Deliverable 4.5

Report:

Quantifying food subsidies to the benthos due to discards

Task 4.4 Report on the quantification of discard flow to the seabed, relative to natural food sources.

Due date of deliverable: month 24 (September 2014)

Due date of report: month 24

Actual submission date: month 26

Coordination: Jochen Depestele (ILVO) & Marie-Joëlle Rochet (ifremer)

(Partner 2, ILVO, Belgium & Partner 7, Ifremer, France)

Main Contributors:

Jochen Depestele

(Partner 2, ILVO, Belgium)

Marie-Joëlle Rochet, Pascal Laffargue

(Partner 7, Ifremer, France)

Eric Stienen

(Research Institute for Nature and Forest, INBO)

Ghislain Dorémus

(Université de La Rochelle, Observatoire PELAGIS, France)

SUMMARY

Discards generated from marine fisheries have significantly affected species populations and community composition of seabirds through mechanisms such as competition, predator–prey interactions and nutrient transfer. Our understanding of the fate of discards beyond seabird scavenging is fragmented, but it is likely that similar mechanisms come into play. This study contributes in resolving this knowledge gap by quantifying the amount and composition of discards that become available to scavengers other than seabirds. The key was nevertheless found in revealing seabird discard consumption, as seabirds are likely the first in taking profit of fishery discards due to their high mobility. Their selective consumption determines the composition and amount of food remaining for others.

The consumption of discards by scavenging seabirds was assessed for the French fishing fleet in the Bay of Biscay. Experimental sea trials were conducted to assess the proportion of discards consumed by foraging guild and discard type. Experimental discard consumption (EDC) was raised to fleet level by foraging guild using the total number of discards by discard type. The raising procedure accounted for the spatio-temporal variability of both foraging guilds and discards, by standardising both distributions to their lowest common resolution. Discards limited inferences in space, whilst the highest temporal resolution was determined by the biennial monitoring of foraging guilds. As EDC of roundfish by Large gulls and Gannets varied considerably, we investigated the main drivers. Consumption increased logarithmically with the number of ship followers for both guilds, but was greatly impaired by competitors for Large gulls. Competition between Large gulls and Gannets reduced the roundfish consumption by threefold, while other guilds such as Kittiwakes, Procellariids and Skuas had only a limited though significant influence. As Large gulls dominated during the first semester (April to September), the consumption of discards and notably roundfish was dictated by this foraging guild. The abundance of ship following Gannets was remarkably higher in the second semester (October to March). This change in flock composition and in numbers of ship followers implied an increase in the consumed proportion of roundfish of 27.9%. The total number of discards that became available to non-avian scavengers was however higher in the first semester, as more discards were produced during this period. Most discards comprised benthic invertebrates, but excluding this discard type revealed that over two thirds of the discards remained roundfish.

TABLE OF CONTENTS

1 INTRODUCTION

Discards generated from marine fisheries are a major food source for seabirds and have been demonstrated to significantly affect seabird ecology (Bicknell et al., 2013). Other marine scavengers also feed upon discards. Elasmobranchs and marine mammals have been scavenging from discards floating on the sea surface or in the water column (Hill & Wassenberg, 2000; Pon et al., 2012). Data on discard consumption in the water column are scarce and its significance on population level is unclear. Once discards have reached the seafloor, they may be consumed by demersal fish and benthic invertebrates (Shephard et al., 2014). In the North Sea for instance, model predictions predicted that discarded carrion from bottom trawl fisheries had only a minimal contribution to benthic invertebrate dynamics. Discards only compensate for 7% of the reduction in benthic biomass production caused by trawling damage (Kaiser & Hiddink, 2007). If positive population effects on benthic scavengers are to be expected from discards, then it was suggested that only pelagic fisheries may cause this contribution. Another study in the North Sea, by contrast, calculated that discards from Nephrops bottom trawling provided up to 37% of the energetic requirements of scavengers (Catchpole et al., 2006). Bottom trawl discards may thus influence scavenger population dynamics, being it on a local scale. The comparison of both studies highlights that our understanding of the fate of discards remains fragmented, and by consequence also our insights in its population effect. Resolving this knowledge gap is imperative for the evaluation of the ecological effects of discard management measures (Borges et al., 2014; Heath et al., 2014), such as a partial discard ban proposed by the European Commission (EC, 2011).

This study contributes in resolving this knowledge gap by quantifying the amount and composition of discards that become available to scavengers other than seabirds. The key however to unravelling discard availability for other scavengers is found in revealing seabird discard consumption. Scavenging seabirds travel long distances in search of food, and tend towards energetically inexpensive locomotion. Their high mobility allows them to be first in taking profit of fishery discards and their selective consumption determines the composition and amount of food remaining for others. Seabirds consume a high proportion of discards with a strong preference for items that are easy to swallow such as roundfish and avoidance behaviour towards species with protrusions, such as benthic invertebrates. While this approach was evaluated for vast areas such as the entire North Sea, local effects may have been levelled off (Catchpole et al., 2006; Furness et al., 2007). Local effects can be due to a range of causes, not in the least spatial discard variability. Very little is known on spatial distribution of discards and this is a likely reason why it was not accounted for in earlier scavenging studies. Changes in discard policies may however prompt changes in the spatio-temporal availability of discards and hence food for scavengers (Rochet et al., 2014). Understanding where and when this food becomes available is thus paramount to gain insights in scavengers' ecology, as well as how much can be attributed to different taxa in different compartment of the ecosystem.

This study explores the possibility of quantifying discard consumption by seabirds on a finer spatial scale than region-wide and presents a framework for quantification. The focal area is the Bay of Biscay (ICES Divisions VIIIa and VIIIb). The investigated fisheries are French fisheries that contribute

the major part of discards in this area, including bottom trawlers, Nephrops trawlers, gill netters, longliners and pelagic fisheries.

2 MATERIAL AND METHODS

2.1 INVESTIGATING DISCARDS AS A FOOD SOURCE

The consumption of discards by scavenging seabirds was assessed using experimental discarding studies, which established a clear link between the number of discards returned to the sea and the number swallowed by seabirds (Arcos & Oro, 2002). Empirical investigations were conducted in the Bay of Biscay to assess the proportion of discards consumed by seabirds (Section 2.2). Experimental discard consumption was raised to fleet level by foraging guild using the total number of discards by discard type. Both the occurrence of foraging guilds and discards varied in space and time. Incorporating these spatio-temporal differences in the raising procedure required that the spatio-temporal distributions of discard types and foraging guilds were standardised by the lowest resolution of either distributions. Discards limited inferences in space, whilst the highest temporal resolution was determined by the biennial monitoring of foraging guilds. Spatio-temporal distribution of the number of ship followers by foraging guild was estimated in several steps. First the spatio-temporal distribution of each foraging guild was determined. Second, we estimated the attraction of seabirds to fishing vessels by foraging guild. The spatio-temporal distribution of the ship followers by foraging guild was subsequently calculated from the spatio-temporal distribution of guild densities and guild-specific attraction to fishing vessels. Once the spatio-temporal distribution was estimated by discard type and foraging guild, we raised the experimental consumption to a region-wide, but spatio-temporally explicit estimate of discard consumption by seabirds. The above described pathway is summarized in Figure 1.
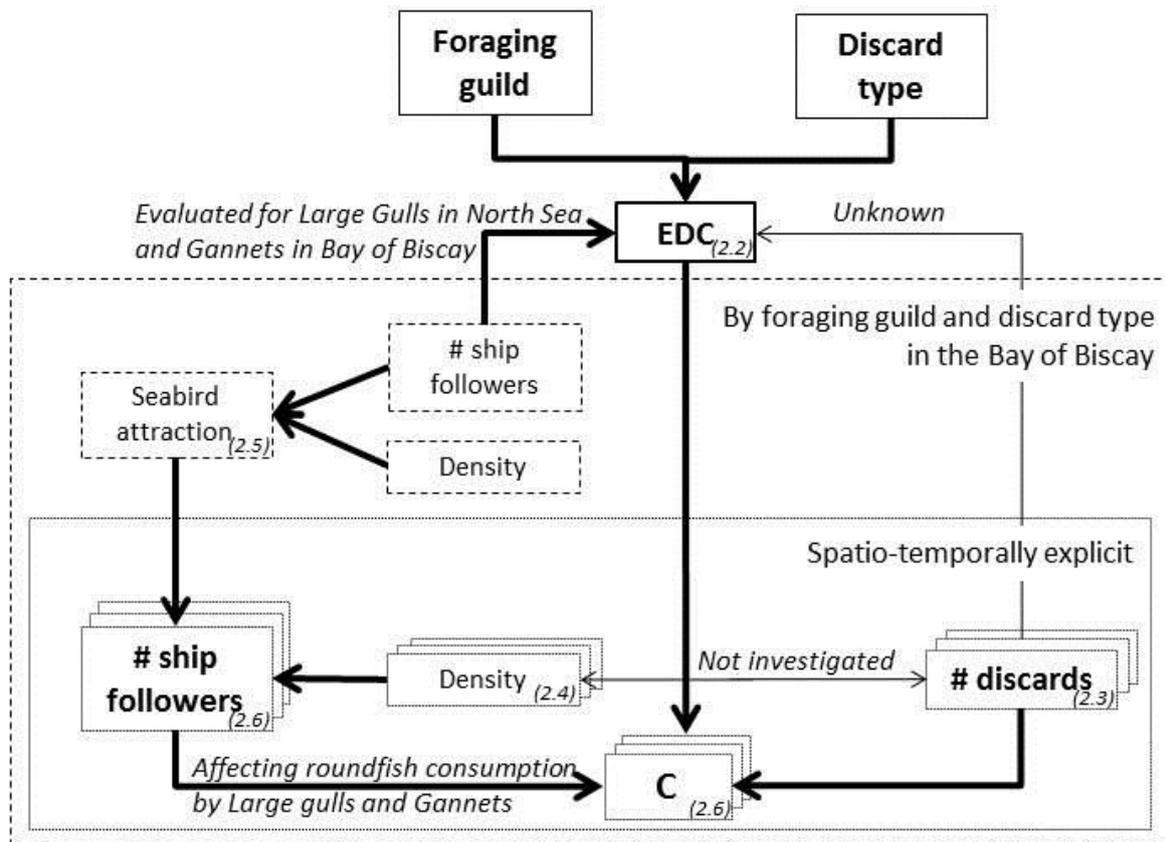
Figure 1 - Pathway of the mechanistic model for the estimation of spatio-temporally explicit discard consumption at fleet level (C) from Experimental Discard Consumption (EDC). Numbers between brackets refer to Material and Methods Sections.

2.2 EXPERIMENTAL DISCARD CONSUMPTION (EDC) BY SEABIRDS

2.2.1 REQUIREMENTS FOR RAISING EDC TO FLEET LEVEL

Experimental discard consumption (EDC) was evaluated as a discard proportion, i.e. the number of discards swallowed to the total number of items thrown. EDC was assessed by (1) discard type and (2) scavenger taxa, following previous approaches (Furness et al., 2007). Discarded items were pooled into five discard types upon morphological similarities (Camphuysen, 1994): benthic invertebrates, cephalopods, depressiform fishes, flatfish and roundfish (Section 0). Pooling was required to enable inferences of experimental discard consumption to fleet level, which comprised >400 discarded taxa. Scavenger taxa were pooled into eight foraging guilds upon similar morphology and discard foraging behaviour (Bicknell et al., 2013; Bodey et al., 2014): Gannets (Sulidae), Large gulls, Small gulls, Unidentified gulls, Kittiwakes (Rissa sp.), Procellariids (Procellariidae), Storm petrels (Hydrobatidae) and Skuas (Stercorariidae) (see species list in Table A 1). These guilds include all scavenging seabird species in the Bay of Biscay, except Auks (Alcidae) and Cormorants (Phalacrocoracidae). They were ignored because of rare occurrences as ship followers (this study; Valeiras, 2003) and rare discard consumers (Käkelä et al., 2007). EDC estimates were based upon

experiments in the Bay of Biscay. When Bay of Biscay estimates were absent, we assumed transferability of EDC estimates from the North Sea.

Previous studies assumed that raising EDC to fleet level increased linearly with increasing number of scavengers (Furness et al., 2007). This linear increase may however level off if discard consumption is hampered by the number of ship followers (intra-guild competition) (Sotillo et al., 2014) or by competition with other foraging guilds (inter-guild competition) (Camphuysen & Garthe, 1997). EDC variability due to intra and inter-guild competition was high for the most eligible discard types consumed by large flocks of ship followers, i.e. roundfish consumption by Gannets and Large gulls in this study (Section 2.5).

2.2.2 *EXPERIMENTAL DISCARD CONSUMPTION*

Experiments were conducted during the International Bottom Trawl Survey (IBTS) on-board the RV Thalassa (4-17 November 2013). Fishing took place between 46° and 50° N and 4° and 11° W, and followed specifications outlined in the ICES protocol (ICES, 2010). Standardised discard samples were composed and contained a mixture of 75 roundfish (N=69, Total Length, TL: 9-31cm) and 50 items of another discard type: cephalopods (N=22, mantle length: 3-18cm), Norway lobster (Nephrops norvegicus) (N=22, carapace length: 1.8-4.4cm) or boarfish (Capros aper) (N=25, TL: 9-17cm) (see species list in Table A 2). Norway lobster was used as a proxy for benthic invertebrates, given the importance of Nephrops trawling in the Bay of Biscay. Discard experiments took place after hauling the gear. Discarded items were sorted by discard type, and randomly returned to the sea over a five minutes interval (1 item per 2.4 seconds). Bird species composition was voice-recorded prior and after each discarded sample, as well as bird species and discard type of each successful capture. Discard experiments (69 over 41 hauls) allowed calculation of the mean EDC of roundfish, benthic invertebrates, cephalopods and boar fish for several foraging guilds in the Bay of Biscay.

EDC variability was high for gannets consuming roundfish. As intra- and inter-guild competition were assumed to be the main drivers of this EDC variability, we fitted a logistic regression curve to the predictor variables 'overall flock size', 'number of birds of each foraging guild' and the 'proportion of Gannets in the flock of competitors'. Skuas were considered as the only potential competitors (Garthe & Hüppop, 1998) (Equation 1).

$$EDC = \log_e \left(\frac{p}{1-p} \right) = \beta_0 + \beta_i X_i \qquad [1]$$

where EDC is the probability of capturing a discarded item, β_0 is the intercept coefficient, β_i the model coefficients for the model matrix of predictor variables X_i. Logistic regression was based on a Generalised Linear Model (GLM) with logit-link function and quasi-binomial error distribution to account for overdispersion. 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 ∆QAIC was >3. Models with ∆QAIC of <3 were essentially equal, resulting in selecting the most parsimonious model. The selected model was further compared to a log-transformation of the predictor variable, testing levelling off at higher predictor values, e.g. log(Gannets+1) instead of Gannets (Limpert et al., 2001).

EDC variability was minor for any other foraging guild in the experiment. However, Large gulls may occur in large flocks in the Bay of Biscay, but our trials did not allow examining subsequent EDC variability, given the small flock sizes encountered (9 +- 22). As our approach requires evaluating EDC variability for large flocks of Large gulls (Section 2.2.1), we used parallel investigations from two data sources in the North Sea. The first series of experiments ('southern North Sea experiments') were conducted on-board the RV Belgica 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 remainder of 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 discard items, composed by two thirds of soles (Solea solea; TL: 6-28cm) and one third roundfish (Merlangius merlangius or Trisopterus sp.; TL: 9-31cm). A total of 150 experiments were realised. Depressiform fishes were also examined (Rajidae, N=52, TL: 30-163cm) by returning them to sea as a single item during 6 discard experiments in December 2011. The second data source from the North Sea was obtained from Camphuysen et al. (1995) ('entire North Sea experiments'). Pooling the experiments from the North Sea and the Bay of Biscay allowed assessing intra- and inter-guild competition for roundfish by Large gulls. Investigations of EDC variability for roundfish consumption by Large gulls followed the modelling procedure outlined above, except that the competition required a different assessment. Due to the social dominance of Gannets in comparison to other competitors (Hudson and Furness, 1989; Camphuysen, 2011), we evaluated two predictor variables for competition, i.e. the proportion of Large gulls in (1) the flock with Gannets and in (2) the flock with other competitors (Kittiwakes, Procellariids and Skuas). North Sea experiments were also used for estimating EDC of Small gulls, flatfish and depressiform fishes, as Bay of Biscay estimates were lacking (Table 1).

Table 1 - Data sources for EDC estimates by foraging guild and discard type. EDC was available for experiments in the Bay of Biscay (BoB) for small gulls, flatfish and depressiformes. EDC was approximated by experiments in the southern North Sea (IVc) and/or the entire North Sea experiments (NS). EDC estimates for roundfish were modelled for Large gulls by experiments in the southern and entire North Sea, and for Gannet in the BoB (black bold rectangle).

	Cephalopods	Benthic invertebrates	Roundfish	Flatfish	Depressiform fishes
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*

*approximated by other foraging guilds; * Assumed negligible

2.3 SPATIO-TEMPORAL DISTRIBUTION OF DISCARD TYPES

Fishery-dependent data of the French fishing fleet have been collected in the Ifremer onboard observer program 'Obsmer' to fulfil data requirements of the European Commission Data Collection Directives (1543/2000 and 1639/2001) and Data Collection Framework (EC, 2008a; 2008b). Catch sampling is stratified by metier and quarter. Metiers are defined by the European level 5 definition (EC, 2008a: 57-59), based on gear type, fishing area and target species assemblage. Landed and discarded numbers of each taxon are sampled by fishing operation. Subsamples were raised to the level of fishing operation, and then to trip on the basis of sampled and total fractions (Dubé et al., 2012; Fauconnet et al., 2011). This study focuses on discard and landing data between 2009-2011 in ICES Divisions VIIIa and VIIIb. The six metiers with the highest discarded amounts were selected according to gear type and target assemblage, i.e. (1) bottom trawls targeting demersal fish and cephalopods (TB-DEF), (2) bottom trawls targeting crustaceans (TB-CRU), (3) midwater trawls targeting small pelagic fish (TM-SPF), (4) midwater trawl targeting demersal fish and cephalopods (TM-DEF), (5) gill nets sensu latu (GN) and (6) longlines (LL). Discarded taxa were pooled into five discard types: benthic invertebrates, cephalopods, depressiform fishes, flatfish and roundfish (Table A 2, Nikolsky, 1963). The 'depressiform' discard type included dorsoventrally flattened fish taxa of the orders Rajiformes, Lophiiformes or Torpediniformes, while flatfish are exclusively Pleuronectiformes. Roundfish were roughly circular in cross-section, e.g. filiform, fusiform, globiform, as opposed to flatfish and skates.

Total trip discards by discard type were raised to total fleet discards for each stratum, i.e. for each of six pre-defined metiers in spatio-temporal units defined below. Extrapolation was based on a ratio estimator with fishing effort as auxiliary variable, i.e. days at sea (ICES, 2007). Numbers were used, because EDCs were expressed as numbers rather than weights.

Temporal strata were pooled to two periods to match seabird distribution data: April to September ('first semester') and October to March ('second semester'). Spatial resolution was defined by merging ICES Statistical Rectangles (1 degree longitude and 0.5 degrees latitude) to enable sufficient discard samples per spatial unit. Rectangles were merged into spatial units (sites) if they occurred in each other's vicinity and reported landings were similar (based on visual inspection of histograms). Each unit was required to include a minimum of ten fishing operations from at least three trips because inter-trip variability is generally larger than within-trip variability (Rochet et al., 2002). Mean sampling coverage of the spatial sites was 1.06% in the first semester and 0.46% in autumn for all metiers (Table 2). This was comparable to the mean sampling coverage of the study area without the spatial segregation (first semester: 0.66, second semester: 0.44) and to other discard observer programs (e.g. Depestele et al., 2011; Rochet et al., 2002).

Table 2 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 unit.

	Spatial sites	Sampling characteristics			Reported fleet characteristics		Sampling coverage (%)		Discarded proportion (roundfish)
		Number of hauls (trips)	Fishing days	Landings (kg)	Fishing days	Landings (t)	Fishing days	Landings	
1st semester									
GN-DEF	16E8, 17E8	40 (22)	26	3270	3368	593	0.77	0.55	0.22
	18E8, 19 E8, 20 E8, 21E8	444 (115)	132	3611	22606	3893	0.58	0.09	0.29
	24E4, 23E6, 21E7, 22 E7, 23E7	246 (49)	67	13117	12257	2426	0.55	0.54	0.56
	24E5, 24E6	57 (13)	16	1836	9375	2053	0.17	0.09	0.29
	Remainder*	38 (12)	19	9575	2913	2039	0.65	0.47	0.10
LLS-DEF	24E5, 23E5, 24E6, 18E6, 21E6, 22 E6, 23E7, 20E8	314 (33)	32	3482	16067	4466	0.20	0.08	0.13
	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
	24E5, 23E6	87 (37)	38	12648	21894	7230	0.17	0.17	0.24
	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
	23E6, 23E7	91 (21)	21	7255	11748	4728	0.18	0.15	0.59
	24E2, 24E3, 23E4, 24E4, 24E5	155 (18)	68	58214	8184	7249	0.18	0.15	0.70
	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
	24E4, 24E5, 23E6	29 (4)	13	12876	327	516	3.98	2.49	0.10
	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
	15E8, 16E8, 17E8, 18E8, 19E8, 20E8	25 (13)	13	21213	396	643	3.28	3.30	0.12
	21E5, 21E7, 22E7, 23E7	87 (23)	26	95922	4436	11338	0.59	0.85	0.15
	23E6, 24E6	38 (22)	18	104242	1133	2690	1.59	3.87	0.02
	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 2 (continued)

	Spatial sites	Sampling characteristics			Reported fleet characteristics		Sampling coverage (%)		Discarded proportion (roundfish)
		Hauls (trip)	Fishing days	Landings (kg)	Fishing days	Landings (t)	Fishing days	Landings	
2nd semester									
GN-DEF	16E8, 17E8	69 (33)	31	6132	2960	838	1.05	0.73	0.39
	18E8, 19 E8, 20 E8, 21E8	453 (114)	140	40353	12226	4239	1.15	0.95	0.40
	22E6, 23 E6, 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.

2.4 SPATIO-TEMPORAL DISTRIBUTION OF FORAGING GUILDS

Aerial and ship-based surveys covered the continental shelf of the Bay of Biscay (ICES Divisions VIIIa/b). Ship-based surveys were realised biennially (April-June; October-November) in 2009-2011 following the protocol outlined in Certain et al. (2011), while aerial monitoring was conducted during the first (May-July) and second semester (December-February) of 2012. Aerial monitoring took place during daylight by two observers looking through bubble windows. Flight height was about 180m above sea level at a speed of 90knots. Visual census was only accomplished in conditions of excellent visibility, i.e. limited wave heights and wind speed < 4 Beaufort. Both aerial and ship-based data (pooled over the years) were processed following the strip transect methodology, assuming that all species were recorded within a strip width of 200m (aerial, Certain et al., 2008) or 300m (ship-based, Tasker et al., 1984). The densities of foraging guilds were estimated by ICES Statistical Rectangle to match the spatial distribution of discard numbers (Section 0). Density calculations were iterated 999 times using random resampling with replacement of bird observations within each rectangle. Density estimates of the aerial and ship-based surveys were compared by calculating the log ratio of the densities in each rectangle, log (aerial /ship-based density), 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 significantly from zero (Fraser et al., 2008). Significant differences occurred for all foraging guilds, although the spatio-temporal patterns and order of magnitude differed. Densities of Auks, for instance, were significantly higher during aerial monitoring in the second semester, confirming Bretagnolle et al. (2004), whereas Large gulls, Procellariids and Kittiwakes had higher densities in the first semester of the ship-based surveys in areas where these guilds were virtually absent during aerial surveys. The spatial distribution of high aerial density estimates of the main scavengers were also more scattered over the Bay of Biscay in the second semester than the ship-based estimates. These significant differences confirm that bird observations are likely biased during ship-based observations (Bretagnolle et al., 2004), inter alia by attraction of scavenging seabirds, we opted to continue with the aerial estimates.

2.5 SEABIRD ATTRACTION TO FISHING VESSELS

Attraction of seabirds to fishing vessels rather than to natural food was estimated by foraging guilds in the Bay of Biscay. Attraction was estimated by the scavenging index of Furness et al. (2007), as the mean numbers of a foraging guild following fishing vessels divided by the mean density of that guild. The mean density was estimated from aerial surveys (Section 2.4). The number of ship followers was recorded on board the RV 'Thalassa' during bottom trawl and pelagic surveys in 2009-2011, covering the entire Bay of Biscay. Bottom trawl surveys 'EVHOE' took place in October and November (second semester), deploying a 36∕47 GOV bottom trawl during 30 min hauls at 4 knots (see ICES (2010) for further details). Trawling during pelagic surveys was conducted between April and June (first semester) with a pelagic trawl of 40 (horizontal) by 20m (vertical). Hauls also lasted 30 min at a speed of 4 knots (Certain et al., 2011). Ship followers were exclusively registered during daylight if they were within a circumference of 200m. Numbers were recorded by species within 10 hours after hauling or after each significant change of environmental conditions as judged by the observers. In total, 88 observations of ship followers were registered in the first semester and 212 during the

second semester. The mean number of hauls preceding registration was 1-2 (first semester) or 1-4 (second semester). The effect of the number of hauls on the total number of ship followers was compared for each survey with a non-parametric Kruskal-Wallis test. Differences between semesters within foraging guilds and between foraging guilds within semester were evaluated with a non-parametric Kruskal-Wallis test, followed by post-hoc comparisons by Mann-Whitney tests with false discovery rate (FDR) corrections (Garcia, 2004).

2.6 FOOD FOR 'OTHER' MARINE SCAVENGERS

The consumption of discards by seabirds was estimated at fleet level through a raising procedure of the number of experimentally discarded items by foraging guild and discard type (Figure 1). The auxiliary variable was the total number of discards by stratum (Section 0). A stratum was defined by spatio-temporal unit (rectangle i, semester j), discard type k and foraging guild l (Equation 2).

$$C_{i,j,k,l} = \frac{D_{i,j,k}}{d_k} * c_{k,l} \qquad\qquad [2]$$

where C and c is discard consumption, and D and d is the total number of discards at fleet and experimental level respectively. Experimental discard consumption of roundfish by Large gulls and Gannets was considerably affected by the composition of the flock of ship followers (Section 2.2). As the number of ship followers and flock composition varied considerably at fleet level, we used this experimental relationship to determine discard consumption by Large gulls and Gannets consuming roundfish. The number of ship followers in each spatio-temporal unit ($F_{i,j,l}$) was estimated from the guild-specific attraction to fishing vessels and local bird densities (Furness et al., 2007; Equation 3).

$$F_{i,j,l} = S_{j,l} * B_{i,j,l} \qquad\qquad [3]$$

where $S_{j,l}$ is the guild-specific biennial scavenging index (Table 3) and $B_{i,j,l}$ the bird density of foraging guild l in spatio-temporal unit i, j. Unidentified gulls in a spatio-temporal unit were attributed to either Small or Large gulls following the ratio of local densities of Small to Large gulls. Experimental discard consumptions were not raised in spatio-temporal units exceeding experimental conditions (>150 ship following Gannets or >220 Large gulls). The total number of discarded items available to marine scavengers other than seabirds was subsequently calculated from Equation 4.

$$R_{i,j} = \left[\sum_k D_k - \sum_k \sum_l C_{k,l}\right]_{i,j} \qquad\qquad [4]$$

where R is the remaining fraction of discards, available to 'other' marine scavengers.

Table 3 - Mean (SD, maximum) of numbers of ship followers, mean density (n/km²) and the guild-specific scavenging index by foraging guild in the Bay of Biscay (VIIIab). The number of hauls, n(hauls), in which the ship followers occurred are indicated with totals of 88 and 212 recordings in the first and second semester respectively.

	Gannets	Large gulls	Small gulls	Kittiwakes	Procellariids	Storm petrels	Skuas
First semester							
n(hauls)	43	72	11	1	31	5	15
Ship followers	4.1	123.7	4.1	0.3	3.3	0.58	0.72
	(8.5, 50)	(233.1, 1506)	(22.9, 152)	(3.2, 30)	(8.5, 60)	(4.3, 40)	(2.4, 15)
Density	0.12	0.21	0.07	0.01	0.06	0.07	0.01
Scavenging index	34.2	589.0	58.6	30.0	55.0	8.3	72.0
Second semester							
n(hauls)	175	176	33	62	67	21	124
Ship followers	109.4	144.0	0.4	5.0	4.9	0.8	3.2
	(183.5, 1000)	(179.9, 800)	(1.1, 1)	(25.9, 340)	(20.7, 175)	(3.9, 42)	(4.8, 31)
Density	0.74	0.26	0.04	0.17	0.02	0.04	0.02
Scavenging index	147.8	553.8	10.0	29.4	245.0	20.0	160.0

3 RESULTS AND DISCUSSION

3.1 EXPERIMENTAL DISCARD CONSUMPTION BY SEABIRDS

Experimental Discard Consumption (EDC) of roundfish was high in all regions for the total flock (EDC>0.37), but this was caused by different foraging guilds (Table 4). Gannets were the main consumers in the Bay of Biscay, while in the southern North Sea discards were mostly consumed by Large gulls. Overall discard consumption in the entire North Sea was due to Large gulls, as well as Procellariids and Kittiwakes. The main contributors to roundfish consumption are reflected in the mean composition of the flocks of ship followers. While Gannets dominated the Bay of Biscay flocks, Large gulls were the most abundant scavengers in the southern North Sea, combined with Kittiwakes and Procelariids for the entire North Sea experiments.

Variability in roundfish consumption is thus highest for foraging guilds occurring in large flocks (Table 4). The number of ship following Gannets followed a logarithmic curve and explained 76% (Pseudo-R^2) of the variability of roundfish consumption in the Bay of Biscay (Figure 2a,Table A3). Roundfish consumption by Large gulls also followed a logarithmic increase with increasing numbers (Figure 2b). The increase in discard consumption by Large gulls was however hampered by the relative abundance of other competitors (Figure 2c,d). Large gulls were about three times less effective in capturing discards with increasing relative abundance of Gannets, and the competition with other guilds also reduced roundfish consumption up to 0.7 times. Both, inter- and intra-guild competition explained up to 62% (Pseudo-R^2) of the variability in discards consumption by Large gulls (Table A3).

Roundfish consumption was higher than the consumption of any other discard type (Table 4). The mean probability of discard consumption by the flock of scavengers was 0.093 for cephalopods and 0.008 for Norway lobsters in the Bay of Biscay. Experimental discard consumption of flatfish was 0.231 as approximated by North Sea experiments. Large gulls were the main consumers of flatfish, whereas Small gulls and Kittiwakes hardly consumed any flatfish. Gannets, Procellariids and Skuas contributed nearly equally to the overall flatfish consumption. The discard consumption of depressiform fish was approximated using experiments in the southern North Sea, revealing that a discarded depressiform fish had a probability of 0.135 of being consumed by Large gulls and were not consumed by Kittiwakes. The consumption by Gannets was assumed equal to Large gull consumption and negligible for Procellariids and Skuas. Consumption by Small gulls was equalled to the consumption by Kittiwakes for cephalopods, benthic invertebrates and depressiform fishes.
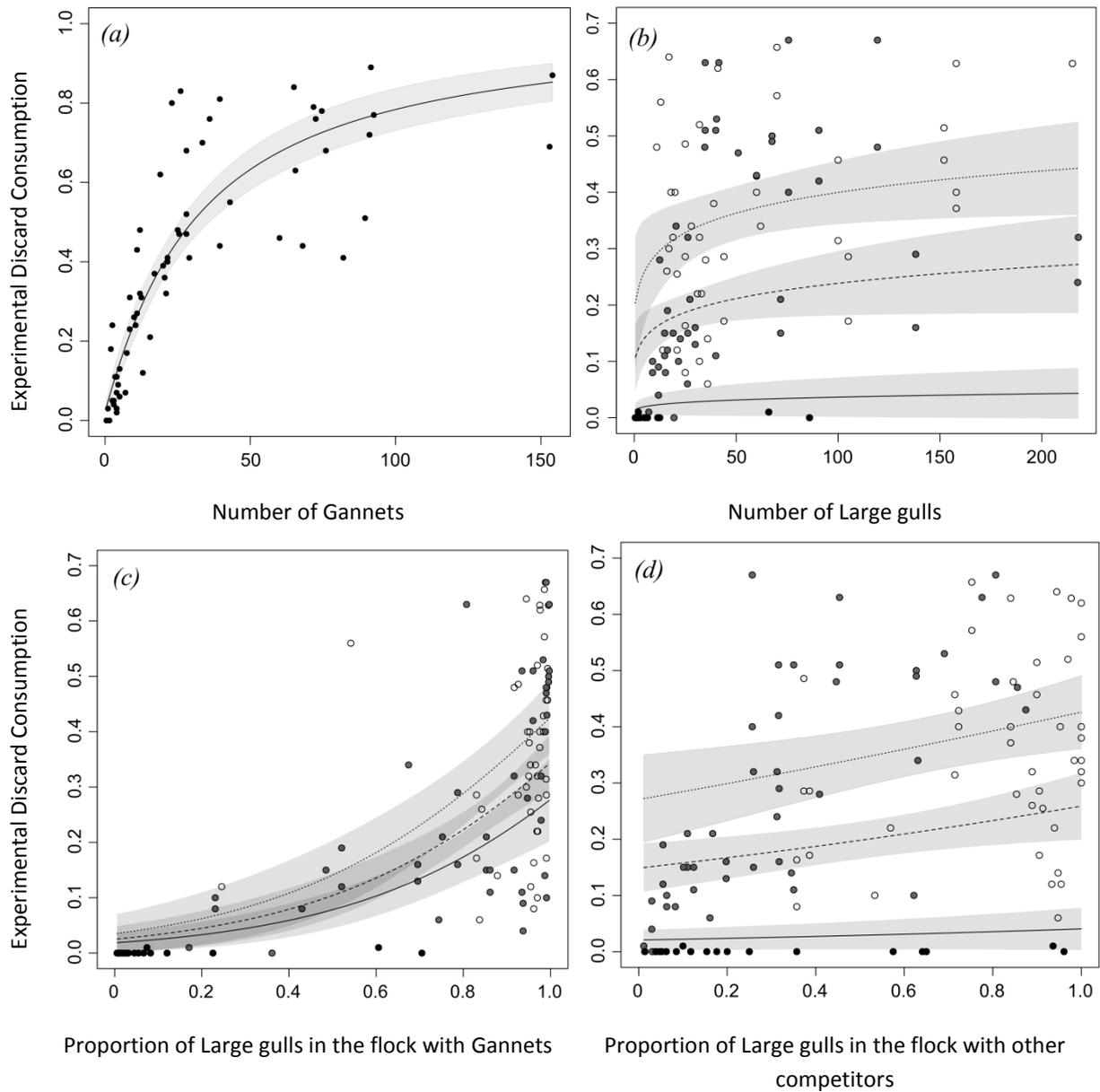
Figure 2 - The probability of roundfish consumption increased logarithmically with the number of ship followers for (a) Gannets and (b) Large gulls (intra-guild competition). Consumption by Large gulls was also affected by inter-guild competition with Gannets and other competitors (Kittiwakes, Procellariids and Skuas). Decreasing relative abundances of Large gulls compared to Gannets reduced consumption by threefold (panel c). The proportion of Large gulls in the flock with Gannets are indicated by a dotted (proportion =1), dashed (proportion=0.75) and solid line (proportion=0.05) in partial plots (b) and (d). Decreasing relative abundances of Large gulls compared to other competitors reduced consumption by a factor 0.7 (panel d). The proportion of Large gulls in the flock with other competitors are also indicated in panel (c) by a dotted (proportion =1), dashed (proportion=0.5) and solid line (proportion=0.05).

Table 4 - Mean number of scavenging seabirds and mean EDC-estimates (SD, maximum) for the Bay of Biscay experiment and experiments in the North Sea (1: experiments on-board RV 'Belgica', 2: Camphuysen et al., 1995). Storm petrels did not consume any discard item.

Number of scavenging seabirds

	Bay of Biscay experiments				southern North Sea[1]		entire North Sea[2]	
	Roundfish	Boarfish	Cephalopods	Norway lobster	Soles/roundfish	Depressiformes	Roundfish	Flatfish
Gannets	29.4 (34.2, 154)	15.1 (15.1, 76)	40.4 (40.0, 154)	31.8 (36.3, 153)	2.4 (8.7, 63)	0.3 (1.0, 3)	9.1 (11.3, 37.4)	9.0 (10.9, 34.5)
Large gulls	3.2 (13.7, 86)	0.8 (2.5, 11.5)	3.5 (12.9, 66)	5.0 (18.6, 86)	67.9 (66.2, 275)	131.7 (51.2, 185)	48.5 (49.0, 217.9)	32.7 (29.4, 217.9)
Small gulls	-	-	-	-	1.1 (1.6, 10)	-	4.0 (5.3, 12.7)	0.1 (-, 0.1)
Kittiwakes	10.6 (13.5, 48.5)	15.1 (15.1, 48.5)	8.6 (13.1, 45)	8.6 (11.4, 45)	10.9 (14.1, 70)	9.7 (4.9, 20)	54.4 (68.8, 270.8)	44.6 (69.2, 270.8)
Procellariids	13.9 (20.9, 95.5)	13.0 (10.4, 37.5)	15.6 (26.6, 95.5)	13.2 (22.0, 84.5)	-	-	140.23 (147.3, 553.8)	194.8 (156.4, 553.8)
Skuas	5.1 (4.4, 24.5)	3.9 (3.5, 12)	6.7 (5.0, 24.5)	4.8 (4.1, 19)	-	-	0.4 (1.0, 4.8)	0.8 (1.3, 4.8)
Storm petrels	0.3 (1.0, 8)	-	0.6 (1.6, 8)	0.3 (0.6, 2)	-	-	-	-
Flock size	62.2 (32.8, 168)	47.8 (16.9, 80)	74.7 (35.8, 168)	63.5 (35.6, 165)	82.3 (67.9, 281)	142.3 (51.6, 195)	254.7 (200.0, 701.8)	295.8 (198.6, 701.8)

EDC estimates (proportions)

	Bay of Biscay experiments				southern North Sea[1]		entire North Sea[2]	
	Roundfish	Boarfish	Cephalopods	Norway lobster	Soles/roundfish	Depressiformes	Roundfish	Flatfish
Gannets	0.379 (0.278, 0.89)	0.048 (0.091, 0.36)	0.058 (0.090, 0.38)	0.006 (0.017, 0.08)	0.032 (0.067, 0.353)	-	0.127 (0.140, 0.52)	0.057 (0.031, 0.108)
Large gulls	0.001 (0.003, 0.01)	0.004 (0.012, 0.04)	0	0.002 (0.006, 0.02)	0.317 (0.294, 0.540)	0.135	0.288 (0.226, 0.91)	0.118 (0.147, 0.5)
Small gulls	-	-	-	-	0.013 (0.017, 0.020)	-	0.032 (0.106, 0.43)	<0.01 (-, 0.01)
Kittiwakes	0.026 (0.040, 0.17)	0	0.005 (0.012, 0.04)	0.001 (0.005, 0.02)	0.060 (0.071, 0.314)	0	0.295 (0.236, 0.81)	0.033 (0.031, 0.09)
Procellariids	0.006 (0.015, 0.08)	0.001 (0.007, 0.04)	0.005 (0.021, 0.1)	0	-	-	0.197 (0.225, 0.72)	0.068 (0.061, 0.19)
Skuas	0.020 (0.040, 0.23)	0.006 (0.018, 0.08)	0.025 (0.052, 0.24)	0	-	-	0.04 (0.069, 0.23)	0.07 (0.106, 0.550)
Total flock	0.421 (0.259, 0.89)	0.055 (0.093, 0.08)	0.093 (0.105, 0.38)	0.008 (0.018, 0.08)	0.370 (0.290, 0.598)	0.135	0.793 (0.192, 1.0)	0.199 (0.157, 0.6)

3.2 SPATIO-TEMPORAL DISTRIBUTION OF DISCARDS

Discarded proportions varied from virtually no discards to proportions >0.6, especially for roundfish (Table 2). Discarded proportions of cephalopods, depressiformes and flatfish were low for all métiers (<10%), except for depressiformes discarded by TB-DEF in northern rectangles in the second semester and for flatfish discarded by TB-DEF in nearly all sites in the first semester and in the southern Bay of Biscay in the second semester. Discarded proportions of benthic invertebrates by bottom trawls targeting crustaceans ranged between 0.45 and 0.71, while proportions by GN-DEF and TB-DEF varied up to 0.47.

The total number of discarded organisms was highest in the north-eastern part of the Bay of Biscay (Figure 3). Here we present differences between roundfish and other discard types, because of their different proportions consumed by seabirds (Section 3.1). Both, roundfish and 'other' discard types were mainly discarded during the first semester. Discards of other discard types in the second semester for instance were <20% of the discards during the first semester. Roundfish discards in the second semester were mainly caused by TB-CRU in 23E6 and 24E5, while TM-SPF contributed largely (>50%) to all other ICES Rectangles. Spatial variability could not be detected for TM-SPF due to a limited number of observations. Apart from TB-CRU and TM-SPF, roundfish discards were located in coastal regions and in offshore fishing grounds at latitude >47°. The discards of 'other' discard types in the first semester was dominated by TB-CRU (>80% of discards of all métiers), as reflected in the spatial distribution pattern (23E6, 24E5, 23E5, 22E6, 21E7 and 20E8). Cephalopods and depressiformes were also discarded by TB-DEF, whereas flatfish discards were also caused by GN-DEF along the coastline of the central Bay of Biscay (19E8-21E8). Roundfish discards in the first semester were about 7 times less than 'other' discard types. They were caused by TB-CRU, as well as TM-SPF and TB-DEF in ICES rectangles 21E5-E8 and 21-23E7. The contribution of TM-DEF and LLS-DEF was <5% to overall discard numbers in all rectangles.
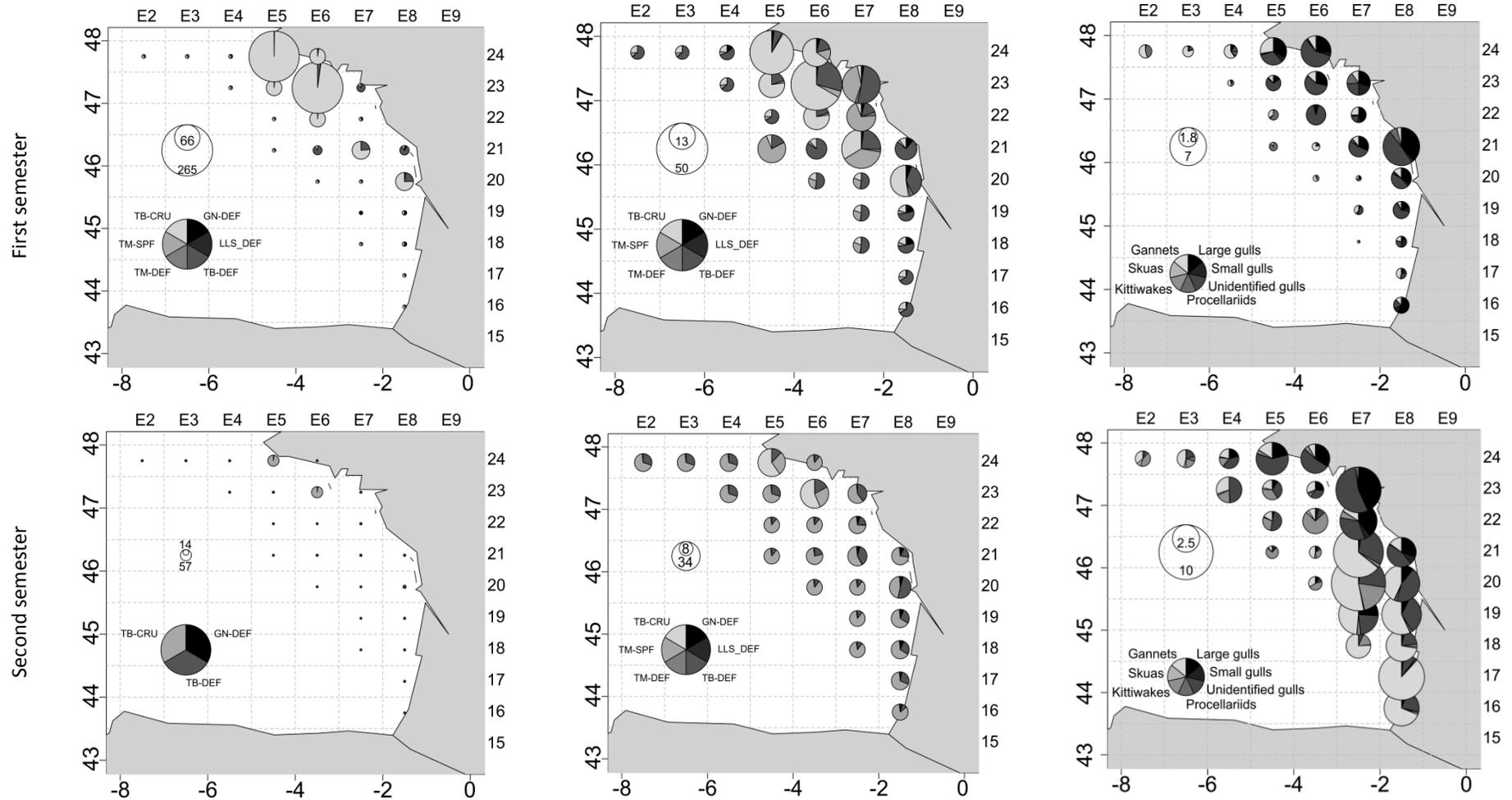
Figure 3 - Numbers of discarded organisms and seabird densities (n/km²) during the first (upper panels) and second (lower panels) semester of 2009-2011 by the major fishing metiers in the Bay of Biscay. Discards are presented by million number of discard items by type: all discard types except roundfish (left) and roundfish (middle). Spatial distribution of seabird foraging guilds is presented in the right panels. Upper en lower panels within each column have the same resolution, but note that resolutions differ between columns.

3.3 SPATIO-TEMPORAL DISTRIBUTION OF FORAGING GUILDS

The highest densities of scavenging seabirds in the Bay of Biscay differed between the first and second semester. The highest densities were located in the north-eastern coastal rectangles in the first semester (~3/km²), whereas higher density estimates were observed in the second semester (~6/km²). The first semester was dominated by Gulls. There were many gull species unidentified, but the proportion of Large gulls to Small gulls highlights the importance of Large gulls in the north-eastern Bay of Biscay during the first semester. Gannets were less abundant, except north of 47.5° latitude. The distribution pattern and the densities of Large gulls was not greatly altered in the second semester, but the densities of Gannets changed considerably. High densities were mainly located in ICES Division VIIIb.

3.4 SEABIRD ATTRACTION TO FISHING VESSELS

The number of hauls that preceded observations did not affect the total number of ship followers during first (χ(4)=1.37, P=0.85) and second semester (χ (6)=11.35, P=0.08). There was no significant difference in total number of ship followers (mean, SD, maximum) between the first (61.5 +- 163.9) and second semester (70.02 +- 132.4) (Z = 0.89, P = 0.37, r = 0.03), but the guild composition of the flock of ship followers differed significantly between semesters. Post-hoc tests with FDR corrections showed a significantly higher number of Gannets (P<0.001, r=0.51) and Skuas (P<0.001, r=0.37) during the second semester (Table 3, Table A4). The flock of ship followers in the second semester was dominated by Large gulls and Gannets (>100 individuals). Kittiwakes, Procellariids and Skuas occurred regularly and occasionally in high numbers. Small gulls and storm petrels were virtually absent. In contrast, the first semester was exclusively dominated by Large gulls, with regular occurrence of Gannets and Procellariids in small numbers. The presence of Small gulls and Skuas was highly variable, while Kittiwakes and Storm petrels rarely followed the vessel. The scavenging index illustrated that Large gulls are highly attracted by fishing vessels at all times of the year, while Gannets, Procellariids and Skuas were especially attracted during the second semester (Table 3, Table A4).

3.5 FOOD FOR 'OTHER' MARINE SCAVENGERS

The food for non-avian predators is determined by the seabird's scavenging behaviour. Virtually all discarded benthic invertebrates remain available in the Bay of Biscay, whereas seabirds focused on the consumption of roundfish (Figure 4). Roundfish consumption was dominated by Large gulls in the first semester, whereas >50% of the discarded roundfish were consumed by Gannets in the second semester, except for the north-eastern Bay of Biscay. The proportion of consumed roundfish was significantly higher (0.69+-0.20 %) in the second semester than in the first (0.40 +/- 0.16 %) (W=222, Z=3.7, P<0.0001, r=0.32). The increased consumption reflects both the higher number of ship following Large gulls as well as the increased abundances of Gannets (Figure 4). The total numbers of discards consumed, as well as the total number of discards available to other marine scavengers were significantly higher in the first semester than in the second (W=1627, Z=3.7, P<0.001, r=0.31). The order of magnitude of the number of discarded items that were returned to the sea was

respectively 7.8 and 5.7 million, and consisted in both period for >75% of roundfish (excluding discards of benthic invertebrates).

4 CONCLUSIONS

This study developed a spatio-temporally explicit framework for the quantification of discards that become available to marine scavengers other than seabirds. The framework was applied to discards from the French fishing fleet in the Bay of Biscay. Discards were categorised into different discard types which were based on seabird's ability to swallow them. Seabird species were pooled into foraging guilds, enabling inferences on seabird's consumption rates across regions and species. Experimental trials were conducted in the Bay of Biscay to evaluate the consumption rates of the main scavenging seabirds and discard types. Experimental discard consumptions were raised to fleet level by foraging guild and discard type, accounting for high EDC-variability for the most eligible discard types and foraging guilds. The raising procedure was applied to spatio-temporal unit with the lowest common resolution, as defined by the distribution of discards and foraging guilds. Discards limited inferences in space, whilst the highest temporal resolution was determined by the biennial monitoring of foraging guilds. The attraction of foraging guild was estimated from the scavenging index, which is a measure for the attraction of seabirds to fishing vessels rather than natural food. It was based on counts of ship following seabirds and their associated densities. The Bay of Biscay case study highlighted clear seasonal differences in consumption rates due to the increased number of ship following Large gulls in the second semester, as well as the increased occurrence of Gannets. The number of benthic invertebrates that were not consumed by seabirds was not surprisingly high. Excluding the invertebrates from the discards highlighted that > two-thirds of roundfish were discarded to the seafloor in comparison to depressiform fishes, flatfish and cephalopods. The case study illustrates the applicability of the framework and assumes transferability to other European regions on the conditions that premises as assemblages of ship following flocks are characterised, as well as the total discarded amounts.
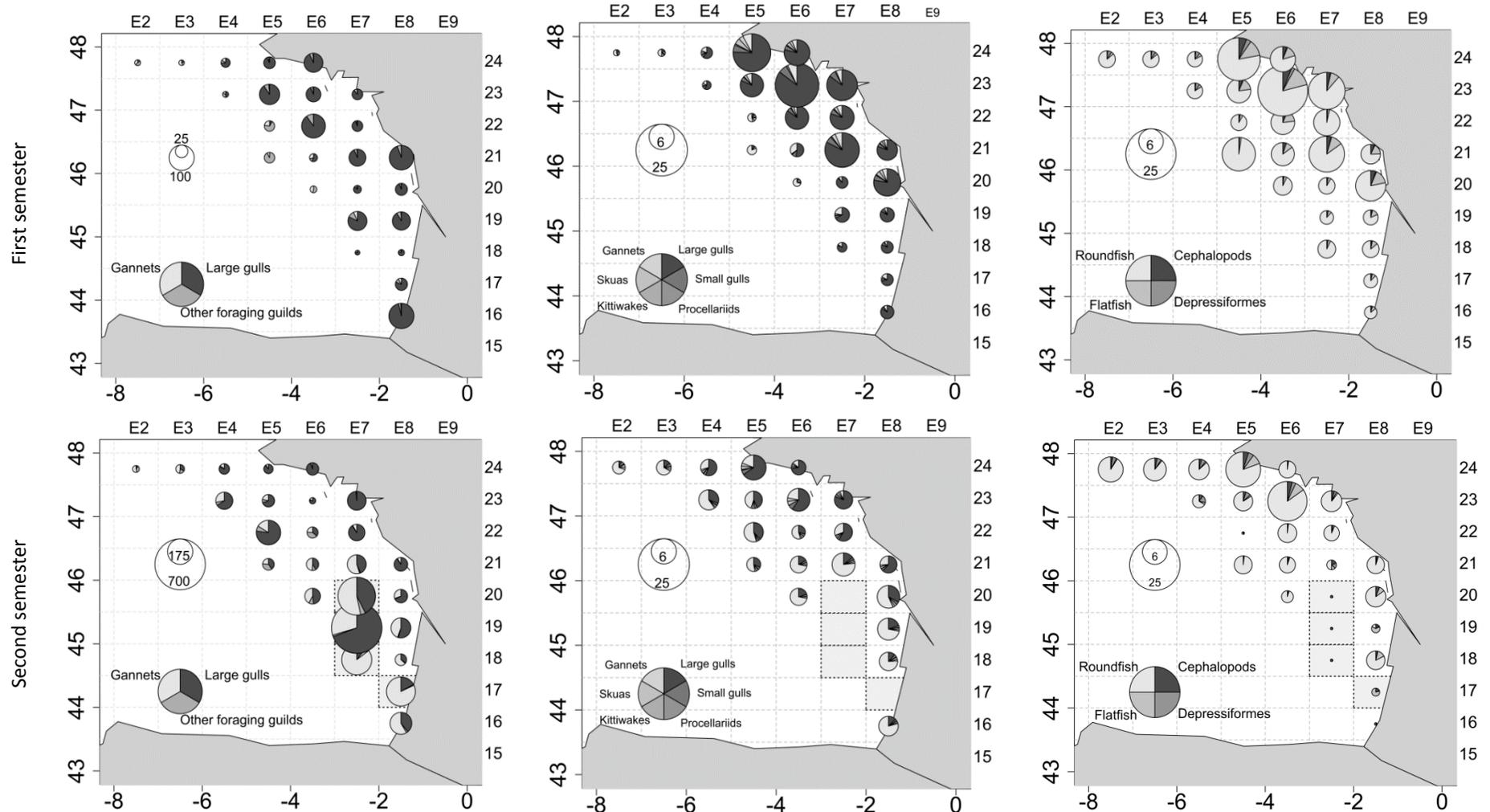
Figure 4 - Numbers of ship followers, consumption of roundfish by foraging guild and number of discards available to other marine scavengers. during the first (upper panels) and second (lower panels) semester of 2009-2011. Discards are presented by million number of discard items. Rectangles that exceeded experimental conditions are indicated with a dotted line (17E8, 18E7, 19E8 and 20E7). Roundfish consumption was not estimated.

5 REFERENCES

Bicknell, A.W.J., Oro, D., Camphuysen, K., Votier, S.C., 2013. Potential consequences of discard reform for seabird communities. J. Appl. Ecol. 50, 649-658.

Bodey, T.W., Ward, E.J., Phillips, R.A., McGill, R.A.R., Bearhop, S., 2014. Species versus guild level differentiation revealed across the annual cycle by isotopic niche examination. J. Anim. Ecol. 83, 470-478.

Borges, F.M., Andonegi, E., Depestele, J., Piet, G., Reid, D., Rindorf, A., Sørensen, T.K., van der Meeren, G.I.. 2014. Priority research areas for evaluating ecosystem consequences of a discard ban. ICES CM 2014/3849-O:16.

Bretagnolle, V., Certain, G., Houte, S., Métais, M., 2004. Distribution maps and minimum abundance estimates for wintering auks in the Bay of Biscay, based on aerial surveys. Aquat. Living Resour. 17, 353-360.

Briggs, K.T., Tyler, W.B., Lewis, D.B., 1985. Comparison of Ship and Aerial Surveys of Birds at Sea. Journal of Wildlife Management 49, 405-411.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. A practical information - theoretic approach. Springer.

Camphuysen, C.J., 1994. Flatfish selection by herring gulls Larus argentatus and lesser black-backed gulls Larus fuscus scavenging at commercial beamtrawlers in the southern North Sea. Neth. J. Sea Res. 32, 91-98.

Camphuysen, C.J., Calvo, B., Durinck, J., Ensor, K., Follestad, A., Furness, R.W., Garthe, S., Leaper, G., Skov, H., Tasker, M.L., Winter C.J.N., 1995. Consumption of discards by seabirds in the North Sea. NIOZ-rapport 1995-5: 1-197.

Camphuysen, C.J., Garthe, S., 1997. An evaluation of the distribution and scavenging habits of northern fulmars (Fulmarus glacialis) in the North Sea. ICES J. Mar. Sci. 54, 654-683.

Camphuysen, C.J., 2011. Northern gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. British Birds 104:60-76

Catchpole, T.L., Frid, C.L.J., Gray, T.S., 2006. Importance of discards from the English Nephrops norvegicus fishery in the North Sea to marine scavengers. Mar Ecol Prog Ser 313, 215-226.

Certain, G., Bretagnolle, V., 2008. Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys. Remote Sensing of Environment 112, 3314-3322.

Certain, G., Masse, J., Van Canneyt, O., Petitgas, P., Doremus, G., Santos, M.B., Ridoux, V., 2011. Investigating the coupling between small pelagic fish and marine top predators using data collected from ecosystem-based surveys.23-39.

Depestele, J., Vandemaele, S., Vanhee, W., Polet, H., Torreele, E., Leirs, H., Vincx, M., 2011. Quantifying causes of discard variability: an indispensable assistance to discard estimation and a paramount need for policy measures. ICES J. Mar. Sci. 68, 1719-1725.

Dubé, B., Diméet, J., Rochet, M.J., Tétard, A., Gaudou, O., Messanot, C., Fauconnet, L., Morizur, Y., Biseau, A., Salaun, M., 2012. Observations a bord des navires de pêche professionnelle Bilan de l'echantillonnage 2011. 1-298.

European Commission. 2008a. Commission decision of 6 November 2008 adopting a multiannual Community programme pursuant to Council Regulation (EC) No 199/2008 establishing a Community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the common fisheries policy. Official Journal of the European Union: 37-88.

European Commission. 2008b. Commission Regulation (EC) No 665/2008 of 14 July 2008 laying down detailed rules for the application of Council Regulation (EC) No 199/2008 concerning the establishment of a Community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. Official Journal of the European Union, L186/3.

European Commission. 2011. Communication from the commission to the European parliament, the council, the European economic and social committee and the committee of the regions. Reform of the Common Fisheries Policy. COM (2011) 417.

Fauconnet, L., Badts, V., Biseau, A., Diméet, J., Dintheer, C., Dubé B., Gaudou, O., Lorance, P., Messanot, C., Nikolic, N., Peronnet, I., Reecht, Y., Rochet, M.J., Tétard, A., 2011. Observations a bord des navires de pêche professionnelle Bilan de l'echantillonnage 2010.

Fraser, H. M., Greenstreet, S. P. R., Fryer, R. J., and Piet, G. J. 2008. Mapping spatial variation in demersal fish species diversity and composition in the North Sea: accounting for species- and size-related catchability in survey trawls. ICES Journal of Marine Science, 65: 531–538.

Furness, R.W., Edwards, A.E., Oro, D., 2007. Influence of management practices and of scavenging seabirds on availability of fisheries discards to benthic scavengers. Mar Ecol Prog Ser 350, 235-244.

Furness, R.W., Ensor, K., Hudson, A.V., 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80, 105-113.

Garcia, L.V., 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105, 657-663.

Garthe, S., Camphuysen, C.J., Furness, R.W., 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. -Prog. Ser. 136, 1-11.

Garthe, S., Hüppop, O., 1998. Foraging success, kleptoparasitism and feeding techniques in scavenging seabirds: does crime pay? Helgoländer Meeresuntersuchungen 52, 187-196.

Groenewold, S., Fonds, M., 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES J. Mar. Sci. 57, 1395-1406.

Grünbaum, D., Veit, R.R., 2003. Black-browed albatrosses foraging on Antarctic krill: density-dependence through lcoal enhancement? Ecology 84, 3265-3275.

Heath, M.R., Cook, R.M., Cameron, A.I., Morris, D.J., Speirs, D.C., 2014. Cascading ecological effects of eliminating fishery discards. Nature Communications 5.

Hill, B.J., Wassenberg, T.J., 2000. The probable fate of discards from prawn trawlers fishing near coral reefs: A study in the northern Great Barrier Reef, Australia. Fish Res. 48, 277-286.

Hudson, A.V., Furness, R.W. 1989. The Behavior of Seabirds Foraging at Fishing Boats around Shetland. Ibis 131. 225-237.

ICES, 2007. Report of the Workshop on Discard Raising Procedures. ICES CM 2007/ACFM:06: 1-57.

ICES. 2010. Report of the International Bottom Trawl Survey Working Group (IBTSWG), 22-26 March 2010, Libon, Portugal. ICES Document CM 2010 SSGESST: 06. 267p .

Kaiser, M.J., Hiddink, J.G., 2007. Food subsidies from fisheries to continental shelf benthic scavengers. Mar. Ecol. Prog. Ser. 350, 267-276.

Käkelä, A., Furness, R.W., Kelly, A., Strandberg, U., Waldron, S., Kakela, R., 2007. Fatty acid signatures and stable isotopes as dietary indicators in North Sea seabirds. Mar Ecol Prog Ser 342, 291-301.

Limpert, E., Stahel, W.A., Abbt, M., 2001. Log-normal distributions across the sciences: Keys and clues. Bioscience 51, 341-352.

Arcos, J.M., Oro, D., 2002. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater Puffinus mauretanicus. Mar Ecol Prog Ser 239, 209-220.

Nikolsky, G.W., 1963. The ecology of fishes. Academic Press, London (UK).

Oro, D., Ruiz, X., 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. ICES J. Mar. Sci. 54, 695-707.

Pon, J.P.S., Garcia, G., Copello, S., Moretinni, A., Lertora, H.P., Pedrana, J., Mauco, L., Favero, M., 2012. Seabird and marine mammal attendance in the Chub mackerel Scomber japonicus semi-industrial Argentinian purse seine fishery. Ocean Coastal Manage. 64, 56-66.

Quinn, G., Keough, M., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge (UK).

Ragnarsson, S.A., Steingrimsson, S.A., 2003. Spatial distribution of otter trawl effort in Icelandic waters: comparison of measures of effort and implications for benthic community effects of trawling activities. ICES J. Mar. Sci. 60, 1200-1215.

Ramsay, K., Kaiser, M.J., Moore, P.G., Hughes, R.N., 1997. Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. The Journal of Animal Ecology 66, 884-896.

Rochet, M.J., Peronnet, I., Trenkel, V.M., 2002. An analysis of discards from the French trawler fleet in the Celtic Sea. ICES J. Mar. Sci. 59, 538-552.

Rochet, M-J., Catchpole, T., and Cadrin, S. 2014. Bycatch and discards: from improved knowledge to mitigation programmes. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsu039.

Shephard, S., Minto, C., Zölck, M., Jennings, S., Brophy, D., and Reid, D. 2014. Scavenging on trawled seabeds can modify trophic size structure of bottom-dwelling fish. – ICES Journal of Marine Science, 71: 398–405.

Sotillo, A., Depestele, J., Courtens, W., Vincx, M., Stienen, E.W.M., 2014. Discards consumption by Herring gulls Larus argentatus and Lesser Black-backed gulls Larus fuscus off the Belgian coast in the breeding season. Ardea.

Stratoudakis, Y., 1999. Recommendations for improving the estimation of the number of seabirds potentially sustained by fisheries discards. Mar Ecol Prog Ser 176, 307-309.

Tasker, M., Jones, P.H., Dixon, T.J., Blake, B.F., 1984. Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. Auk 101, 567-577.

Valeiras, J., 2003. Attendance of scavenging seabirds at trawler discards off Galicia, Spain. Sci. Mar. 67, 77-82.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A.V., Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I., Thompson, D.R., 2004. Changes in fisheries discard rates and seabird communities. Nature 427, 727-730.

ACKNOWLEDGMENTS

6 APPENDICES

Table A 1- Pooling of seabird scavenging taxa in foraging guilds. Categorization was based on morphology and discard foraging behaviour.

Foraging guilds	Taxa list
Sulidae	*Morus bassanus*
Large gulls	*Larus fuscus, Larus maritimus, Larus argentatus, Marus michahellis, Larus cachinnans, Larus hyperboreus*
Small gulls	*Larus minutus, Larus melanocephalus, Larus sabini, Larus canus, Larus audouinii, 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* sp.*, Calonectris diomedea, Fulmarus glacialis, Calonectris* sp.*, Puffinus* sp.*, Puffinus gravis, P. griseus, P. yelkouan, 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 A 2 - List of taxa included in the discard types (Section 0). Bold taxa were used in the experimental discarding study in the Bay of Biscay (Section 2.2). Categorization was based on morphology which is related to handling time of consumers.

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***
Depressiformes (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 A2 (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 A3 - 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 Gannets	3.02 (0.54)	5.49	<0.0001
Proportion of Large gulls in the flock with 'other' competitors	0.69 (0.26)	2.71	<0.001

Table A4 - Effect size (r) and significance (P-value) of differences in number of ship followers between seasons within a bird category (diagonal), between bird categories in autumn (values above diagonal) and in spring (values below diagonal). Non-significant results are indicated in bold.

	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
	P<0.001	P<0.01	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001
Large gulls	r=0.58	**r=0.10**	r=0.74	r=0.66	r=0.75	r=0.60	r=0.66
	P<0.001	**P=0.11**	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001
Small gulls	r=0.38	r=0.71	**r=0.02**	r=0.21	**r=0.08**	r=0.47	r=0.19
	P<0.001	P<0.001	**P=0.70**	P<0.001	**P=0.14**	P<0.001	P<0.001
Procellariids	**r=0.12**	r=0.63	r=0.26	**r=0.06**	r=0.26	r=0.25	**r=0.01**
	P=0.15	P<0.001	P<0.01	**P=0.37**	P<0.001	P<0.001	**P=0.88**
Storm petrels	r=0.48	r=0.76	**r=0.12**	r=0.37	**r=0.07**	r=0.50	r=0.25
	P<0.001	P<0.001	**P=0.10**	P<0.001	**P=0.24**	P<0.001	P<0.001
Skuas	r=0.36	r=0.72	**r=0.05**	r=0.23	r=0.18	r=0.37	r=0.24
	P<0.001	P<0.001	**P=0.55**	P<0.01	P<0.05	P<0.001	P<0.001
Kittiwakes	r=0.54	r=0.78	r=0.22	r=0.43	**r=0.12**	r=0.27	r=0.30
	P<0.001	P<0.001	P<0.01	P<0.001	**P=0.21**	P<0.001	P<0.001