patterns (+1 to -1), and were calculated for seven distance classes. The distance class was set at 110 km, the shortest distance between rectangle midpoints in the Bay of Biscay. Moran's I correlograms visualised the spatial correlation by plotting Moran's I index by distance classes (Borcard et al., 2011) and were plotted for foraging guilds, ship followers, fishery discards and discard consumption. The correlograms were categorised into three basic profiles depending on the significance of Moran's I at several distances: (i) autocorrelation only in the smallest distance classes ('patchy' distribution), (ii) positive autocorrelation in short distance classes coupled with negative values in large distance classes ('linear gradient') and (iii) no significant Moran's I coefficients ('random') (Diniz-Filho et al., 2003). To better understand the emerging pattern in the ship followers, the overlap coefficient *H* (Horn, 1966) was calculated for bird densities of each seabird taxon *k* and fishing vessels:

$$H_{i,j,k} = 2\frac{p_k p_V}{p_k^2 + p_V^2} \quad [8]$$

where p_k is the relative proportion of bird taxon *k* in location *i* and period *j* and p_V the relative proportion of fishing vessels. Proportions p_k and p_V were rescaled to a maximum of 1. This coefficient indicated an exact overlap of birds and fishing vessels at a value of 1, and a complete absence of overlap at zero.

3. Results

3.1 Scavenging seabirds and ship followers

Period 1 was dominated by high densities of large gulls in the northeastern and coastal parts of the Bay of Biscay; the densities were not significantly altered in period 2 ($Z = 1.68$, $P = 0.10$, $r = 0.14$). The densities of gannets increased significantly in period 2 ($Z = 2.65$, $P < 0.01$, $r = 0.23$) and were mainly located in ICES Division VIIIb.

The scavenging index and the attraction radius illustrated that large gulls were highly attracted to fishing vessels at all times of the year, while gannets, procellariids and skuas were especially attracted to fishing vessels during period 2 (Tables 2, S6). The number of ship followers (mean, SD) did not differ significantly between the first (61.5, 163.9) and period 2 (70.02, 132.4) ($Z = 0.89$, $P = 0.37$, $r = 0.03$), but its guild composition and spatial organisation did (Tables 2, 3, S6). Period 1 was dominated by large gulls with regular occurrence of gannets and procellariids in smaller numbers. The flock of ship followers in period 2 was dominated by large gulls and gannets (>100 individuals).

3.2 Experimental Discard Consumption by ship followers

Roundfish consumption was higher than the consumption of any other discard type (Figure 2, Table S4 in Supp. Mat.[1]) and varied with flock composition for large gulls and gannets. Roundfish consumption by gannets followed a logarithmic increase with the number of ship followers, which explained 76% (Pseudo-R^2) of model variability (Figure 3a, Table S5 in Supp. Mat.[1]). Roundfish consumption by large gulls also followed a logarithmic increase with increasing number of ship followers (Figure 3b), but this increase was counteracted by the relative abundance of other competitors (Figure 3c, d): large gulls were about three times less efficient in capturing discards with increasing relative abundance of gannets, and 1.4 times more efficient than other guilds. Both intra and inter-guild competition explained up to

62% (Pseudo-R^2) of the variability in roundfish consumption by large gulls (Table S5 in Supp. Mat.[1]).

3.3 Fishery discards from the French fishing fleet

In both periods, the largest number of discards (represented by benthic invertebrates and roundfish) was observed in the northeastern part of the Bay of Biscay (Figure 4, Figure S1 in Supp. Mat.[1]). Discarding was particularly apparent during period 1 in the rectangles coinciding with the 'Grande Vasière' area, a sedimentary mud bank of 12 000 km² which is known to be *Nephrops* fishing grounds (ICES Rectangles 24E5-6, 23E5-6, 22E6, 21E7 and 20E8). In both periods, benthic discards typically reflected the activity of *Nephrops* trawlers in the Grande Vasière. In period 1 roundfish discards came from *Nephrops* trawlers as well as pelagic and demersal trawlers in rectangles 21E5-8 and 21-23E7 (Figure 4, Figure S1 in Supp. Mat.[1]). In period 2 roundfish discards by *Nephrops* trawlers were concentrated in 23E6 and 24E5, while roundfish discards in all other rectangles were most numerous from demersal and pelagic trawlers.

3.4 Spatio-temporal variation in discard consumption by seabirds

3.4.1 Regional discard consumption

Over 500 million individuals were discarded in the Bay of Biscay, 27% of them were consumed by seabirds. Two-thirds of the discards occurred during period 1, but consumption by seabirds peaked during period 2, representing up to half of the discarded material. Both the higher number of discards and the lower discard consumption implied that a significantly higher number of discards became available to non-avian marine scavengers in period 1 ($W=1627$, $Z=3.7$, $P<0.001$, $r=0.31$), i.e. 287 million individuals or 77 % of all discarded individuals per year. Both periods showed a high spatial variation. Discard consumption ranged between 7 and 47 % of the total number of discarded individuals across rectangles in period 1, and between 17 and 85 % in the second. Almost none of the discarded benthic invertebrates were consumed by seabirds, making all of them available to scavengers in the sea. This contrasts strongly with the consumption of discarded roundfish (Figures 5, 6). In period 2 the proportion of roundfish consumed by seabirds (mean, SD) was significantly higher (0.69, 0.20) than in period 1 (0.40, 0.16) (W=222, Z=3.7, P<0.0001, r=0.32). This increase was mainly caused by the increased abundance of gannets following the ships, which accounted for >50 % of the consumption of roundfish in period 2.

3.4.2 Unexplained variation

Estimations of discard consumption by foraging guild and discard type were highly variable across rectangles and periods, as indicated by a mean CV of 4.34 (SD 2.62). Over 50% of the variation was due to the estimates for bird attraction (Table 2), while the estimates of EDC (Table S4 in Supp. Mat.[1]) and discards contributed at least to 30 % and 10 % of the variation and bird densities less than 5 %. Note that none of the CVs of the EDC estimates were <0.5 (Table S4 in Supp. Mat.[1]). The CVs of roundfish consumption by large gulls varied between 1.68 and 2.14 across rectangles. CVs for gannets varied between 1.97 and 2.17. Variation in roundfish consumption by large gulls and gannets contributed less to the overall variation in discard consumption (between 16 % and 30 % across rectangles and periods).

3.4.3 Spatial pattern analysis

The spatial patterns of discard consumption were predominantly patchy, reflecting the patchy distribution of the fishery discards, except for roundfish (Table 3). Roundfish consumption by seabirds imposed different patterns in the amount of discards that became available to scavengers in the sea. In period 1, roundfish discard distribution was patchy

(Moran's I of 0.27) while the main scavengers following ships were randomly distributed (Moran's I of 0.09 and -0.01 for gannets and large gulls). The pattern of roundfish discard consumption was also patchy (Moran's I of 0.20) and largely followed the distribution of roundfish discards (Figure 4, 5). The random distribution of large gulls following ships resulted from the patchy distribution of large gulls and the patchy distribution of fishing vessels (Moran's I of 0.22). Fishing vessels were concentrated in coastal regions, whereas large gulls also occurred further away from the coast, which is reflected in a highly variable overlap of seabirds and fishing vessels (Figure 7). In period 2, the spatial pattern of discard consumption was driven by a significant linear gradient of gannet densities, causing a shift of roundfish consumption towards the south. Gannets overlapped with fisheries distribution in some rectangles, but also occurred in high abundances in rectangles with few vessels (Figure 7).

4. Discussion

One-quarter of the discards from commercial fisheries in the Bay of Biscay were consumed by seabirds in 2009, 2010 and 2011. Great variability in discard consumption by ship followers was observed across foraging guilds, discard types, time periods and locations. The proposed framework for modelling the partitioning of discards consumed by seabirds and those left for sea-dwelling scavengers accounts for temporal and intra-regional spatial variability of discard consumption by scavenging seabirds. This increases our ability to estimate the order of magnitude by which discard partitioning affects biomass transfer through the food web (Catchpole et al., 2006; Kaiser and Hiddink, 2007). Despite these improvements to the framework, our estimates of discard consumption remain imprecise. In the following sections we discuss the main causes for this unexplained variation and recommend solutions. The last section illustrates the usefulness of a modelling framework to quantify the importance of spatial scale in estimating discard availability as a food source for scavenging seabirds and sea-dwelling scavengers.

4.1 A modelling framework for discard partitioning

In the 1990s, spatial and temporal variation of discard consumption by seabirds was experimentally demonstrated by conducting sea trials in different seasons and areas in the North Sea (Garthe et al., 1996). No comparable, large-scale programme has been undertaken since then, presumably for logistical and financial reasons. The alternative modelling framework presented here may alleviate the need for such resource-intensive large-scale programmes. However, the spatial and temporal variations of our results are conditional upon the framework assumptions, particularly those related to (i) the approximations used to estimate the number of ship followers in each spatio-temporal entity and (ii) the detection of variation in EDC. The potential sources of unexplained variation and methodological uncertainty are discussed for these two aspects, and solutions are suggested to deal with them.

4.1.1 Scavenging seabirds and ship followers

The overlap between bird densities and fishing vessels showed high variability (Figure 7). This increased the complexity of understanding the relationship between fishing vessels and seabirds at rectangle scale, hence complicating the estimation of the number of ship followers. The association between birds and fishing vessels is not fully understood in the Bay of Biscay (Certain et al., 2011), and the influence of fishing vessels on seabird movement patterns has only recently been shown in other regions (Bartumeus et al., 2010). The high variability in ship follower estimates was not surprising, as such variability has been reported in previous studies in the Bay of Biscay (Valeiras, 2003) and other regions (Louzao et al., 2011). Because of the limited number of observations in the present study, calculations of the number of ship followers were limited to biannual estimates at the scale of the entire Bay of Biscay. This implies that spatial variation in bird attraction to vessels was not accounted for. The larger number of ship following gannets in period 2 was likely due to winter migration of gannets into the Bay of Biscay (Kubetzki et al., 2009) which created a seasonal pattern in seabird-fishery interactions. Although the seasonal pattern was clearly detected, the complex spatial coupling between seabirds and fishing vessels was not so clear (Louzao et al., 2011). The unexplained variation in the number of ship followers is hypothesised to be largely due to spatial variation in birds being attracted to fishing vessels, creating the need for a rectangle-specific scavenging index.

The assumption that birds are equally attracted to fishing vessels across all rectangles ignored the actual foraging strategy of the birds. This may explain the high variation in the number of ship followers registered in this and other studies. A bird’s foraging strategy is hierarchically structured in large-scale areas and patches of Area-Restricted Search (ARS) behaviour nested within these large-scale areas (Fauchald, 2009). The locations and characteristics of the large-scale areas are strongly influenced by environmental features and their linkage with natural prey (50 km in the Bay of Biscay; Certain et al., 2011). Birds look for conspecifics or indicators of a concentrated food source (e.g. fishing vessels) to locate their prey indirectly within each of the large-scale areas and thus within the rectangles in this study (Pettex et al., 2010; Fauchald et al., 2011; Votier et al., 2011). This process, known as local enhancement, leads to increased foraging success along with increasing bird densities and densities of prey or indicators of food sources such as fishing vessels and hydrographic features promoting the availability of natural prey (Skov and Durinck, 2001; Grünbaum and Veit, 2003; Certain et al., 2011; Votier et al., 2013; Thiebault et al., 2014). A thorough understanding of these local processes is required to estimate rectangle-specific bird attraction, and may emerge from recent developments in coupling high-resolution fisheries data with seabird tracking data (Bodey et al., 2014*b*; Thiebault et al., 2014). Rectangle-specific attraction can be readily incorporated in the framework presented here; such additional data will likely reduce the major source of variability when estimating discard consumption by birds.

4.1.2 Experimental Discard Consumption

The variation of EDC was largely explained by intra and inter-guild competition when consumption of a discard type by a foraging guild was highly variable and higher than an arbitrary threshold. Indeed, the composition of the ship-following flock greatly affects a species' ability to capture discards, depending on their social behaviour and feeding strategy (Sotillo et al., 2014). The unexplained variation for other discard types than roundfish and/or for other foraging guilds than gannets and large gulls may also be caused by competition (Camphuysen and Garthe, 1997).

This study suggests that intra and inter-guild competition is the main driver of the variation reflected in the CVs, since other drivers of EDC variability were controlled for during the sea trials, namely the discharge rate and discard composition. The experimental discharge rate was fixed at 1 individual per 2.4 seconds during a 5-min interval to avoid over-estimation in discard consumption by testing single discarded individuals (Garthe and Hüppop, 1998). This discharge rate reflected discharge rates in gill net or long line fisheries, but may be lower than the pulsed discharges of metiers such as demersal and pelagic trawling. The discharge rate and the time interval between discarding events significantly affect EDC (Pierre et al., 2010) and may have induced bias in the estimates at fleet level. The size of the discarded individuals also significantly affects EDC for all discard types and foraging guilds. Gannets for instance prefer roundfish discards $\geq$ 25 cm, while kittiwakes can barely digest discards of this size (Garthe and Hüppop, 1998). The discard size ranges in the experiments generally matched the size ranges of the fleet discards, e.g. between 7 - 20 cm for roundfish in pelagic and 8-26 cm in *Nephrops* trawling (Table S7 in Supp. Mat.[1]). Size-specific EDC was not included in this study due to a lack of length measurements for all identified discard individuals (>400 taxa). The high diversity of discarded individuals also required separating the individuals into discard types (Garthe et al., 1996), and composition. Experimental discard composition consisted of 60% roundfish, which reflected the discard composition of demersal trawlers (approximately 60-70% roundfish discards) and gill netters in period 1, but less so for *Nephrops* or pelagic trawlers. The latter fisheries represented 17 % and 100 % of roundfish discards respectively. Roundfish discards consisted of a wide range of morphologies, including gadoids as well as compressiform fish (e.g. boarfish). EDC of compressiform fish differed greatly (Table S4 in Supp. Mat.[1]), but its effect on the overall consumption of the discards was limited in the Bay of Biscay, as compressiform fish contributed to less than 2 % of the discards at fleet level.

In conclusion, the major sources of EDC uncertainty are linked to metier-specific discarding practices, i.e. discharge rate, time between discarding events and discard composition (as a combination of discarded lengths and species-specific morphologies). The present study could not cover all metier-specific aspects; we therefore recommend that future experiments account for the variation of metier-specific discharging procedures as well as discard composition when estimating EDC. The effect of different discharging rates and discard composition may gain momentum particularly when changes occur as a consequence of the EU landing obligation (EU, 2013).

4.2 Spatial scale considerations when partitioning discards in the food web

Biomass discarded from commercial fishing vessels provides food to species that would otherwise not be able to access it. Discarding thus creates shortcuts in trophic relationships, in turn leading to higher productivity of the most efficient scavengers (Heath et al., 2014*b*). Seabird populations are directly affected by discarding practices (Votier et al., 2004). Whether discarding also leads to similar direct population effects for sea-dwelling scavengers requires a complex analysis. For instance population changes of benthic scavengers depend on the amount of biomass that is first removed by seabirds and the spatial scale at which the removal is estimated, as benthic scavengers are less mobile than seabirds and therefore less able to access all of the discards. A credible example below illustrates that the potential contribution of discards to the benthic scavenger's diet can vary according to spatial resolution.

In the Grande Vasière as a whole, scavenging benthic invertebrates represent about 21% of the total benthic biomass. Dominant species are *Nephtys caeca*, *Glycera rouxii*, *Natatolana borealis* and *Nephrops* sp. (Le Loc'h et al., 2008). The scavenger biomass totals approximately 60 000 tonnes (Ricciardi and Bourget, 1998; Le Loc'h et al., 2008). At a yearly consumption rate (Q/B) of 11.2, discards in the Grande Vasière may contribute to 1.6 % of the total food requirements of the scavenging benthic community, or 1.0 % after seabird predation (Lassalle et al., 2011). These calculations illustrate that discards have only a small potential to subsidise the food available to the benthic scavenging community in the Grande Vasière as a whole. Similar findings were presented for ICES Divisions VIIIa and VIIIb located in the Bay of Biscay (Lassalle et al., 2011), for an area of 125 000 km² covering parts of the central and southern North Sea (7% in Kaiser and Hiddink, 2007) and for the southern North Sea (1-3% in Groenewold and Fonds, 2000).

These findings contrast with those of Catchpole et al. (2006), who suggest that discards can lead to population increases of certain benthic scavengers. Their study area was confined to a local fishing ground of 2 504 km², where >80 vessels were occasionally concentrated at the same time. Extrapolating from that data, if all the discards in the Grande Vasière not eaten by seabirds were consumed by *Nephrops* alone, discarding could fulfil 14% of their food requirements. However, *Nephrops* trawling is mainly concentrated in the northern rectangles of the Grande Vasière (24E5, 23E5 and 23E6), with ~80% of the landings being caught there. Between 9% and 15% of the food requirements of *Nephrops* can be provided by discards in those rectangles, based on rectangle-specific estimates of *Nephrops* biomass inferred from commercial catches. In contrast, between 12% and 42% of the food requirements of *Nephrops* may be fulfilled by discards in the southern rectangles (20E8, 21E7 and 22E6) where bottom and pelagic trawling also largely contribute to discarded biomass (Figure 4, 5).

Unquestionably, several additional factors also affect the potential of discards to subsidise the food supply of certain species in the benthic food web. Some of these factors are composition, aggregation and competitive abilities of the scavenger community (Groenewold and Fonds, 2000), trawling-induced mortalities (Kaiser and Hiddink, 2007) and differences in survival potential between discarded taxa (Depestele et al., 2014). Although these aspects are not covered in the current study, the abovementioned examples show that on a large scale, discards contribute little to the food requirements of the total scavenging benthic communities (estimated at <2 % in the Grande Vasière), but on a local scale, they may provide a substantial contribution to the food requirements of certain scavengers (up to 42 % in certain ICES Rectangles). These results suggest that on a large scale, reductions in discards resulting from the landing obligation may affect the food availability of seabird communities more than benthic communities.

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Tables

Table 1. Data sources for estimates of Experiment Discard Consumption (EDC) by foraging guild and discard type. EDC estimates were based on experimental trials in the Bay of Biscay (BoB), except for the grey and hatched cells. Data sources of the grey cells were based on experiments in the North Sea (NS); hatched cells indicate experimental trials in the southern North Sea (IVc). EDC estimates of roundfish were modelled for large gulls and gannets (black bold rectangle). Note that assumptions are indicated by an asterix.

		Discard type				
		Cephalopods	Benthic invertebrates	Roundfish	Flatfish	Depressiform fishes
Foraging guild	Small gulls	BoB*	BoB*	NS	NS	BoB*
	Procellariids	BoB	BoB	BoB	NS	NS**
	Skuas	BoB	BoB	BoB	NS	NS**
	Kittiwakes	BoB	BoB	BoB	NS	**IVc**
	Large gulls	BoB	BoB	**IVc / NS**	NS	**IVc**
	Gannets	BoB	BoB	**BoB**	NS	NS*

*Assumed negligible; **approximated by other foraging guilds

Table 2. Mean number of ship followers, mean density, scavenging index and the attraction radius by foraging guild in the Bay of Biscay. The number of hauls, n(hauls), in which the ship followers occurred is indicated with totals of 88 and 212 records in periods 1 and 2, respectively. The scavenging index marks the area in which a foraging guild is attracted to a fishing vessel rather than to naturally-occurring food sources (Furness et al., 2007, Equation 2). CVs are given between brackets.

	Gannets	Large gulls	Small gulls	Kittiwakes	Procellariids	Storm petrels	Skuas
Period 1							
n(hauls)	43	72	11	1	31	5	15
n(Ship followers)	4.1 (2.07)	123.7 (1.88)	4.1 (5.59)	0.3 (10.67)	3.3 (2.58)	0.58 (7.41)	0.72 (3.33)
Density (n/km²)	0.12 (0.0050)	0.21 (0.0043)	0.07 (0.0014)	0.01 (0.0002)	0.06 (0.0031)	0.07 (0.0043)	0.01 (0.0002)
Scavenging index (km²)	34.2 (2.05)	589.0 (1.88)	58.6 (5.54)	30.0 (9.38)	55.0 (2.58)	8.3 (7.44)	72.0 (3.42)
Attraction radius (km)	3	14	4	3	4	2	5
Period 2							
n(hauls)	175	176	33	62	67	21	124
n(Ship followers)	109.4 (1.68)	144.0 (1.25)	0.4 (2.75)	5.0 (5.18)	4.9 (4.22)	0.8 (4.88)	3.2 (1.50)
Density (n/km²)	0.74 (0.0076)	0.26 (0.0083)	0.04 (0.0041)	0.17 (0.0031)	0.02 (0.0002)	0.04 (0.0010)	0.02 (0.0004)
Scavenging index (km²)	147.8 (1.68)	553.8 (1.25)	10.0 (3.14)	29.4 (5.16)	245.0 (4.26)	20.0 (4.98)	160.0 (1.50)
Attraction radius (km)	7	13	2	3	9	3	7

Table 3. Categorisation of spatial patterns in guild densities, the number of ship followers, fishery discards and discard consumption. Spatial patterns were categorised in three groups, based on Moran's I correlograms: linear gradient (dark grey cells), patchy (grey cells) or random pattern (white cells). The patchy pattern of scavenging seabirds, for instance, implies that animals are aggregated together while in a random pattern they do not. Patchy patterns may occur at several locations throughout the Bay of Biscay, while a linear gradient indicates that most aggregations are grouped in one location, such as the linear gradient for gannets in period 2 (see guild density of gannets in period 2 in Figure 4).

	Foraging guilds		Ship followers	
	Period 1	Period 2	Period 1	Period 2
Gannets	0.28*	0.35* -0.49*	0.09	0.35** -0.45*
Large gulls	0.21*	0.19*	-0.01	-0.02
Small gulls	0.22*	0.21	-0.08	0.01
Kittiwakes	0.25*	-0.12	0.26**	0.08
Procellariids	-0.04	0.52*** -0.13***	0.18*	0.38***
Stormpetrels	0.29**	0.46***	0.19	0.05
Skuas	0.07	0.13	0.17	0.10

	Fishery discards		Discard consumption	
	Period 1	Period 2	Period 1	Period 2
Roundfish	0.27**	0.05	0.20*	0.28**
Flatfish	0.23*	0.00	0.22*	0.00
Depressiform fishes	0.31**	0.47***	0.31**	0.47***
Cephalopods	0.20*	0.11	0.20*	0.11
Benthic invertebrates	0.12	0.08	0.12	0.08

Significance levels: * < 0.05, ** <0.01, *** <0.001

Figure captions

Figure 1. Modelling framework to estimate discard consumption by seabirds per location and time period. Equations (eq) are described in Section 2.2. Parallelograms present spatio-temporal input or output estimates; the rhombus refers to a decision process and rectangles to processing steps. Grey shaded areas were estimated at the scale of the Bay of Biscay: attraction to fishing vessels and Experimental Discard Consumption (EDC). When EDC was (> 0.15) and its Coefficient of Variation (CV) was high (> 0.5), the intra- and interguild competition was modelled to explain the variation in EDC.

Figure 2. Mean number of ship followers (upper) and mean EDC estimates (lower) of experimental discarding in the Bay of Biscay and the North Sea (sNS: southern North Sea, NS: North Sea). Number of ship followers and composition relate to the experiments in which discard types were discharged. Discard types included benthic invertebrates (B), cephalopods (C), depressiform fish (D), flatfish (FF) and roundfish (RF). Foraging guilds included skuas, small gulls, procellariids, kittiwakes, large gulls and gannets.

Figure 3. Probability of roundfish consumption for gannets (a) and large gulls (b, c, d). Probabilities are given in function of the number of ship-following gannets (a), ship-following large gulls (b), the proportion of interference competitors (c) and the proportion of exploitation competitors (d). The proportion of large gulls in the flock with interference competitors are indicated by a dotted (proportion =1), dashed (proportion=0.75) and solid line (proportion=0.05) in partial plots (b) and (d). The proportion of large gulls in the flock with exploitation competitors are also indicated in panel (c) by a dotted (proportion =1), dashed (proportion=0.5) and solid line (proportion=0.05).Black dots: Bay of Biscay, grey dots: North Sea, open circles: southern North Sea.

Figure 4. Numbers of discarded organisms and seabird densities (n/km²) during period 1 (upper panels) and period 2 (lower panels) in 2009, 2010 and 2011 in the Bay of Biscay. Discards are presented in numbers of discarded individuals (in millions; reflected by the pie chart sizes) by the major fishing metiers and by discarded type: roundfish (left panels) and all other discard types (middle panels). Seabird densities are presented in number per km² (reflected by the pie chart sizes in the right panels). Pie chart sizes in the upper and lower panels within each column have the same scale, but scales differ between columns.

Figure 5. Ship followers, consumption of discarded roundfish and discards which are available to non-avian marine scavengers during period 1 (upper panels) and period 2 (lower panels) in 2009, 2010 and 2011 in the Bay of Biscay. The size of the pie charts indicate the number of ship followers at a fishing vessel (two left panels), the number (in millions) of discarded roundfish that are consumed by a foraging guild (two middle panels) and the number of discards (in millions) which were not consumed and thus become a potential food source for sea-dwelling scavengers (two right panels). Predictions of roundfish consumption in the rectangles outlined with a dotted line were outside model boundaries and therefore disregarded (see ‘Materials and methods’ section). Benthic invertebrates were not presented because most of them are not consumed by seabirds (Figure 2, 6).

Figure 6. Partitioning the number of discarded items in the Bay of Biscay between the part that was consumed by seabirds and the remainder. Y-axes are expressed in number of discards (in millions). The total numbers of cephalopod (C), depressiform fishes (D) and flatfish (FF) discards respond to the primary axis; benthic invertebrates (B) and roundfish (RF) to the secondary axis. Hatched bars refer to period 2.

Figure 7. Box-and-whisker plots of the overlap coefficient of Horn (1966) of bird densities and number of fishing vessels by ICES Rectangles in the Bay of Biscay. Plots are presented by foraging guilds for period 1 (left) and period 2 (right). The boxes indicate the interquartile range (IQR, between 25^{th} and 75^{th} percentile). The line within the box represents the median and the whiskers mark the lowest and highest value within 1.5 * IQR. Outliers are plotted as individual points.

Figure 1

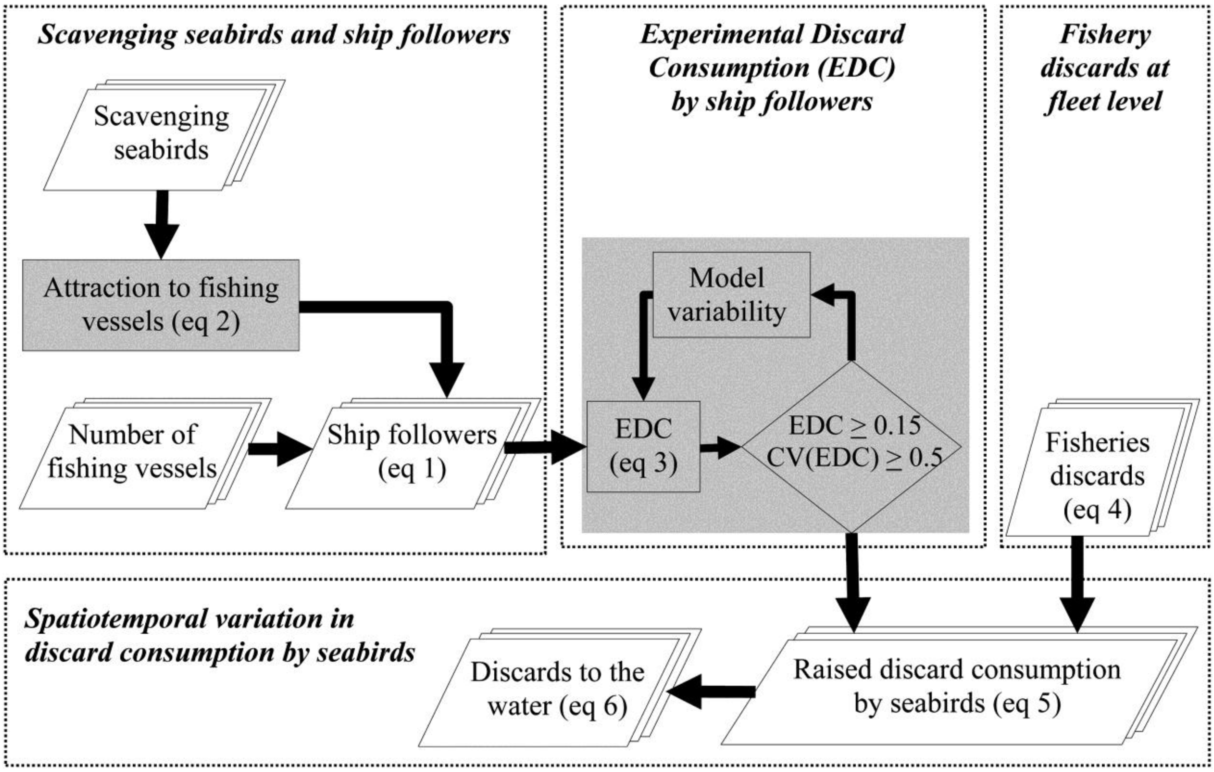

Scavenging seabirds and ship followers
Scavenging seabirds
Attraction to fishing vessels (eq 2)
Number of fishing vessels
Ship followers (eq 1)
Experimental Discard Consumption (EDC) by ship followers
Model variability
EDC (eq 3)
EDC ≥ 0.15
CV(EDC) ≥ 0.5
Fishery discards at fleet level
Fisheries discards (eq 4)
Spatiotemporal variation in discard consumption by seabirds
Discards to the water (eq 6)
Raised discard consumption by seabirds (eq 5)

Figure 2

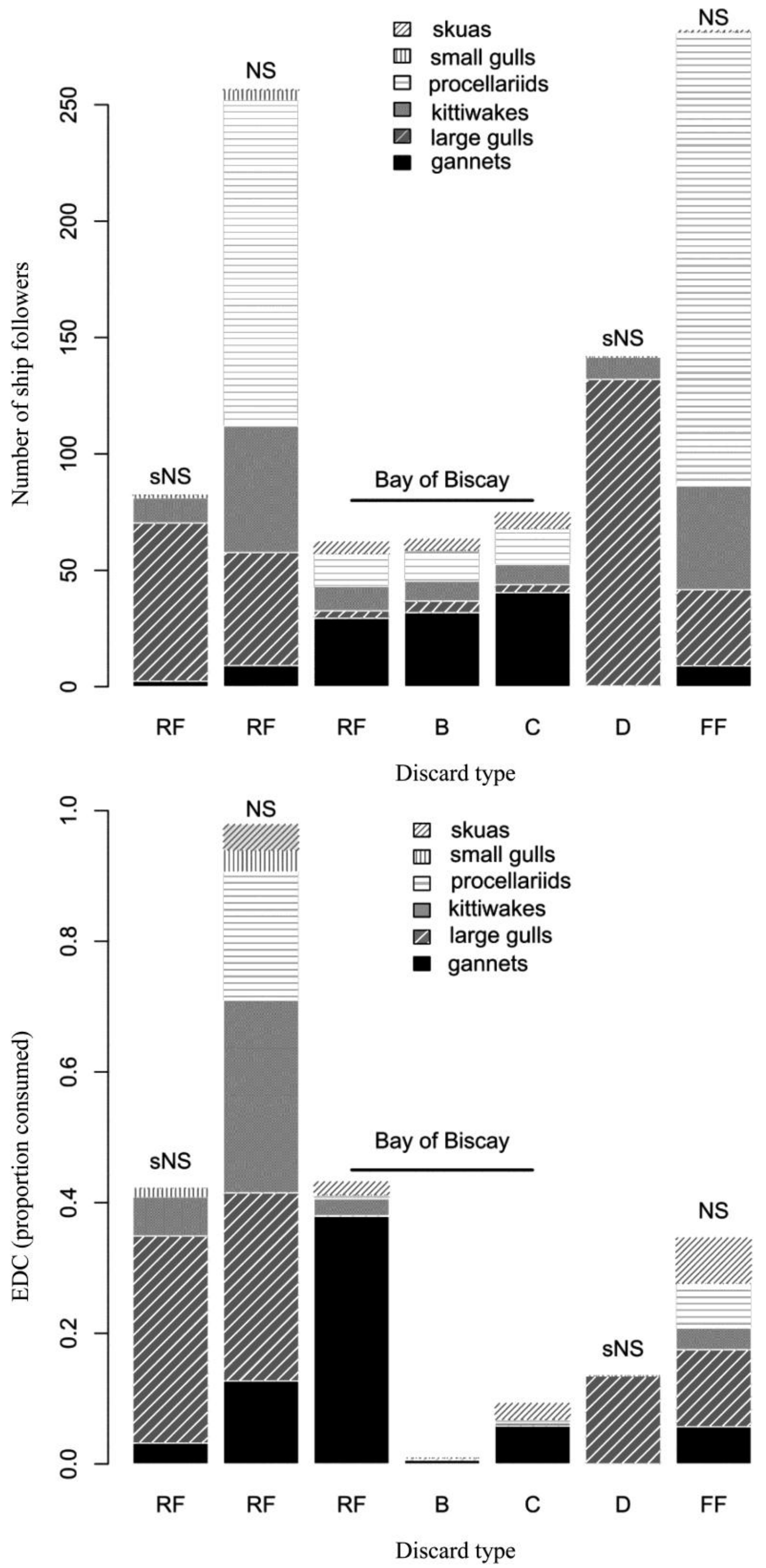
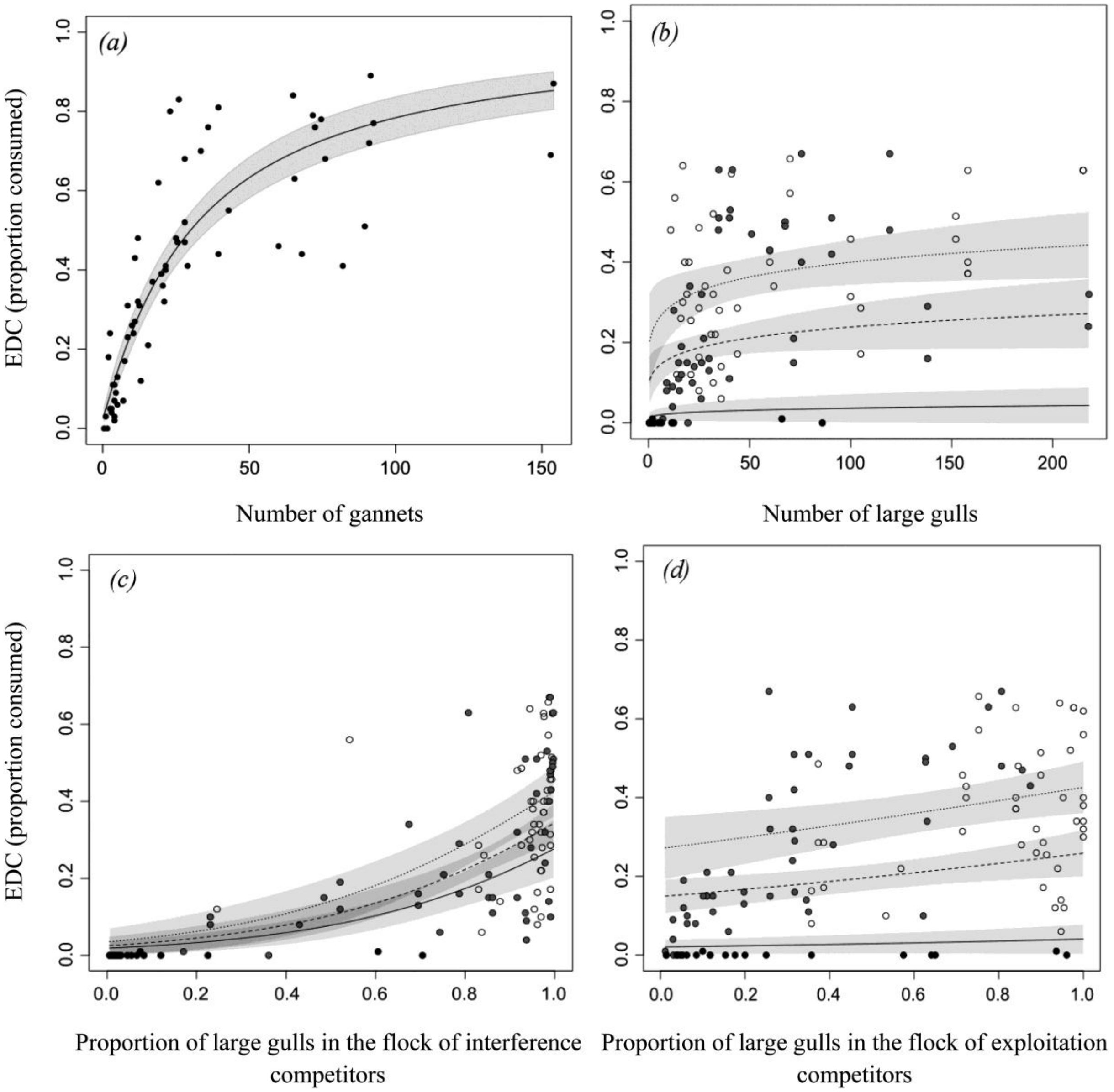

skuas
small gulls
procellariids
kittiwakes
large gulls
gannets
Number of ship followers
0
50
100
150
200
250
sNS
NS
Bay of Biscay
sNS
NS
RF
RF
RF
B
C
D
FF
Discard type
EDC (proportion consumed)
0.0
0.2
0.4
0.6
0.8
1.0
NS
skuas
small gulls
procellariids
kittiwakes
large gulls
gannets
Bay of Biscay
sNS
NS
sNS
RF
RF
RF
B
C
D
FF
Discard type

Figure 3



(a)
(b)
(c)
(d)
EDC (proportion consumed)
Number of gannets
Number of large gulls
Proportion of large gulls in the flock of interference competitors
Proportion of large gulls in the flock of exploitation competitors

Figure 4

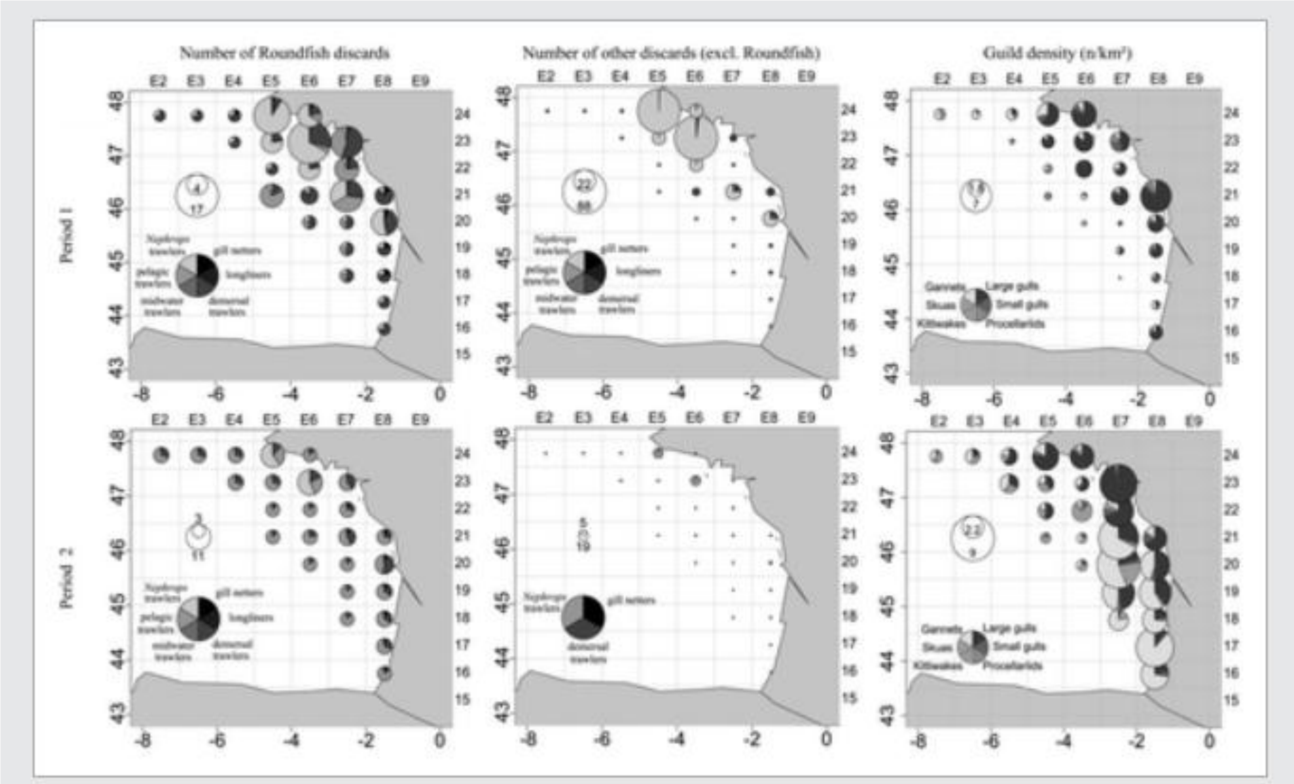


Figure 5

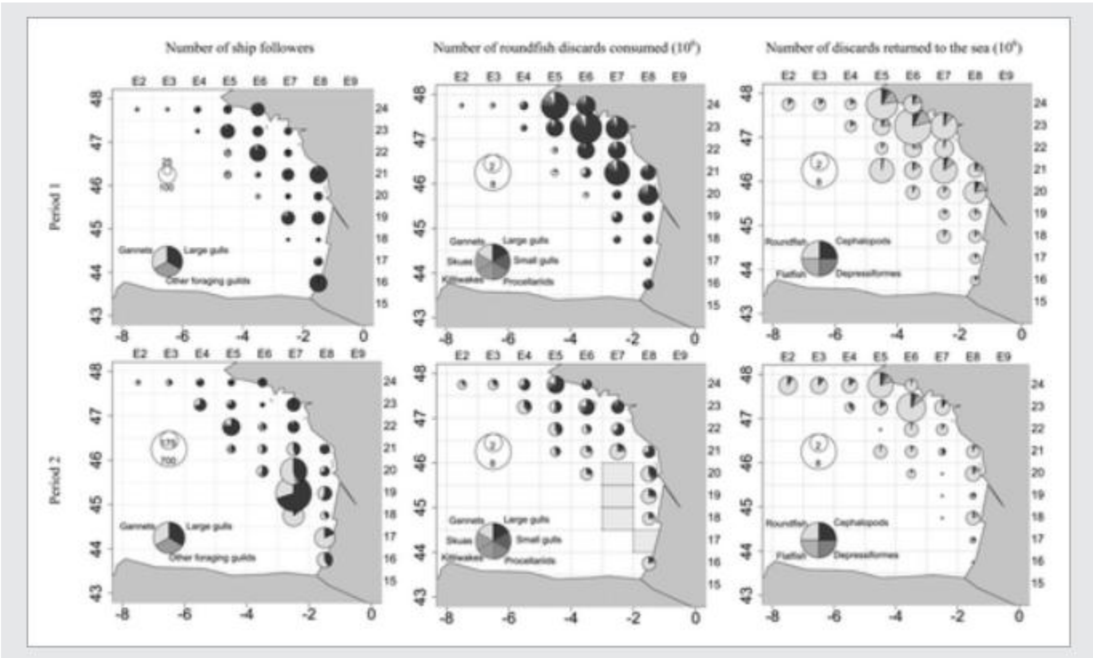
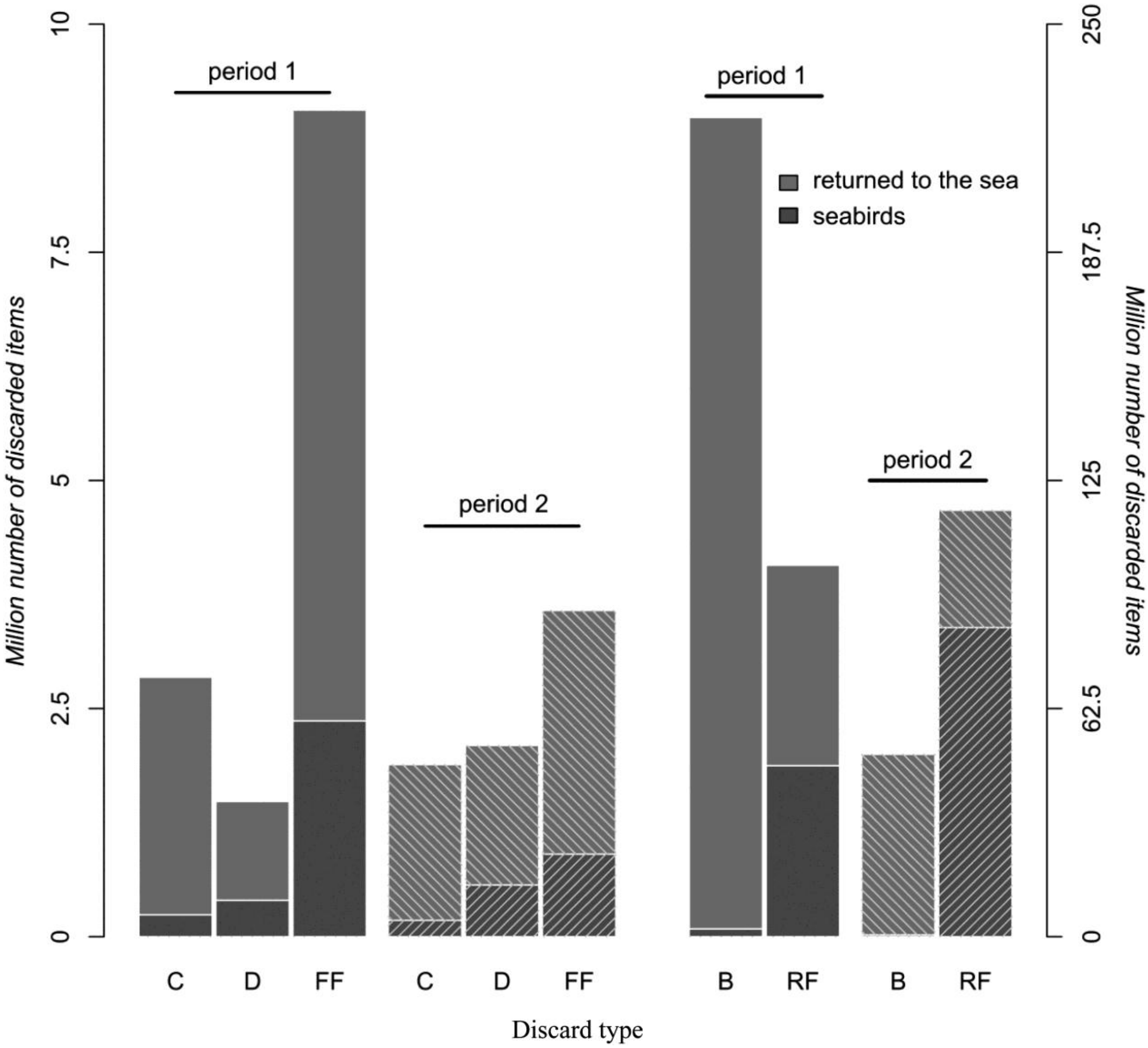
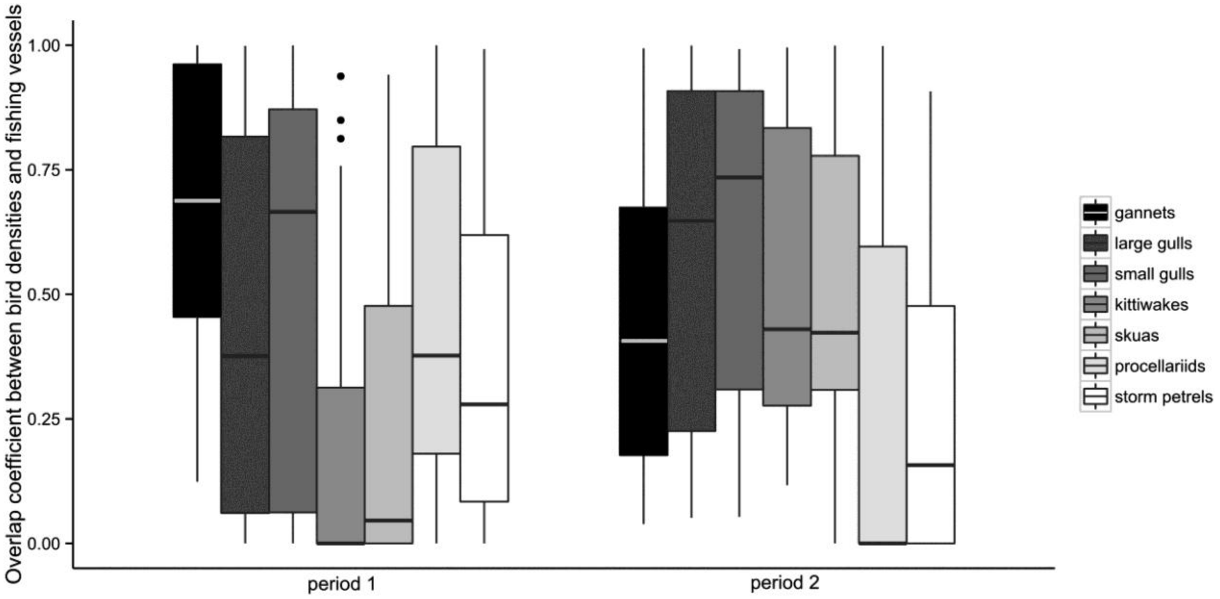


Figure 6



period 1
period 2
period 1
period 2
returned to the sea
seabirds
Million number of discarded items
Million number of discarded items
0
2.5
5
7.5
10
0
62.5
125
187.5
250
C
D
FF
C
D
FF
B
RF
B
RF
Discard type

Figure 7



Overlap coefficient between bird densities and fishing vessels
1.00
0.75
0.50
0.25
0.00
period 1
period 2
gannets
large gulls
small gulls
kittiwakes
skuas
procellariids
storm petrels

Supplementary material

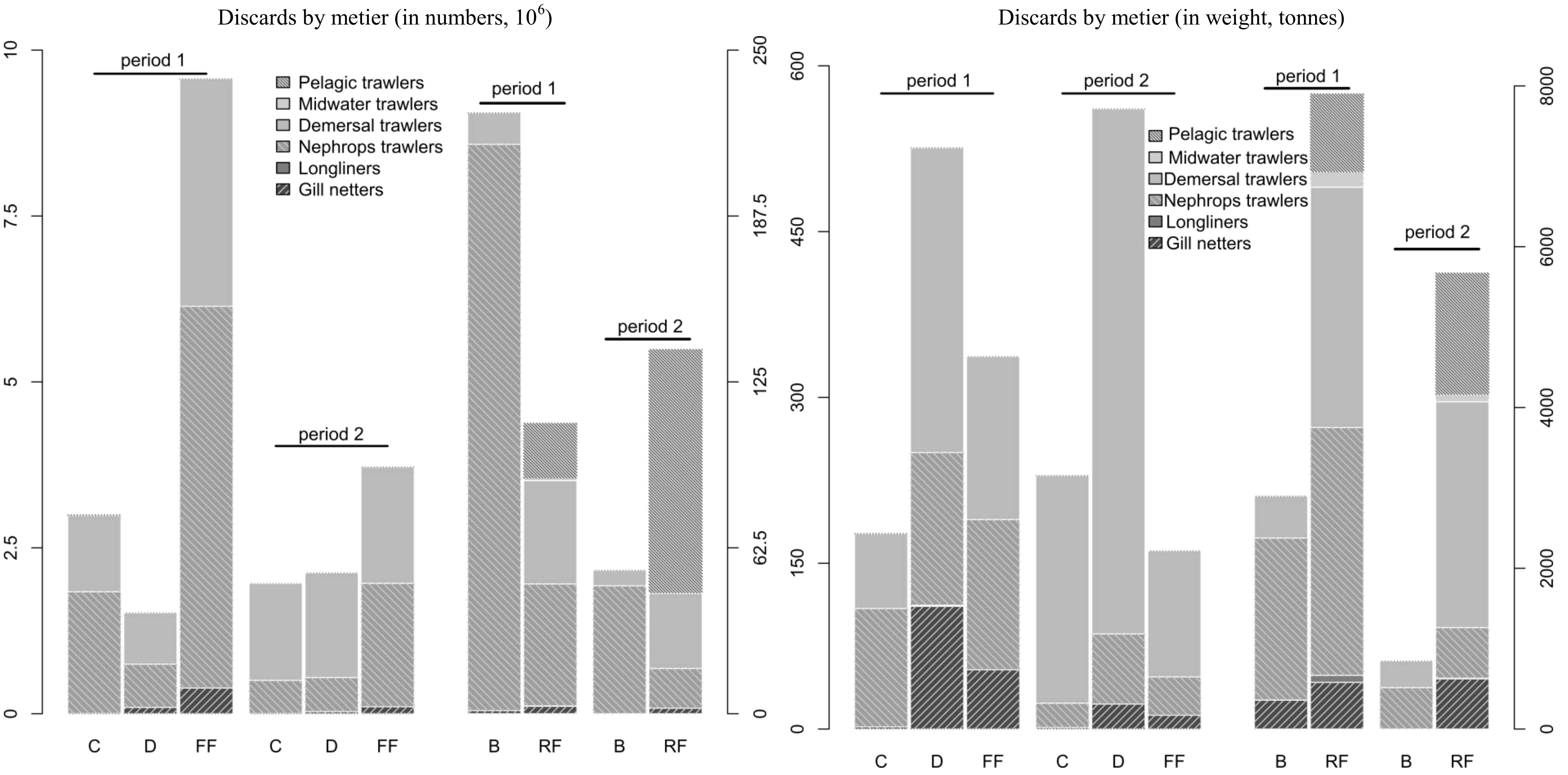


Figure S1. Discards by the six main fishing metiers in the Bay of Biscay. The total number of discards (left) are expressed in number of discards (in millions) (Y-axis). The total numbers of cephalopod (C), depressiform fishes (D) and flatfish (FF) discards respond to the primary axis; benthic invertebrates (B) and roundfish (RF) to the secondary axis. The total weight of discards (right) are expressed in tonnes. The primary axis relates to C, D and FF; while B and RF were reflected in the second axis.

Table S1. List of taxa included in the discard types (Section 2.3). Taxa in bold typeface were used in the experimental discarding study in the Bay of Biscay. Categorization was based on morphology which is related to the handling time of the scavenger.

Discard types	Taxa list
Benthic invertebrates	*Aequipecten opercularis*, *Aphroditidae*, *Asterias rubens*, *Atelecyclus undecimdentatus*, *Atrina pectinata*, *Buccinum undatum*, *Callinectes* sp., *Callinectes ornatus*, *Callista chione*, *Cancer pagurus*, *Carcinus maenas*, *Caridea*, *Caryophyllia (Caryophyllia) smithii*, *Cerastoderma edule*, *Chaceon affinis*, *Charonia lampas*, *Chlamys* sp., *Chlamys islandica*, *Corystes cassivelaunus*, *Crangon crangon*, *Crassostrea gigas*, *Crepidula fornicata*, *Crustacea*, *Dendrophyllia cornigera*, *Echinoidea*, *Echinus esculentus*, *Galathea*, *Galathea trigosa*, *Galatheidae*, *Glycymeris glycymeris*, *Goneplax rhomboides*, *Hippocampus* sp., *Hippocampus hippocampus*, *Homarus gammarus*, *Liocarcinus depurator*, *Liocarcinus navigator*, *Lutraria lutraria*, *Macropodia tenuirostris*, *Maja brachydactyla*, *Maja squinado*, *Marsupenaeus japonicus*, *Mimachlamys varia*, *Munida intermedia*, *Munida rugosa*, *Munnidae*, *Mytilus* sp., *Mytilus edulis*, *Natantia* sp., *Necora puber*, ***Nephrops norvegicus***, *Ostrea edulis*, *Pagurus alatus*, *Pagurus bernhardus*, *Palaemon serratus*, *Palinurus* sp., *Palinurus elephas*, *Palinurus mauritanicus*, *Panulirus laevicauda*, *Parapenaeus longirostris*, *Paromola cuvieri*, *Pecten jacobaeus*, *Pecten maximus*, *Polybius henslowii*, *Portunidae*, *Portunus* sp., *Psammechinus miliaris*, *Pteroeides griseum*, *Rhizostoma pulmo*, *Scyllarides delfosi*, *Scyllarus arctus*, *Scyphozoa*, *Solenidae*, *Squilla mantis*, *Tritonia hombergii*
Cephalopods	*Alloteuthis*, *Alloteuthis media*, *Cephalopoda*, ***Eledone* sp.*, Eledone cirrhosa, Eledone moschata***, ***Illex* sp.*, Illex coindetii***, ***Loligo* sp.*, Loligo forbesi, Loligo vulgaris***, *Octopodidae*, *Octopus* sp., *Octopus vulgaris*, *Ommastrephidae*, *Rossia macrosoma*, *Sepia* sp., *Sepia elegans Sepia officinalis*, *Sepia orbignyana*, *Sepiola* sp., *Sepiola affinis Sepiola atlantica*, *Teuthoidea*, *Todarodes sagittatus*, ***Todaropsis eblanae***
Depressiform fish (excl. flatfish)	*Amblyraja radiata*, *Dasyatis pastinaca*, *Dipturus batis*, *Dipturus oxyrinchus*, *Leucoraja circularis*, *Leucoraja fullonica*, *Leucoraja naevus*, *Lophiidae*,*Lophius* sp., *Lophius budegassa*, *Lophius piscatorius*, *Mobula hypostoma*, *Myliobatis* sp., *Myliobatis aquila*, *Raja* sp., *Raja asterias*, *Raja brachyura*, *Raja clavata*, *Raja microocellata*, *Raja montagui*, *Raja undulata*, *Rajidae*, *Rhinoptera bonasus*, *Torpedo*sp., *Torpedo marmorata*, *Torpedo nobiliana*, *Torpedo torpedo*
Flatfish	*Arnoglossus* sp., *Arnoglossus imperialis*, *Arnoglossus laterna*, *Arnoglossus thori*, *Buglossidium luteum*, *Citharus linguatula*, *Dicologlossa cuneata*, *Glyptocephalus cynoglossus*, *Hippoglossoides platessoides*, *Lepidorhombus* sp., *Lepidorhombus boscii*, *Lepidorhombus whiffiagonis*, *Limanda ferruginea*, *Limanda limanda*, *Microchirus* sp., *Microchirus variegatus*, *Microstomus kitt*, *Pegusa lascaris*, *Phrynorhombus norvegicus*, *Platichthys flesus*, *Pleuronectes platessa*, *Pleuronectiformes*, *Scophthalmus maximus*, *Scophthalmus rhombus*, *Solea* sp., *Solea senegalensis*, *Solea solea*, *Soleidae*, *Zeugopterus punctatus*
Roundfish	*Acanthostracion quadricornis, Agonus cataphractus, Alepocephalus, Alepocephalus bairdii, Alepocephalus rostratus, Alopias vulpinus, Alosa alosa, Alosa fallax, Ammodytes, Ammodytes marinus, Ammodytes tobianus, Ammodytidae, Anarhichas, Anguilla anguilla, Aphanopus carbo, Aphia minuta, Apogon nigrocincta, Apogon noumeae, Apristurus,* ***Argentina silus, Argentina sphyraena****, Argyropelecus olfersii, Argyrosomus regius, Aspistor quadriscutis, Atherina presbyter, Auxis rochei rochei, Bagre bagre, Balistes capriscus, Balistidae, Belone belone, Beryx decadactylus, Beryx splendens, Blennius, Blennius ocellaris, Boops boops, Brama brama, Brosme brosme, Callionymus, Callionymus lyra, Callionymus maculatus, Callionymus reticulatus,* ***Capros aper****, Carangidae, Caranx latus, Centrolabrus exoletus, Centrolophus niger, Centrophorus squamosus, Centroscymnus coelolepis, Centroselachus crepidater, Cepola macrophthalma, Cetorhinus maximus, Chelidonichthys, Chelidonichthys cuculus, Chelidonichthys lucernus, Chelidonichthys obscurus, Chelon labrosus, Chimaera monstrosa, Chlorophthalmus agassizi, Chromis chromis, Cichlasoma bimaculatum, Ciliata mustela, Clupea harengus, Coelorinchus caelorhincus, Coelorinchus labiatus, Conger, Conger conger, Coris julis, Coryphaenoides guentheri, Coryphaenoides rupestris, Ctenolabrus rupestris*

Table S1. (continued).

Discard types	Taxa list
Roundfish	*Cubiceps gracilis, Cyclopterus lumpus, Dalatias licha, Deania calcea, Dicentrarchus, Dicentrarchus labrax, Dicentrarchus punctatus, Diplodus annularis, Diplodus cervinus, Diplodus puntazzo, Diplodus sargus, Diplodus sargus cadenati, Diplodus vulgaris, Echiichthys vipera, Enchelyopus cimbrius, Engraulis encrasicolus, Entelurus aequoreus, Epigonus telescopus, Epinephelus itajara, Etmopterus princeps, Etmopterus spinax, Euthynnus alletteratus, Eutrigla gurnardus, Gadiculus argenteus, Gadiculus argenteus argenteus, Gadiformes, Gadus morhua, Gaidropsarus macrophthalmus, Gaidropsarus mediterraneus, Gaidropsarus vulgaris, Galeorhinus galeus, Galeus melastomus, Galeus murinus, Ginglymostoma cirratum, Gobiidae, Gobius niger, Gymnammodytes semisquamatus, Halargyreus johnsonii, Helicolenus dactylopterus, Heptranchias perlo, Hexanchus griseus, Hoplostethus atlanticus, Hoplostethus mediterraneus, Hoplostethus mediterraneus mediterraneus, Hydrolagus, Hydrolagus mirabilis, Hygophum benoiti, Hymenocephalus italicus, Hyperoplus lanceolatus, Isurus oxyrinchus, Katsuwonus pelamis, Labridae, Labrus, Labrus bergylta, Labrus mixtus, Lamna nasus, Lampetra fluviatilis, Lepadogaster, Lepidion eques, Lesueurigobius friesii, Lithognathus mormyrus, Liza, Liza aurata, Liza ramada, Liza saliens, Macroramphosus scolopax, Macrourus berglax, Malacocephalus laevis,* ***Melanogrammus aeglefinus****, Menticirrhus americanus, Merlangius merlangus,* ***Merluccius merluccius****,* ***Micromesistius poutassou****, Mola mola, Molva, Molva dypterygia, Molva macrophthalma, Molva molva, Mora moro, Morone saxatilis, Mugil, Mugil cephalus, Mugil curema, Mugilidae, Mullidae, Mullus, Mullus barbatus, Mullus surmuletus, Muraenesocidae, Mustelus, Mustelus asterias, Mustelus mustelus, Mustelus punctulatus, Myoxocephalus scorpioides, Neocyttus helgae, Nezumia aequalis, Osmerus eperlanus, Pagellus, Pagellus acarne, Pagellus bogaraveo, Pagellus erythrinus, Pagrus pagrus, Petromyzon marinus, Phycis blennoides, Phycis phycis, Pollachius pollachius, Pollachius virens, Polyprion americanus, Pomacanthidae, Pomacentridae, Pomatoschistus microps, Pomatoschistus minutus, Prionace glauca, Prionotus, Remora remora, Rhizoprionodon, Salmo salar, Salmo trutta fario, Salmo trutta trutta, Sarda sarda, Sardina pilchardus, Sarpa salpa, Schedophilus medusophagus + S. ovalis, Sciaena umbra, Scomber colias, Scomber japonicus,* ***Scomber scombrus****, Scomberesox saurus saurus, Scomberomorus, Scomberomorus brasiliensis, Scomberomorus regalis, Scombridae, Scorpaena, Scorpaena elongata, Scorpaena notata, Scorpaena porcus, Scorpaena scrofa, Scorpaeniformes, Scyliorhinidae, Scyliorhinus, Scyliorhinus canicula, Scyliorhinus stellaris, Scymnodon ringens,* ***Sebastes****, Sebastes norvegicus, Sebastidae, Seriola, Seriola carpenteri, Seriola rivoliana, Serranus, Serranus cabrilla, Sparidae, Sparus, Sparus aurata, Spondyliosoma cantharus, Sprattus sprattus, Squalidae, Squalus acanthias, Symphodus melops, Symphodus tinca, Synchiropus phaeton, Syngnathidae, Syngnathus acus, Taurulus bubalis, Thunnus, Thunnus alalunga, Thunnus albacares, Thunnus obesus, Thunnus thynnus, Trachinus draco, Trachinus radiatus, Trachipterus arcticus, Trachipterus trachypterus, Trachurus, Trachurus mediterraneus, Trachurus picturatus,* ***Trachurus trachurus****, Trachyrincus murrayi, Trachyrincus scabrus, Trachyscorpia cristulata cristulata, Trachyscorpia cristulata echinata, Triakidae, Trichiurus lepturus, Trigla, Trigla lyra, Triglidae, Trigloporus lastoviza,* ***Trisopterus****, Trisopterus esmarkii, Trisopterus luscus, Trisopterus minutus, Umbrina canariensis, Umbrina cirrosa, Xiphias gladius, Zenopsis conchifer, Zeus faber*

Table S2. Pooling of seabird scavenging taxa in foraging guilds. Categorisation was based on morphology and discard foraging behaviour.

Foraging guilds	Taxa
Sulidae	*Morus bassanus*
Large gulls	*Larus fuscus, Larus maritimus, Larus argentatus, Larus michahellis, Larus cachinnans, Larus hyperboreus*
Small gulls	*Larus minutus, Larus melanocephalus, Larus sabini, Larus canus, Larus ridibundus, Sterna* sp.*, Sterna albifrons, Sterna hirundo, Sterna paradisaea, Sterna sandvicensis, Sterna dougallii*
Unidentified gulls	*Larus* sp., which could not be classified as large or small gull
Rissa sp.	*Rissa tridactyla*
Procellariidae	*Calonectris diomedea, Fulmarus glacialis, Calonectris* sp.*, Puffinus* sp.*, Puffinus gravis, P. griseus, P. puffinus, P. mauretanicus, Thalassarche melanophris*
Hydrobatidae	*Hydrobates* sp., *Hydrobates pelagicus*, *Oceanites* sp., *Oceanodroma* sp., *Oceanodroma leucorhoa*
Stercorariidae	*Stercorarius* sp.*, Stercorarius skua, Stercorarius parasiticus, Stercorarius pomarinus*

Table S3. Data used in this study for the major metiers in the Bay of Biscay. Samples were aggregated across ICES Statistical Rectangles to ensure a sufficient number of samples per spatio-temporal entity. (i) bottom trawls targeting demersal fish and cephalopods (TB-DEF), (ii) bottom trawls targeting crustaceans (TB-CRU), (iii) midwater trawls targeting small pelagic fish (TM-SPF), (iv) midwater trawl targeting demersal fish and cephalopods (TM-DEF), (v) gill nets *sensu latu* (GN-DEF) and (vi) longlines (LLS-DEF).

		Sampling characteristics			Reported fleet characteristics		Sampling coverage (%)		Discarded proportion (roundfish)
	Spatial sites	Number of hauls (trips)	Fishing days	Landings (kg)	Fishing days	Landings (t)	Fishing days	Landings	
period 1									
GN-DEF	16E8, 17E8	40 (22)	26	3270	3368	593	0.77	0.55	0.22
GN-DEF	18E8, 19E8, 20E8, 21E8	444 (115)	132	3611	22606	3893	0.58	0.09	0.29
GN-DEF	24E4, 23E6, 21E7, 22E7, 23E7	246 (49)	67	13117	12257	2426	0.55	0.54	0.56
GN-DEF	24E5, 24E6	57 (13)	16	1836	9375	2053	0.17	0.09	0.29
GN-DEF	Remainder*	38 (12)	19	9575	2913	2039	0.65	0.47	0.10
LLS-DEF	24E5, 23E5, 24E6, 18E6, 21E6, 22E6, 23E7, 20E8	314 (33)	32	3482	16067	4466	0.20	0.08	0.13
LLS-DEF	Remainder*	29 (6)	6	436	5146	2652	0.12	0.02	0.24
TB-CRU	23E5, 22E5, 24E6, 21E7, 20E8	108 (36)	51	20211	13344	5748	0.38	0.35	0.38
TB-CRU	24E5, 23E6	87 (37)	38	12648	21894	7230	0.17	0.17	0.24
TB-CRU	Remainder*	48 (23)	30	9078	6264	2056	0.48	0.44	0.50
TB-DEF	21E6, 21E7, 20E8, 21E8	206 (57)	62	19562	19371	7866	0.32	0.25	0.46
TB-DEF	23E6, 23E7	91 (21)	21	7255	11748	4728	0.18	0.15	0.59
TB-DEF	24E2, 24E3, 23E4, 24E4, 24E5	155 (18)	68	58214	8184	7249	0.18	0.15	0.70
TB-DEF	Remainder*	83 (33)	42	13722	12580	7666	0.33	0.18	0.78
TM-DEF	21E7, 22E7, 23E7, 20E8	30 (12)	20	3314	1515	1423	1.32	0.23	0.93
TM-DEF	24E4, 24E5, 23E6	29 (4)	13	12876	327	516	3.98	2.49	0.10
TM-DEF	Remainder*	10 (5)	9	4968	1184	813	0.76	0.61	0.39
TM-SPF	20E6, 18E6, 19E6, 20E7	18 (9)	8	18365	258	916	3.10	2.01	0.25
TM-SPF	15E8, 16E8, 17E8, 18E8, 19E8, 20E8	25 (13)	13	21213	396	643	3.28	3.30	0.12
TM-SPF	21E5, 21E7, 22E7, 23E7	87 (23)	26	95922	4436	11338	0.59	0.85	0.15
TM-SPF	23E6, 24E6	38 (22)	18	104242	1133	2690	1.59	3.87	0.02
TM-SPF	Remainder*	31 (14)	14	59360	398	1819	3.52	3.26	0.13

*The remainder category includes all other rectangles in ICES Division VIIIa/b not listed for the investigated metier.

Table S3. (continued).

		Sampling characteristics			Reported fleet characteristics		Sampling coverage (%)		Discarded proportion (roundfish)
	Spatial sites	Hauls (trip)	Fishing days	Landings (kg)	Fishing days	Landings (t)	Fishing days	Landings	
period 2									
GN-DEF	16E8, 17E8	69 (33)	31	6132	2960	838	1.05	0.73	0.39
	18E8, 19E8, 20E8, 21E8	453 (114)	140	40353	12226	4239	1.15	0.95	0.40
	22E6, 23E6, 24E6, 20E7, 23E7	198 (49)	44	9537	7992	2723	0.55	0.35	0.09
	21E7, 22E7	20 (6)	12	7792	7567	3708	0.16	0.21	0.16
	Remainder*	23 (12)	14	1905	3534	2189	0.40	0.09	0.27
LLS-DEF	24E4, 24E5, 24E6, 23E6, 23E7, 21E8, 20E8	15 (3)	3	226	7219	2953	0.04	0.01	0.02
	Remainder*	13 (5)	5	876	4123	2338	0.12	0.04	0.11
TB-CRU	24E5, 23E6	93 (37)	44	10339	12958	3519	0.34	0.29	0.36
	Remainder*	12 (8)	9	1374	5679	1643	0.16	0.08	0.23
TB-DEF	17E8, 18E8, 19E8	102 (18)	37	19231	5012	4740	0.74	0.41	0.58
	20E8	67 (16)	26	2869	5397	2715	0.48	0.11	0.47
	21E6, 21E8, 22E7	29 (13)	13	2892	7683	4669	0.17	0.06	0.55
	23E6, 23E7, 21E7	32 (10)	14	8465	13789	8256	0.10	0.10	0.57
	24E2, 24E3, 24E4, 24E5, 23E4, 23E5	164 (17)	57	57897	18555	9813	0.31	0.59	0.61
	Remainder*	30 (14)	19	8107	7173	5057	0.26	0.16	0.59
TM-DEF	21E7, 22E7, 23E7	18 (10)	10	14381	1781	2038	0.56	0.71	0.05
	Remainder*	33 (9)	18	13820	1551	1443	1.16	0.96	0.15
TM-SPF	All rectangles	26 (9)	9	51403	2025	6625	0.44	0.78	0.44

*The remainder category includes all other rectangles in ICES Division VIIIa/b not listed for the investigated metier.

Table S4. Mean number of scavenging seabirds and mean EDC estimates (CV) for the Bay of Biscay experiment and experiments in the North Sea (1: experiments on-board Research Vessel 'Belgica', 2: Camphuysen et al., 1995). Storm petrels did not consume any discarded individuals.

		Bay of Biscay experiments				southern North Sea[1]		entire North Sea[2]	
		Roundfish	Boarfish	Cephalopods	Norway lobster	Roundfish	Depressiformes	Roundfish	Flatfish
Number of scavenging seabirds	Gannets	29.4 (1.16)	15.1 (1.00)	40.4 (0.99)	31.8 (1.14)	2.4 (3.63)	0.3 (3.33)	9.1 (1.24)	9.0 (1.21)
	Large gulls	3.2 (4.28)	0.8 (3.13)	3.5 (3.69)	5.0 (3.72)	67.9 (0.97)	131.7 (0.39)	48.5 (1.01)	32.7 (0.90)
	Small gulls	-	-	-	-	1.1 (1.45)	-	4.0 (1.33)	0.1 (-)
	Kittiwakes	10.6 (1.27)	15.1 (1.00)	8.6 (1.52)	8.6 (1.33)	10.9 (1.29)	9.7 (0.51)	54.4 (1.26)	44.6 (1.55)
	Procellariids	13.9 (1.50)	13.0 (0.80)	15.6 (1.71)	13.2 (1.67)	-	-	140.23 (1.05)	194.8 (0.80)
	Skuas	5.1 (0.86)	3.9 (0.90)	6.7 (0.75)	4.8 (0.85)	-	-	0.4 (2.50)	0.8 (1.63)
	Storm petrels	0.3 (3.33)	-	0.6 (2.67)	0.3 (2.00)	-	-	-	-
	Flock size	62.2 (0.53)	47.8 (0.35)	74.7 (0.48)	63.5 (0.56)	82.3 (0.83)	142.3 (0.36)	254.7 (0.79)	295.8 (0.67)
		Bay of Biscay experiments				southern North Sea[1]		entire North Sea[2]	
		Roundfish	Boarfish	Cephalopods	Norway lobster	Roundfish	Depressiformes	Roundfish	Flatfish
EDC estimates	Gannets	0.379 (0.73)	0.048 (1.90)	0.058 (1.55)	0.006 (2.83)	0.032 (2.09)	-	0.127 (1.10)	0.057 (0.54)
	Large gulls	0.001 (3.00)	0.004 (3.00)	0	0.002 (3.00)	0.317 (0.93)	0.135 (-)	0.288 (0.78)	0.118 (1.25)
	Small gulls	-	-	-	-	0.013 (1.31)	-	0.032 (3.31)	<0.01 (-)
	Kittiwakes	0.026 (1.54)	0	0.005 (2.40)	0.001 (5.00)	0.060 (1.18)	0	0.295 (0.80)	0.033 (0.94)
	Procellariids	0.006 (2.50)	0.001 (7.00)	0.005 (4.20)	0	-	-	0.197 (1.14)	0.068 (0.90)
	Skuas	0.020 (2.00)	0.006 (3.00)	0.025 (2.08)	0	-	-	0.04 (1.73)	0.07 (1.51)
	Total flock	0.421 (0.62)	0.055 (1.69)	0.093 (1.13)	0.008 (2.25)	0.370 (0.78)	0.135 (-)	0.793 (0.24)	0.199 (0.79)

Table S5. Explanatory factors of EDC variability of roundfish: parameters estimates with standard errors (S.E.) and p-values for the final model for gannets and large gulls.

	Parameter estimate (S.E.)	*t-value*	*p-value*
Gannets			
Intercept	-3.74 (0.29)	-12.75	<0.0001
Log(gannets +1)	1.09 (0.08)	12.16	<0.0001
Large gulls			
Intercept	-4.79 (0.46)	-10.37	<0.0001
Log(large gulls+1)	0.23 (0.10)	2.30	<0.05
Proportion of large gulls in the flock with interference competitors	3.02 (0.54)	5.49	<0.0001
Proportion of large gulls in the flock with exploitation competitors	0.69 (0.26)	2.71	<0.001

Table S6. Effect size (r) of differences in number of ship followers between seasons within a bird category (diagonal), between bird categories in period 2 (values above diagonal) and in period 1 (values below diagonal). Non-significant results are indicated in bold (α = 0.05).

	Gannets	Large gulls	Small gulls	Procellariids	Storm petrels	Skuas	Kittiwakes
Gannets	r=0.51	r=0.13	r=0.73	r=0.63	r=0.74	r=0.56	r=0.62
Large gulls	r=0.58	**r=0.10**	r=0.74	r=0.66	r=0.75	r=0.60	r=0.66
Small gulls	r=0.38	r=0.71	**r=0.02**	r=0.21	**r=0.08**	r=0.47	r=0.19
Procellariids	**r=0.12**	r=0.63	r=0.26	**r=0.06**	r=0.26	r=0.25	**r=0.01**
Storm petrels	r=0.48	r=0.76	**r=0.12**	r=0.37	**r=0.07**	r=0.50	r=0.25
Skuas	r=0.36	r=0.72	**r=0.05**	r=0.23	r=0.18	r=0.37	r=0.24
Kittiwakes	r=0.54	r=0.78	r=0.22	r=0.43	**r=0.12**	r=0.27	r=0.30

Table S7. Length ranges (min-max) of the main discarded species and discard types (bold) in the Bay of Biscay in 2010 (modified from Fauconnet et al., 2011). Total length is measured for fish, carapax length for *Nephrops norvegicus* and mantle length for cephalopods. The maximum lengths were subdivided into the maximum length of >10,000 individuals and the overall maximum length in brackets.

	Reported species	*Length range (cm)*	*Reported species*	*Length range (cm)*
Demersal trawlers	**Roundfish**	**10-43 (57)**	**Cephalopods**	**3-30(32)**
	Mackerel	19-33 (37)	Cuttlefish	3-12(19)
	Whiting	10-22(36)	Squid	4-30(32)
	Hake	15-43(57)	**Flatfish**	**7-21(27)**
	Pouting	10-39 (39)	Sole	7-21(27)
	Monkfish	11-30 (35)		
	Horse mackerel	10-19 (36)		
Nephrops trawlers	**Roundfish**	**8-26 (27)**	**Invertebrates**	**13-33 (42)**
	Hake	18-23 (33)	Norway lobster*	1.3-3.3 (4.2)
	Monkfish	8-20 (57)	**Flatfish**	**8-23 (25)**
	Pouting	9-26 (27)	Sole	8-23 (25)
	Red mullet	11-(16)	**Cephalopods**	**3-(12)**
	Horse mackerel	10-15 (36)	Squid	3-(12)
	Whiting	9-(27)		
Midwater trawlers	**Roundfish**	**8-33 (52)**	Pollack	(34)
	Monkfish	8-33 (39)	**Elasmobranchs**	**8-43 (50)**
	Haddock	15-33 (40)	Cuckoo ray	8-43 (50)
	Red gurnard	13-29 (34)	**Flatfish**	**10-34 (42)**
	John dory	12-(27)	Megrim	10-34 (42)
	Horse mackerel	8-30 (40)	**Cephalopods**	**5-(18)**
	Whiting	13-30 (40)	Squid	5-(18)
	Hake	14-(43)		
	Cod	20-(52)		
Pelagic trawlers	**Roundfish**	**7-20 (92)**		
	Anchovy	10-17 (19)	Sardine	13-(24)
	Mackerel	8-20 (45)	Chub mackerel	11-(27)
	Horse mackerel	7-16 (43)	Sprat	8.5-13.5 (16.5)
	Garfish	29-(92)	Blue whiting	13-(61)
	Seabass	44-(62)	Hake	18-(54)
Gill netters	**Roundfish**	**13-26 (93)**	**Invertebrates**	**6-(17)**
	Pollack	27-(36)	Spiny spider crab	6-(17)
	Hake	18-(93)	**Flatfish**	**16-23 (67)**
	Black sea-bream	25-(32)	Sole	16-23 (67)
	Meagre	18-(67)	Sand sole	20-23 (38)
	Seabass	20-(51)	Senegalese sole	21-(33)
	Pouting	13-26 (49)	Plaice	16-(37)
	Whiting	16-(49)	Wedge sole	17-(24)
Longliners	**Roundfish**	**22-34 (74)**	Garfish	73-(74)
	Seabass	34-(35)	Pouting	20-(30)
	Whiting	22-34 (37)	**Elasmobranchs**	**42-(47)**
	Mackerel	26-(35)	Blonde ray	42-(47)