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Contribution to the Theme Section 'Non-breeding distribution and movements of North Atlantic seabirds'

Light-level geolocators reveal spatial variations in interactions between northern fulmars and fisheries

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ABSTRACT: Seabird–fishery interactions are a common phenomenon of conservation concern. Here, we highlight how light-level geolocators provide promising opportunities to study these interactions. By examining raw light data, it is possible to detect encounters with artificial lights at night, while conductivity data give insight on seabird behaviour during encounters. We used geolocator data from 336 northern fulmars *Fulmarus glacialis* tracked from 12 colonies in the North-East Atlantic and Barents Sea during the non-breeding season to (1) confirm that detections of artificial lights correspond to encounters with fishing vessels by comparing overlap between fishing effort and both the position of detections and the activity of birds during encounters, (2) assess spatial differences in the number of encounters among wintering areas and (3) test whether some individuals forage around fishing vessels more often than others. Most (88.1%) of the tracks encountered artificial light at least once, with 9.5 ± 0.4 (SE) detections on average per 6 mo non-breeding season. Encounters occurred more frequently where fishing effort was high, and birds from some colonies had higher probabilities of encountering lights at night. During encounters, fulmars spent more time foraging and less time resting, strongly suggesting that artificial lights reflect the activity of birds around fishing vessels. Inter-individual variability in the probability of encountering light was high (range: 0–68 encounters per 6 mo non-breeding season), meaning that some individuals were more often associated with fishing vessels than others, independently of their colony of origin. Our study highlights the potential of geolocators to study seabird–fishery interactions at a large scale and a low cost.

KEY WORDS: Seabird–fishery interactions · Global location sensor · GLS · *Fulmarus glacialis* · Activity budget · Discards · Management policy

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1. INTRODUCTION

Fishing activities affect the ecology of many marine species (Humphries & Huettmann 2014, Diaz Pauli & Sih 2017), including both target-fish populations (Ivanova et al. 2020) and their predators, such as seabirds (Cianchetti-Benedetti et al. 2018). Seabird–fishery interactions can affect seabirds through different degrees of reliance on fisheries in their foraging strategies (Bearhop et al. 2001), distribution (Bartumeus et al. 2010) and population dynamics (Oro et al. 2004). These interactions can take various forms but are often negative for seabirds. This applies notably to bycatch, where the incidental capture of non-targeted species (e.g. seabirds, marine mammals) can severely impact seabird populations in many ecosystems (Wagner & Boersma 2011). Moreover, bycatch is often highly biased by sex and age (Gianuca et al. 2017), which can increase the impacts of bycatch on seabird populations (Barbraud et al. 2012, Gianuca et al. 2017). Seabird–fisheries interactions can also be indirect through competition for food resources, as the birds and fishers often exploit the same prey. This competition can lead to declines in seabird populations (Crawford et al. 1985, Wagner & Boersma 2011, Barbraud et al. 2018, Grémillet et al. 2018) or hinder seabird foraging efficiency (Bertrand et al. 2012). However, fisheries can also have positive effects on seabirds, for instance when triggering an increase in prey abundance if competitors or predators are fished (Wagner & Boersma 2011, Jurinovic et al. 2019), or by providing discards and offal (Le Bot et al. 2018).

Fishery discards (the proportion of catch that is not retained on board, such as fish below legal landing size, unmarketable species or species above quota restrictions) have been a major ecological issue since the intensification of fishing. In the North Atlantic, gradual regulations and technological improvements since the end of the 1980s (Kelleher 2005, Clark et al. 2020) have encouraged a more sustainable fishing industry, but some discarding still occurs (Watson 2017, Weimerskirch et al. 2020). This includes discarding of offal (organs and processing waste that are removed from the catch and thrown back into the sea) that represents an easily handled and highly calorific source of food for seabirds (Tasker 2000). Many studies have tried to quantify the consequences of seabirds feeding on fishery discards: by assessing spatial overlap between seabirds and fisheries (Cianchetti-Benedetti et al. 2018, Jurinovic et al. 2019, Clark et al. 2020); making direct observations onboard fishing vessels (Yeh et al. 2013); or using animal-borne cameras (Votier et al. 2013). More recently, another technique has been used, based on the raw light data recorded by light-level geolocators (global location sensors, GLS) — small data devices recording light to determine twice-daily positions of birds during the non-breeding season (Krüger et al. 2017). Given that nocturnal fisheries typically use intense light sources on deck, evidence of close encounters with these artificial light sources is recorded by geolocators attached to those individuals coming close to fishing boats at night. These devices also record conductivity (indicating contact with water) that can be used to infer bird behaviour during encounters (hereafter referred to as activity).

The intensity of interactions between seabirds and fisheries varies among species and areas (Furness 2003, Krüger et al. 2017, Grémillet et al. 2019, Jurinovic et al. 2019). It is important to understand how such differences are affected by factors such as fishing intensity (Clark et al. 2020) or discarding regulations (Sturludottir 2018). Reduced discards, for example, may benefit some seabird species through a reduction of bycatch risk (Bicknell et al. 2013). In addition, discards might be nutritionally inferior to natural prey (Grémillet et al. 2008), so that stricter discarding regulations would force the birds to concentrate their foraging efforts on more valuable food sources. For generalist seabirds, reduced discards may have negative effects in the absence of alternative sources of food (Bicknell et al. 2013). Reduced availability of discards may lead to prey switching, with some species predating other seabirds, their chicks and eggs (Regehr & Montevecchi 1997) or increasing kleptoparasitism (Martínez-Abraín et al. 2003), which can result in population-level impacts for affected species (Heubeck et al. 1999, Votier et al. 2008).

Among seabirds, procellariforms are often attracted to fisheries (Thompson 2006), and studies of these seabird–fishery interactions (Cianchetti-Benedetti et al. 2018, Weimerskirch et al. 2020) provide extensive evidence of discard consumption (Phillips et al. 1999, Sturludottir 2018). Previous studies using geolocators on procellariforms suggest that conductivity data provide reliable measures of activity during the non-breeding season, with prolonged dry periods indicating flight, prolonged wet periods indicating resting on the sea surface, and rapidly alternating between wet and dry indicating foraging (Gutowsky et al. 2014, Krüger et al. 2017).

In this study, we aimed to identify and quantify encounters between fisheries and northern fulmars *Fulmarus glacialis* in relation to broad-scale differences in fishing intensities within the North-East

Atlantic and Barents Sea. Our objectives were to (1) test the hypothesis that light detections correspond to encounters with fishing vessels in our study system, (2) assess whether birds change their activity when encountering artificial lights, (3) look at spatial variations in the probability and duration of encounters and (4) investigate the degree to which individuals might specialise in foraging near fishing vessels during the non-breeding season.

To achieve these aims, northern fulmars were equipped with GLS in different colonies across the North-East Atlantic and the Barents Sea. Previous studies have shown that several procellariform species, including northern fulmars, tend to overlap with fisheries (Camphuysen & Garthe 1997, Copello & Quintana 2009, Krüger et al. 2017) and are attracted by artificial lights (Rodríguez & Rodríguez 2009, Troy et al. 2013). If artificial light detections at night correspond to encounters with fishing vessels, we predicted that there will be high overlap between the positions of the detections and fishing effort (Krüger et al. 2017). In addition, we predicted that, if they take advantage of discards and offal from fishing vessels, fulmars will spend more time foraging during encounters (Camphuysen & Garthe 1997, Krüger et al. 2017). In contrast, if fulmars mostly follow boats that are not fishing, without feeding on discards, we predicted that they will spend more time flying (conductivity of 0) during the encounters. As fishing effort and discard ban policies vary between wintering areas (Kelleher 2005), we expected spatial variations in the number and duration of encounters (Bodey et al. 2014). For example, fulmars might stay longer in the vicinity of fishing vessels that are discarding larger quantities because of an increased prey abundance (Tasker 2000, Weimerskirch et al. 2000). Finally, from a conservation perspective, while conductivity data provide input on fulmar behaviour during encounters (e.g. they might be more vulnerable to bycatch if they are foraging than if they are only following vessels), it is also important to know whether some individuals, or individuals from specific colonies, encounter fishing vessels more often than others do, as increased encounters can influence population vulnerability to bycatch, and this information can be used to design conservation measures (Granadeiro et al. 2014, Patrick et al. 2015, Tyson et al. 2015).

2. MATERIALS AND METHODS

2.1. Study species and logger deployment

A total of 336 northern fulmars from 13 colonies (Fig. 1) were equipped with light-level geolocators (GLS) between 2007 and 2018. Colonies used in this study covered a large range of the overall fulmar distribution in the North-East Atlantic (Mallory et al. 2020). Icelandic colonies closer than 150 km to each other were grouped due to their proximity (Breidafjordur and Reykjanes, Langanes, Skjálfandi and Grimsey, Papey and Hólmanes). Birds were captured at their nest during one breeding season, banded and fitted with Migrate Technology (w65, c65, c65_super, f100, c250, c330), BAS (mk13, mk14, mk18, mk15, mk19, mk3, mk4, mk7) or Biotrack (mk4093, mk4083, mk3006, mk3005) loggers mounted on a plastic ring (see Table S1 in the Supplement at www.int-res.com/articles/suppl/meps13673_supp.pdf). Instrumented individuals were recaptured 1–5 yr later to recover the GLS. Some individuals were equipped several times.

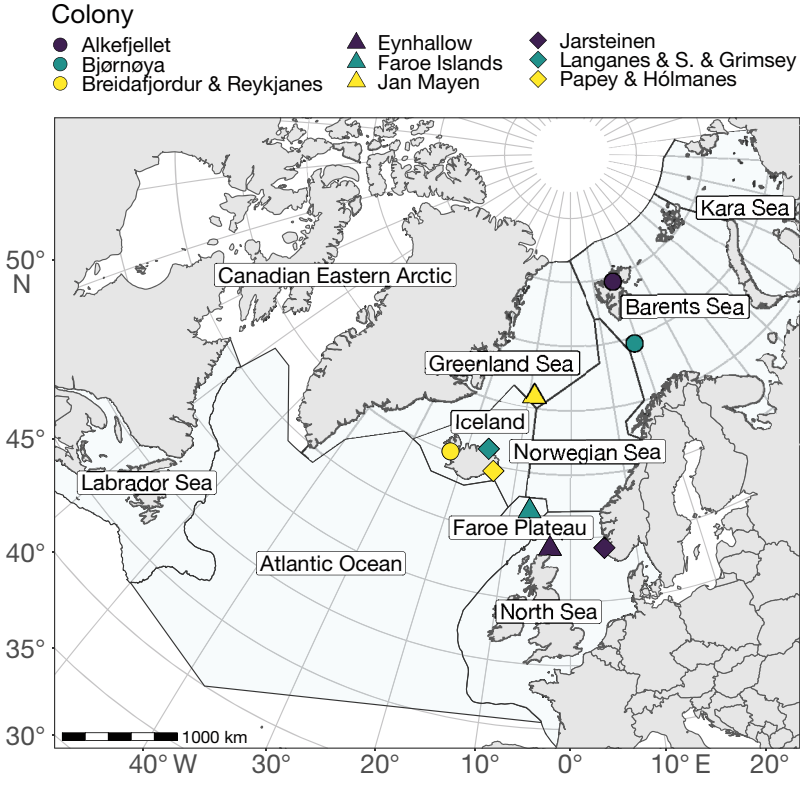

Fig. 1. Boundaries of the 10 northern fulmar wintering areas and locations of the studied colonies. S.: Skjálfandi

2.2. Processing of GLS data

We used a dataset based on 569 GLS deployments (out of a total of 593) that provided light data for the full deployment duration. Herein, a 'track' refers to a time period of 1 yr, from one breeding season to the next. Some individuals were equipped with a geolocator for longer than 1 yr; therefore, 1 deployment could record several successive annual tracks. The number of tracks per individual was on average 2.3 ± 0.1 SE (range 1–8 tracks ind.$^{-1}$).

We focused on the non-breeding season (October to March) when birds are not central-place foragers and are therefore less constrained in their movements. Excluding the summer was also relevant to include high-latitude colonies that experience midnight sun, which prevented the detection of artificial light encounters.

Loggers sampled light every 3 s, and recorded the maximum value in each 5 or 10 min interval. Different logger models recorded light differently. BAS and Biotrack loggers recorded light values from 0 (night) to a threshold value of 64 (day), whereas Migrate Technology loggers recorded light levels in lux. Loggers also sampled conductivity every 3, 6 or 30 s, and recorded the number of wet samples in each 5 or 10 min bin between 0 (dry) and a maximum value of 200, 50 or 20 (wet). Conductivity data were standardized (from 0 to 1) to be comparable among the logger types.

Positions were estimated using a threshold method, where light data were used to first characterize local times for sunrise and sunset, and from these, estimate 2 positions per 24 h based on time of apparent midnight and noon for longitudes, and length of night and day for latitudes. Unrealistic positions were removed as described by Bråthen et al. (2021), using speed, angle and zone filters. In addition, the determination of latitudes (but not longitudes) is inaccurate during equinoxes when day length is similar everywhere on the globe. Therefore, positions estimated during the equinox periods (8 September to 20 October and 20 February to 3 April) were also removed (Frederiksen et al. 2012, Bråthen et al. 2021). Finally, many locations could not be estimated when the birds were situated within the polar night area. These successive filters led to a heavily biased dataset, owing to the non-random distributions of data gaps (both in time, during the equinoxes, and in space, in the areas affected by the polar night). To alleviate this bias, all filtered-out locations were re-estimated using an algorithm that interpolates missing locations between 2 known locations. Briefly, this algorithm, building on a linear interpolation method originally proposed by Technitis et al. (2015), uses available additional information (e.g. light levels, land masks, longitudes during the equinoxes) to determine a plausible location for each timestamp at which a location is missing. The technical details can be found in Fauchald et al. (2019).

2.3. Encounter detection

To retain only periods of night in the raw light dataset, we used time of sunrise and sunset (hereafter twilight events), obtained when calculating positions. To avoid detecting potential remaining sunlight, we applied 2 corrections. Firstly, we removed light data 30 min around each twilight event. We then applied a correction during the polar night period, as some twilight can occur around the solar noon. Consequently, we removed all light data from the 60 min around the estimated time of solar noon during the polar night. Solar noon was estimated by using the solar noon times 10 d before and after each polar night period.

We used a light intensity threshold method to detect encounters of fulmars with artificial lights as described by Krüger et al. (2017). Since the light sensitivity of different loggers varied (Fig. S1 in the Supplement), we used 3 different thresholds. Biotrack mk3006 and mk 3005, and BAS mk15, mk19, mk3, mk4 and mk7 formed the 'Biotrack-high' group. For these, we used the same threshold of 10 as in Krüger et al. (2017), then we adjusted the threshold for other recording modes to have comparable data in terms of number and duration of encounters. Therefore, we used a threshold of 5 for the 'Biotrack-low' group (Biotrack mk4093 and 4083, and BAS mk13, mk14 and mk18) and 20 for Migrate Technology loggers.

To avoid overestimating the number of encounters, we assessed whether 2 light detections belonged to the same encounter by using the Bout-Ending Criterion method in the R package 'DiveMove' (Sibly et al. 1990, Luque & Guinet 2007). This method was originally designed for diving vertebrates (Sato et al. 2001) to detect whether successive dives belong to the same dive bout (a succession of dives, preceded and followed by longer breaks). We adapted the method to calculate the amount of time under which 2 light peaks could be considered as belonging to the same encounter (Text S1 in the Supplement).

The encounter detection process is summarized in Fig. 2. The positions of encounters were mapped using an azimuthal equidistant projection centred on the centroid of all fulmar positions. Their density was mapped into a raster where each cell is 200 km wide.

This resolution was chosen based on the accuracy of GLS data (Phillips et al. 2004). We focused on the spatial rather than temporal variation because preliminary analyses showed only little interannual variation in the location of wintering areas (Fig. S2).

2.4. Fishery data

We used open-access data available from the Global Fishing Watch website (https://globalfishingwatch.org/). These data provide the cumulative number of fishing hours per pixel and per day on a 0.01° pixel grid between 2012 and 2016. Data were merged into a raster where each cell is 200 km wide to be compared to the raster containing the density of encounters. Areas with high fishing intensity did not vary from year to year (Fig. S3), as mentioned in other studies (Guiet et al. 2019). We therefore pooled all years together. We also pooled all fishing vessel types, because our dataset contains mainly trawlers and fixed gears (Fig. S4). Fishing effort was calculated as the sum of fishing hours per grid cell, and we included all fishing gear types available in the dataset.

2.5. Spatial analyses and wintering area definition

To reduce the bias generated by varying numbers of tracks among colonies, and by variation in night duration (due to season and latitude), we applied a weighting correction to each detection:

$$WD = \frac{1}{P_n \times N_w} \times \frac{1}{\min\left(\frac{1}{P_n \times N_w}\right)} \quad (1)$$

where P_n is the proportion of night-time per 24 h on the date of the detection, N_w is the number of winter tracks recorded in the colony from which the bird originated, and WD is the weighted value of the detection.

We used the method described by Cuthbert et al. (2005) to calculate an overlap index quantifying the

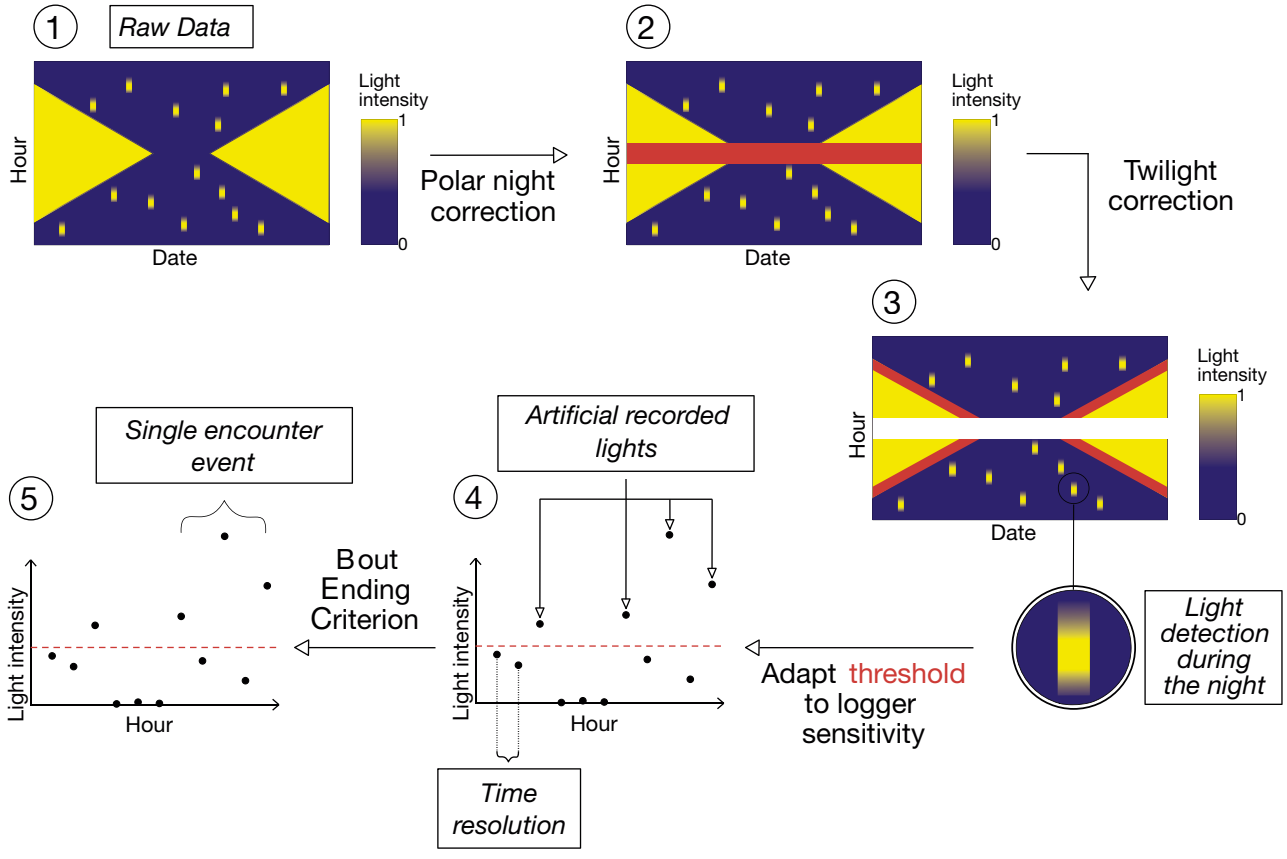

Fig. 2. Raw light data filtration and artificial light detection method: example for 1 individual encountering polar night. The first 3 panels represent the maximum light intensity per hour along date (*x*-axis) and time (*y*-axis). Yellow dots at night represent artificial lights. Panel 2 shows the filtration of twilight around noon during the polar night. Panel 3 shows the filtration of twilight before sunrise and after sunset events. Panels 4 and 5 represent the light intensity over time, showing an example of detections and encounter for 1 individual

spatial overlap between fulmar light detections and fishing vessels. The index was obtained by multiplying 2 rasters, one representing the fishing effort (sum of fishing hours), and the second representing the density of light encounters calculated as the sum of WD values in each cell. The weighting correction of detection was used for mapping and overlap index only.

Using QGIS v3.12.2 (https://qgis.org), we defined wintering areas (Fig. 1) with different exposure levels to fishing activities. These areas were based on regions presented in the Large Marine Ecosystem report of the Protection of the Arctic Marine Environment (PAME, working group of the Arctic Council) (Skjoldal et al. 2013), to which we added 3 additional regions in the south to cover the entire study area.

2.6. Assessing fulmar activity from conductivity data

We used conductivity data to assess fulmar activity. Conductivity measures whether the geolocator (on the bird's leg) is in saltwater ('wet') or not ('dry'). During the non-breeding season, a bird that was not in contact with saltwater was assumed to be flying; if the leg was constantly immersed, the bird was assumed to be resting on the sea surface, and if it was alternating between short wet and dry periods, the bird was assumed to be foraging (Lecomte et al. 2010).

To analyse fulmar activity budgets, we aggregated the conductivity data by individual and by encounter with artificial lights and calculated the proportion of time spent in each type of activity. We classified standardized conductivity values (see Section 2.2) in 3 activity types, as described by Lecomte et al. (2010): flying (conductivity <0.05), resting on the water (>0.95) and actively foraging (intermediate values). For each individual, we randomly selected control periods of the same duration as the cumulative duration of all encounters for that individual and in the same wintering area but for which no encounter was detected.

2.7. Statistical analyses

We used R version 3.6.3 for all statistical analyses (R Core Team 2020). All R code used for the analyses is available at https://github.com/benjamindps/Detections-of-seabird-fishery-interactions-using-GLS. A generalized linear mixed-effects model (GLMM) with a binomial distribution was used to test whether the probability of encountering artificial lights per night varied among wintering areas and colonies. A second GLMM with a binomial distribution was used to test for differences in encounter duration between colonies or wintering areas. More specifically, we tested the effect of the wintering areas and colonies on the probability of having short encounters (≤10 min) versus long encounters (>10 min), the median duration being 10 min. Three wintering areas with very low numbers of detections had to be removed for this model to ensure convergence (between 4 and 12 detections for Kara Sea, Labrador Sea and Canadian Eastern Arctic, versus 90–1992 detections for the other wintering areas). All models were built using the 'lme4' package (Bates et al. 2015) in R, including individual ID as a random effect to take the non-independence in the data into account.

We then investigated the changes in fulmar behaviour when encountering artificial lights using activity data. Each individual (n = 293; 3 loggers failed to record conductivity) was characterized by activity data (proportion spent flying, foraging or resting) during encounters and during a randomly selected control period (i.e. when no light was detected; see Section 2.6 for details). No test was appropriate for comparing activity when encountering artificial lights and in control groups (e.g. distribution of the data was not symmetrical around the median as required for non-parametric Wilcoxon signed-rank tests, and/or the distribution of the differences between paired data was not normal as required for paired *t*-tests), and we therefore based our discussion on bootstrap confidence intervals (CIs). We calculated the 95% CIs of the mean proportion of time spent in each activity (flying, foraging, resting) during encounters and in the control group using non-parametric bootstraps ('boot' and 'boot.ci' functions in the 'boot' package, Davison & Hinkley 1997, Canty & Ripley 2020). Non-overlapping CIs between the encounter and control groups were interpreted as significant differences. Results were exactly the same using Wilcoxon or *t*-tests, and we are therefore confident that our results and conclusions are robust.

Finally, to test whether the probability of encountering artificial light was consistent within individuals and within colonies, a repeatability test was performed using the 'rpt' function of the 'rptR' package (Stoffel et al. 2017). Repeatability was calculated as:

$$R = \frac{V_G}{V_G + V_R} \quad (2)$$

where V_G is the among-individual (or among-colony) variance component, and V_R is the within-individual (or within-colony) variance component when modelling the log-transformed (to fit normal distribution) number of encounters per 6 mo non-breeding period with individual and colony as random effects.

3. RESULTS

Loggers detected artificial light at night at least once in the period October–March in 657 tracks by 296 individuals (note that activity data were only available for 293 individuals), out of a total of 751 tracks by 336 individuals (Table 1A). For these birds, the average number of encounters per track was 9.5 ± 0.4 (SE) (Fig. S5) with a mean duration of 35.6 ± 0.7 min (Fig. S6).

3.1. Overlap between light encounters and fishing effort

Four wintering areas (Barents Sea, North Sea, Norwegian Sea and Iceland) contained most of the light detections (86.1% after weighting with Eq. 1), with the Barents Sea representing the highest proportion of detections (31.3%, Table 1B, Fig. 3A,B). In contrast, there were very few detections in the Atlantic Ocean (6.3%), Canadian Eastern Arctic (0.1%) and Labrador Sea (0.2%).

The fishing effort (defined as the sum of fishing hours per grid cell) was higher in Iceland, the Barents Sea, the North Sea (Fig. 3C). Applying the overlap index (Fig. 3D) confirmed that recorded light detections during the night spatially overlapped with the fishing effort. Again, this overlap was the strongest around Iceland, in the Barents Sea and the North Sea. Regarding the Norwegian Sea, we observed a low fishing effort combined with a moderate number of encounters, which led to a low overlap index.

3.2. Bird activity during light detections

We observed marked shifts in fulmar activity during light encounters (Fig. 4). Fulmars increased their time spent foraging by 37% and decreased their time spent resting and flying by 30 and 7%, respectively (Fig. 4).

Table 1. (A) Summary of the deployments and encounters per northern fulmar colony (see Fig. 1 for abbreviations). (B) Number of encounters in each wintering area. Weighted detection (WD) represents the value of a given light detection after the weighting process (Eq. 1)

(A)

	Colony									
	Breida-fjordur & R.	Langanes & S. & G.	Papey & H.	Jan Mayen	Faroe Islands	Eynhallow	Jarsteinen	Alkefjellet	Bjørnøya	Total
Number of tracks	17	127	11	102	28	318	26	32	90	751
Number of individuals	17	51	11	46	19	127	14	13	38	336
Tracks without detections	8	33	4	7	4	29	9	0	0	94
% with no detections	47.1	26.0	36.4	6.9	14.3	9.1	34.6	0	0	12.5
Number of encounters	95	418	34	729	68	2430	113	394	1479	5760
Sum of WD	2933.3	6159.9	2674.9	5849.3	3235.1	4502.9	6712.6	4639.7	4821.8	41 535.5
% of WD	7.1	14.8	6.4	14.1	7.8	10.8	16.2	11.2	11.6	100

(B)

	Wintering area									
	Canadian E. Arctic	Labrador Sea	Atlantic Ocean	Greenland Sea	Iceland	Faroe Plateau	North Sea	Norwegian Sea	Barents Sea	Kara Sea	Total
Number of encounters	12	5	231	253	351	90	1789	1023	1992	4	5750
Number of bird nights	1280	1242	25 435	7894	14 541	3181	31 714	20 582	15 415	541	121 825
Sum of WD	61.5	76.5	2602	2404	6359	573	8299	7916	12 868	17	41 176
% of WD	0.1	0.2	6.3	5.8	15.4	1.4	20.2	19.2	31.3	0.04	100

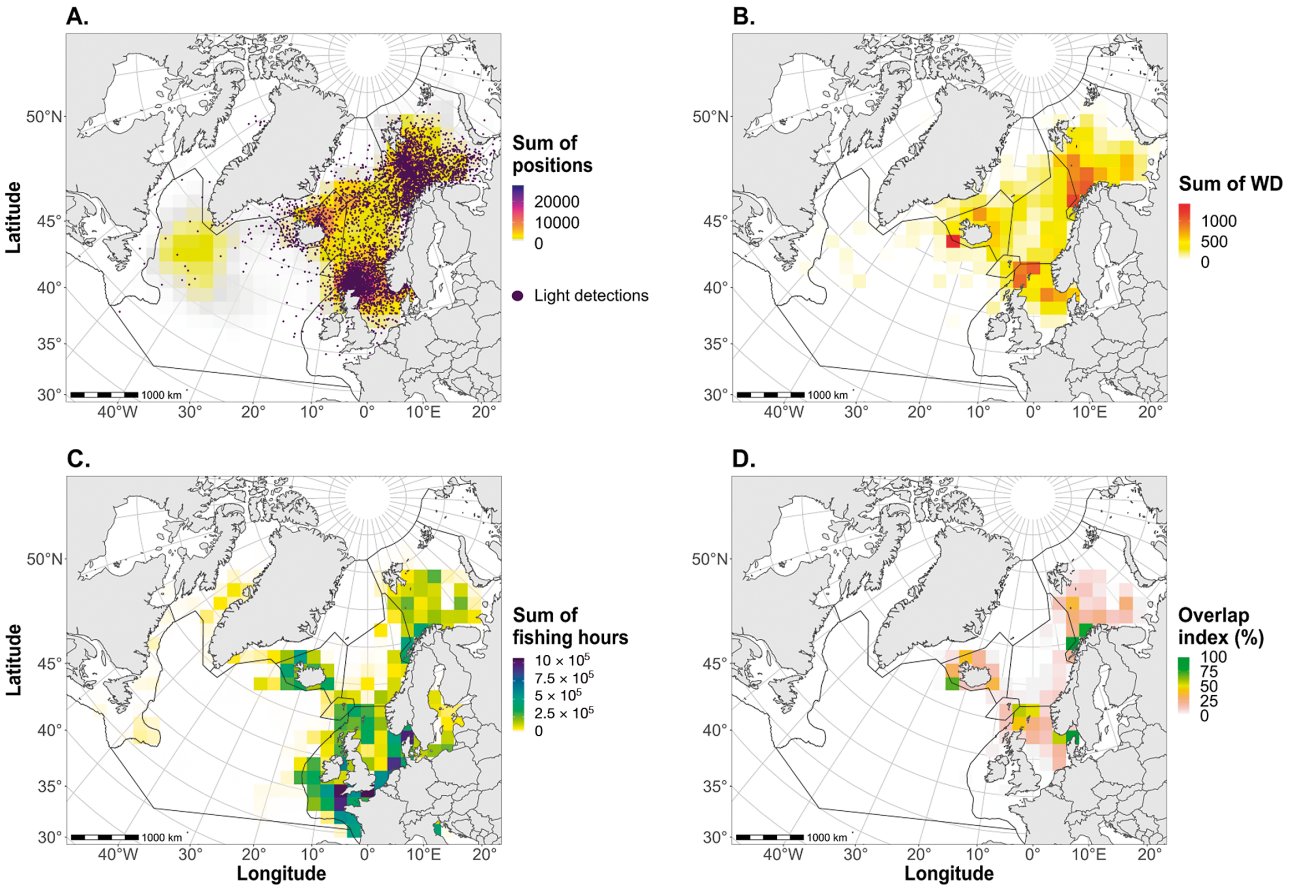

Fig. 3. Light detections at night overlap with fishing effort. (A) Positions of light detections. Each point represents 1 detection. The colour gradient represents the density of fulmar positions during the non-breeding season. (B) Raster of light detections after weighting (WD: weighted detection, i.e. the value of a given light detection after the weighting process). (C) Raster of the fishing effort (sum of the fishing hours per grid cell) recorded between 2012 and 2016. (D) Overlap between vessel density and light detections at night. Raster cells are 200 km wide. Azimuthal equidistant projection centred on the centroid of all fulmar positions

3.3. Spatial variations

Fulmars had, on average, a 0.04 (4 %) probability of encountering artificial lights per night (i.e. 4788 nights with at least 1 light encounter for a total of 121 825 individual-nights). Independent of the total night duration, this probability varied among colonies and among wintering areas (Table 2A, Fig. 5). More specifically, birds from Bjørnøya (average probability of 0.09), Alkefjellet (0.06) and Eynhallow (0.04) had the highest probabilities of encountering light at night, while birds from the Faroe Islands (0.01), Langanes/Skjálfandi/Grimsey (0.02) and Papey/Hólmanes (0.02) had the lowest probabilities (Fig. 5A). There were also differences in the probabilities of birds encountering artificial lights in the different wintering areas (Table 2A). The highest encounter probability was found in the Barents Sea (0.07; Fig. 5B) and the lowest in the Atlantic Ocean, Labrador Sea and Canadian Eastern Arctic (0.01; Fig. 5B). The probability of having short (≤10 min) or long (>10 min) encounters with artificial lights did not vary among colonies or wintering areas (Table 2B).

3.4. Consistency of the probability of encountering artificial lights at night

The frequency distribution of the number of encounters per non-breeding season (Fig. S5) shows that most tracks had a small number of detections, while some tracks had higher numbers (range: 0–68 encounters per 6 mo non-breeding season). The repeatability test revealed that 23.2 ± 9.7 % (mean ± SE) of the variation in the number of encounters per non-breeding season can be explained by the colony and 36.4 ± 5.7 % by the individual, independent of their colony (both likelihood ratio tests: $p < 0.001$). These repeatability values suggest that birds from some colonies were more likely to encounter artificial

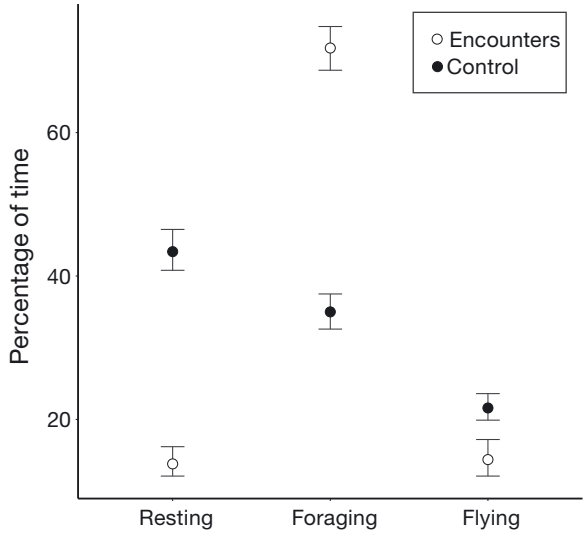

Fig. 4. Night activity budgets of 293 northern fulmars during encounters with artificial lights and in 'control' periods (i.e. with no light encounters). Activities are defined based on global location sensor (GLS) conductivity data and the proportion of time spent wet (flying if <5%, resting if >95%, active foraging otherwise; see Section 2 for details). Symbols represent the mean ± CI % of time spent in each activity

Table 2. Model selection for (A) the probability of encountering artificial light per night and (B) the probability that light encounters at night last ≤ or >10 minutes. Np: number of model parameters; Dev: deviance; AIC: Akaike's information criterion; ΔAIC: difference in AIC between a given model and the model with lowest AIC; colony: breeding colony of each individual; WArea: wintering area; night duration: total duration of the night; class: type of GLS logger (see Section 2 for details). Bird identity was included in all models as a random effect. For (A), the total sample size (number of individual-nights) was 121 825 from 336 individuals. For (B), the total sample size (number of encounters) was 5729 from 296 individuals encountering artificial lights. Three wintering areas with very few observations were removed from this analysis to allow model convergence (see Section 2.7 for details)

Model	Np	Dev	AIC	ΔAIC
(A) Probability of encountering artificial light per night				
Colony + WArea + Night duration	20	36 211.9	36 251.9	0.0
WArea + Night duration	12	36 311.5	36 335.5	83.6
Colony + Night duration	11	36 354.1	36 376.1	124.2
Night duration	3	36 743.5	36 479.5	227.6
Colony + WArea	19	37 066.9	37 104.9	853.0
WArea	11	37 178.9	37 200.9	949.0
Colony	10	37 264.4	37 284.4	1032.5
1 (intercept only)	2	37 392.2	37 396.2	1144.3
(B) Probability that light encounters at night last ≤ or >10 min				
1 (intercept only)	2	7828.9	7832.9	0.0
Class	4	7826.6	7834.6	1.7
WArea	8	7820.2	7836.2	3.3
WArea + Class	10	7817.4	7837.4	4.5
Colony	10	7826.0	7846.0	13.1
Colony + Class	12	7822.9	7846.9	14.0
Colony + WArea + Class	18	7814.4	7850.4	17.5

lights at night, and that, independent of their colony, some birds were also more likely to encounter lights.

4. DISCUSSION

A previous study at a single South Atlantic colony (Krüger et al. 2017) highlighted the potential for using light data from GLS to detect nocturnal seabird–fishery interactions. Applying this same method to a multi-colony international study, we demonstrate how this low-cost technique can provide important insights into seabird–fisheries interactions across large-scale areas such as the North-East Atlantic. The clear overlap between light detections and fishing effort (Fig. 3D) matches the areas where fishing is the most intense in Europe (i.e. the North and Barents Seas and Iceland). This overlap, in addition to the increased foraging activity during encounters, strongly suggests that the detection of artificial light by bird-borne light-loggers can be used to investigate interactions between seabirds and fisheries in our system.

While detecting abnormal lights in the raw light data is a straightforward process, one limitation is that the nature of the light source is not known. In our study system, we were challenged by the presence of polar night at high latitudes. It could happen that no clear sunrise and sunset were detected, and that crepuscular light still appeared in the raw light data. This was fixed by filtering light data around the solar noon. For studies outside polar areas, any detection of daylight period (if some sunrise and sunset events are missed while processing the data) can be fixed by filtering detections that have the same duration as the daylight. Regarding artificial lights, we cannot exclude that we detected light sources other than fishing boats, either from other commercial vessels or offshore oil platforms, both of which also attract seabirds (Wiese et al. 2001, Ronconi et al. 2015). This could, for example, be the case in the Norwegian Sea, where we found a significant number of light detections despite a low level of fishing effort (Fig. 3). Likewise, some of the detections in the North Sea may come from

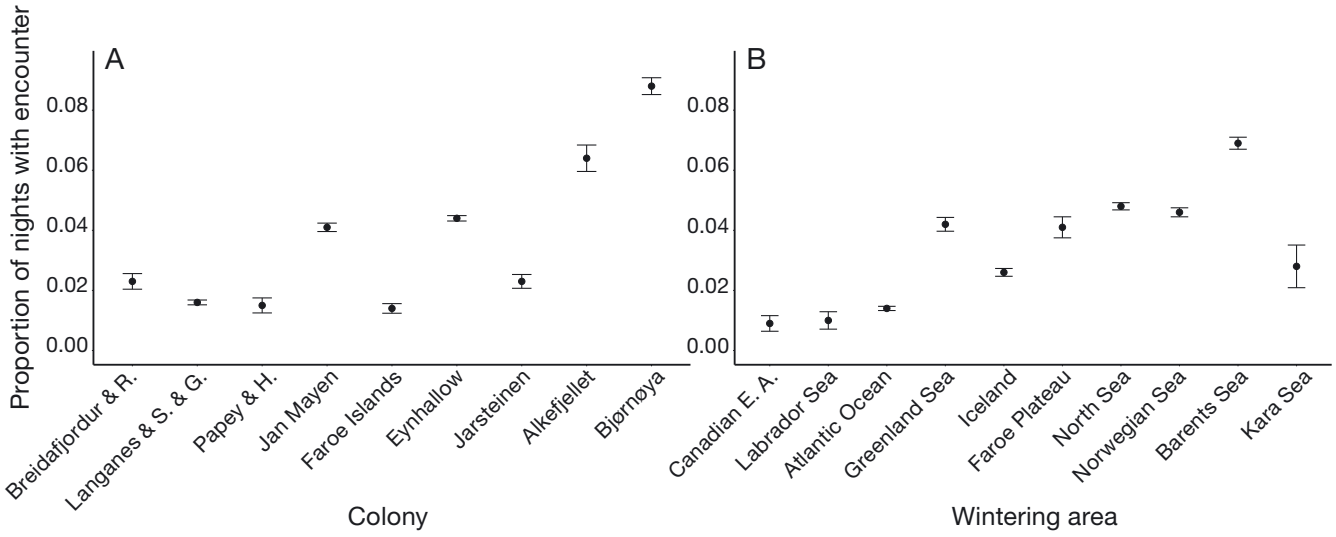

Fig. 5. Variation in the probability of encountering artificial light at night. Observed mean ± SE probability (A) per northern fulmar colony and (B) per wintering area. See Fig. 1 for full colony and area names

ships other than fishing vessels, as ship traffic is heavier there than in other wintering areas (Jalkanen et al. 2016), yet the overlap between detections and fishing effort remained quite high, supporting the hypothesis that fulmars mostly encountered fishing vessels. In the English Channel and the Celtic Sea (i.e the southeast part of the North Sea wintering area in the present study), the overlap was very low despite a high vessel density (i.e. high fishing effort and ship traffic; Jalkanen et al. 2016), most likely due to few of the tracked birds using these areas (Fig. 3A). At sea, fulmars might also encounter lights from wind turbine fields, although we did not find any evidence in the literature that the lights of wind turbine fields attract seabirds. Finally, other artificial light sources might come from coastal areas. During the non-breeding season, fulmars are mostly on the open seas, but sometimes visit their colonies; however, none of their colonies were affected by light pollution, and the activity data did not reflect colony visits (= conductivity of 0). We are therefore confident that potential coastal light encounters are negligible and more generally that the artificial lights encountered are a good proxy of the encounters with fishing vessels, as supported by the activity data. To further validate our technique, it is interesting to note that lights can be used to detect fishing boats at a very different scale: satellites are now used to monitor fishing activities at nighttime by detecting the lights of fishing boats, in particular those that do not broadcast their positions (Waluda et al. 2002, Park et al. 2020, Li et al. 2021).

The description of the encounters highlighted the fact that in wintering areas with different levels of fishing effort, the duration of such events may not change (there was no effect on the probability that encounters last more or less than 10 min), although their probability of occurring increased in wintering areas with higher fishing effort. Attraction of seabirds to fisheries in relatively small geographical areas has previously been demonstrated (Garcia-Barcelona et al. 2010), but to our knowledge, these interactions have not previously been assessed at as large a spatial scale as covered in the present study (i.e. the whole North-East Atlantic).

Not all of the colonies studied had the same exposure to fisheries. Colonies in which birds are the most likely to interact with fisheries were the ones located near fishing hotspots, respectively the North Sea for Eynhallow and the Barents Sea for Bjørnøya and Alkefjellet. There were also important inter-individual variations which accounted for more than 59 % in the probability of encountering fishing vessels (combining repeatability at individual and colony levels, which is consistent with other studies (Patrick et al. 2015, Gianuca et al. 2017, Krüger et al. 2017). The tendency for some individual fulmars to be more closely associated with fishing boats than others has also been demonstrated through analysis of higher-resolution GPS tracking and fisheries data in Scottish waters (Pirotta et al. 2018). This variation is likely to be partly related to sex and age class (Votier et al. 2013, Jimenez et al. 2016, Gianuca et al. 2017, Krüger et al. 2017). In terms of conservation, a sex-biased bycatch mortality can lead to changes in sex ratios and therefore a decline of the effective population size (Weimerskirch et al. 2005, Donald 2007). In a meta-analysis of global patterns of bycatch,

Gianuca et al. (2017) found that mortality was skewed towards adults, further exacerbating deleterious effects on seabird populations. However, North Atlantic studies tend to be under-represented in Gianuca et al. (2017) and other bycatch studies (see Pott & Wiedenfeld 2017). Studies that have been conducted in this region have highlighted that fulmars are commonly caught in a range of different fisheries (Anderson et al. 2011, Fangel et al. 2017, Bærum et al. 2019). Currently, the extent of these biases and the scale of threats are hard to estimate due to insufficient data on bycatch, although it is one of the greatest threats to seabirds (Croxall et al. 2012). Light-based assessments of interactions with vessels can now be integrated into individual-based demographic studies to further evaluate the basis and consequences of observed individual variation in interactions.

Even though we successfully identified a seabird–fishery overlap, it does not obviously mean that fulmars took advantage of fishing vessels to feed. Conductivity data helped us to highlight these interactions. Depending on the species and the studied area, some previous results indicated changes in behaviour during fishery encounters (Nel et al. 2002), while others did not (Grémillet et al. 2019). As we expected, fulmars showed behavioural changes during their interactions with fishing vessels. These modifications were specific to the encounter period and coincided, in every studied wintering area, with more time spent foraging around the boat and less time spent resting on the water. This is in line with onboard observations of fulmars (Hedd et al. 2016) and previous results on procellariforms (Nel et al. 2002).

Fulmars are attracted to fishing vessels (Skov & Durinck 2000), with specific high concentrations of individuals around fisheries (Wahl & Heinemann 1979). Pirotta et al. (2018) recently quantified the extent to which individual fulmars associated with vessels during the breeding season, when higher-resolution GPS tracking data can be obtained. Our study is the first to provide colony-specific estimates of variation in the number of encounters between northern fulmars and fisheries during the non-breeding season at an individual scale (i.e. 9.5 ± 0.4 SE encounters per 6 mo of non-breeding season, varying from 0 to 68). Using the same method on another procellariform, Krüger et al. (2017) found that the number of nights with fishing vessel encounters was in the same order of magnitude (between 20 and 30 for the whole year) in the South Atlantic Ocean, where fishing effort is high and there is no discard ban policy. Moreover, this raises questions concerning the prevalence of discards and offal in fulmar diet. In gannets, only 42% of the foraging behaviour around fishing vessels could be considered as direct foraging on fishery offal (Votier et al. 2013). In our study, although we could only detect the interactions occurring at night, their number remained relatively low. Thus, it seems likely that offal and discards represent a low proportion of fulmar diet during the non-breeding season according to our results. This is highly contrasting with diet studies conducted during the breeding season on birds captured both at the colony and at sea, where up to 72 and 40% of the diet, respectively, consisted of fishery discards (Lilliendahl & Solmundsson 1997, Phillips et al. 1999). Additionally, fishery discards available to seabirds also fluctuate over longer time scales; in the North Sea, the number of seabirds that could be supported by fishery discards has declined by 39% between 1990 (peak of fishery discards) and 2010 (Sherley et al. 2020). Further investigations would be needed to study the seasonal and interannual variations in the importance of discards in fulmar diet.

In the present study, we analysed only night data and indirect measurements of fulmar behaviour due to methodological constraints. We suggest that future studies should combine GLS light data with other sources of information like direct onboard observations of fulmar interactions with fisheries, which could provide information about bycatch mortality and any related biases that are crucial for conservation. Comparing day and night encounter probabilities could be useful to evaluate the role of artificial lights in attracting fulmars. Some seabird species that nest in burrows are actively attracted by artificial lights at night (Montevecchi 2006), but this is less common for birds nesting on the ground, including fulmars. In addition, knowing that procellariforms have well-developed olfaction and may use this sense rather than vision to search for food (Nevitt 2000), it is possible that they are more attracted by the fishing activity itself than by the light. Diet analyses would also help to assess potential differences in the reliance on fisheries among different wintering areas and between seasons. More recent methods to obtain dietary information, such as stable isotopes, DNA metabarcoding or fatty-acid analyses, could also be useful and have proven to be efficient in reconstructing the amount of discards eaten by seabirds (Mariano-Jelicich et al. 2017, McInnes et al. 2017, Conners et al. 2018). The nature of observed individual variation should also be explored further in relation to management policies that are typically only

considered at larger population scales (Croxall et al. 2012, Gianuca et al. 2017). Finally, the activity shift observed during encounters that led to foraging around fisheries could have fitness consequences that remain to be investigated.

In conclusion, we found that fulmars encountered fisheries at night during the non-breeding season. The probability of encounter was highly variable between individuals but was higher in wintering areas with intense fishing effort. Fulmars tended to forage more and rest less during these periods. We provided a useful methodological framework to study seabird–fishery interactions at larger scale, which is crucial to understand and compare the consequences of management policies for entire seabird populations.

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