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Original Article

Gannets are not attracted to fishing vessels in Iceland—potential influence of a discard ban and food availability

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Fisheries produce large amounts of waste, providing food subsidies for scavengers. Discards influence seabird movement, demography and community structure, but little is known about seabird–fishery interactions where discarding is banned. Here, we investigate how northern gannets *Morus bassanus* respond to fishing vessels in Iceland, where discarding commercial species is illegal, but birds may still access bait, offal, or catch. We GPS-tracked 82 foraging trips for 36 breeding gannets from two colonies (Skrúður and Hellisey) and obtained time-matched vessel locations. We classified bird behaviour using Hidden Markov Models and then tested the effect of vessel distance on behavioural state-switching using multi-state Markov models. Fishing vessels were present during 94% of foraging trips. However, the likelihood of gannets switching from travelling to foraging was unaffected by vessel proximity, regardless of gear type or activity. When encountering vessels, gannets rarely foraged but instead were more likely to continue travelling. When controlling for population size, gannet foraging trips at both colonies were shorter than expected, suggesting favourable conditions. The lack of behavioural responses to vessels among Icelandic gannets is likely driven by the discard ban and availability of pelagic fishes. Our findings have implications for understanding bycatch risk and the consequences of discard reforms.

Keywords: behavioural response, biologging, foraging, GPS tracking, *Morus bassanus*, northern gannet, Predictable Anthropogenic Food Subsidies (PAFS), scavenging, seabird–fisheries interactions, Vessel Monitoring Systems (VMS)

Introduction

Fisheries provide food subsidies in the form of discards, attracting large numbers of scavengers (Oro *et al.*, 2013). Seabirds are one of the most conspicuous consumers of fisheries waste (Sherley *et al.*, 2019), with at least 52% of seabird species eating discards (Oro *et al.*, 2013). While reducing discards is key for a sustainable fishing industry, this may considerably impact the large numbers of scavenging individuals (Bicknell *et al.*, 2013). On the other hand, many birds that feed at vessels are killed as bycatch (Lewison *et al.*, 2004) and reducing discarding may in turn reduce mortality. As a result, understanding the consequences of variation in discard availability is valuable for the study of marine ecology, as well as for ecosystem approaches to fisheries management (Zeller *et al.*, 2018).

Subsidies from fishing vessels affect seabird diet (Votier *et al.*, 2004), movement patterns (Bodey *et al.*, 2014), population dynamics (Oro *et al.*, 2004), species distributions (Arcos and Oro, 1996), and community composition (Church *et al.*, 2018). Seabird–fishery interactions are therefore important, yet complex. For instance, they vary among species (Collet *et al.*, 2017), populations (Petyt, 1995; Granadeiro *et al.*, 2011), and individuals (Votier *et al.*, 2010; Patrick *et al.*, 2015), with fishing vessels being a key resource in some regions while of little importance in others. For example, Scopoli's shearwaters *Calonectris diomedea* in the western Mediterranean follow fishing boats for food (Soriano-Redondo *et al.*, 2016), while most in the central Mediterranean do not (Cianchetti-Benedetti *et al.*, 2018). Similarly, in waters around New Zealand, White-capped albatrosses *Thalassarche steadi* overlap strongly with vessels (Torres *et al.*, 2011), while Campbell albatrosses *Thalassarche impavida* show limited attraction (Sztukowski *et al.*, 2017). The reasons for such variation in attraction to fishing vessels are not fully understood but may relate to differences in discard availability, naturally occurring foods, or both (Votier *et al.*, 2004).

Most research into fisheries interactions takes place in areas with high discarding rates, such as the United Kingdom (Votier *et al.*, 2013), the Mediterranean (Soriano-Redondo *et al.*, 2016), and the Benguela Current region (Tew Kai *et al.*, 2013). As such, comparing responses to fishing vessels in regions with differing discard availability could provide valuable insights into scavenging behaviour and the potential impacts of changing discarding practice. For example, in Iceland, discarding is banned for all species of commercial value (Popsescu and Poulsen, 2012; Marchal *et al.*, 2016), and other measures have been introduced to reduce discarding, including increased trawl net mesh size (Sturludottir, 2018), transferable quotas (Woods *et al.*, 2015), a penalty-free allowance for landing undersized fish (Sturludottir, 2018), and real-time closures in response to undersized fish (Björnsson *et al.*, 2015). Illegal discarding occurs despite these measures, but estimated rates are low at 0.9% for cod *Gadus morhua* and 2% for haddock *Melanogrammus aeglefinus* (Valtýsson, 2014), compared to 8–22% for haddock in the late 20th century (Sturludottir, 2018). While there are no other species-specific estimates of discard rates for Iceland, overall discard rates were estimated at 2.8% in 2010 (Valtýsson, 2014; Zeller *et al.*, 2018). The fate of discards in Iceland is also unknown, aside from records of discard consumption by northern fulmar *Fulmarus glacialis* (Lilliendahl and Solmundsson, 1997; Sturludottir, 2018). Offal dumping, where waste from gutting marketable catch is disposed of, is permitted but has not been quantified (G. M. Sigurðsson, pers. comm.). Overall, discards are not widely available to birds in Icelandic waters, but there is little known about seabird–fishery interactions there.

Northern gannets *Morus bassanus* are a regular scavenger in some parts of their range (Votier *et al.*, 2010, 2013), but their interactions with fishing boats have not been studied in Icelandic waters. Gannets vary regionally in scavenging tendency, with strong responses to vessels in the Celtic sea (Bodey *et al.*, 2014; Patrick *et al.*, 2015), where discarding rates are high, but limited attraction in the North Sea (Camphuysen *et al.*, 1995b). There may also be seasonal differences in discard use in some regions, with more gannets observed feeding on discards in the North Sea in winter than in summer (Camphuysen *et al.*, 1995a). This spatial and temporal variation in scavenging behaviour is poorly explained and may be related to variation in the availability of discards and alternative foods.

As well as discards, fisheries present other foraging opportunities. Offal may available in Iceland, but gannets rarely feed on this, instead preferring discarded whole fish, particularly gadoids (Camphuysen *et al.*, 1995a). Gannets may also take bait or catch from longlines (García Barcelona *et al.*, 2010), while fish corralled into nets provide a focal point for diving (Petyt, 1995). These behaviours bring gannets in contact with fishing gear, with the potential for injury and death, particularly for those attending longliners (Oliveira *et al.*, 2015). At trawlers, collision with warp cables and entanglement are risks (Watkins *et al.*, 2008). Bycatch data for gannets in Iceland is limited to gillnets (Anderson *et al.*, 2011), with few caught, but elsewhere in their range where discarding is common (Portugal, Canada, and the United States), gannets experience high bycatch from gillnets, longlines, trawls, and seines (Žydelis *et al.*, 2013; Oliveira *et al.*, 2015). As seabird mortality risk at vessels is increased by discarding or dumping offal while gear is still in the water (Pierre *et al.*, 2010; Maree *et al.*, 2014), understanding the role of discarding in attracting gannets to vessels could help to explain the regional variation in gannet bycatch rates.

To investigate whether gannets are attracted to forage at fishing vessels in a region where discarding is banned, we GPS-tracked chick-rearing adults at two Icelandic colonies. Here, we used Hidden Markov Models to classify gannet behaviour and then investigated the influence of vessel proximity on changes between these behavioural states using multi-state Markov models. We also examined responses to different gear types with differing levels of potential foraging opportunities during hauling or due to variation in potential spillage of fish or illegal discarding. We also calculated foraging trip duration, range, and distance travelled as measures of foraging effort and compared this against estimates from other gannet colonies to indicate natural food availability.

Methods

Study sites and sampling

GPS tracking took place in July 2016 and 2017 at two colonies in Iceland: Skrúður (64.900°N, 13.632°W) and Hellisey (63.361°N, 20.366°W). Skrúður had 6051 apparently occupied nests (AONs) in 2013. Hellisey had 3374 AONs in 2014 but is part of the Vestmannaeyjar archipelago, which had 15 044 AONs in 2013/2014 (Garðarsson, 2019). We captured chick-rearing gannets at the nest using a pole and noose and attached Mobile Action Technology "i-gotU" GPS loggers to the central tail feathers with Tesa® tape. We deployed 48 loggers and retrieved 38 after 1–3 d. Two loggers failed, yielding 36 datasets with GPS locations every minute (Skrúður 2016–2017 and Hellisey 2017) or 2 min (Hellisey 2016). GPS loggers weighed 20 g (i-gotU 120) or 35 g (i-gotU 600), which were 0.7% or 1.2% of the lightest bird. In 2016, ten birds were equipped with i-gotU 120 GPS loggers, accelerometers (Gulf Coast Data Concepts X16-mini) and altimeters (MSR-145W), totalling 54 g (1.9% of the lightest bird). The acceleration and altitude data are not used in this study. Previous studies found no effects of similar loggers on foraging trip duration or body mass for chick-rearing gannets (Hamer *et al.*, 2000). We collected diet samples for tracked adults that spontaneously regurgitated food, and chick diet was surveyed concurrently during annual ringing. Protocols were completed with the permission of the Icelandic Institute of Natural History with ethical approval from the University of Exeter (2016/1519).

Gannet foraging trips

We extracted foraging trips from bird-borne GPS loggers when birds exceed 2 km from the colony using the "raster"

(Hijmans, 2018) R package. We removed trips of one GPS fix, partial trips (no return within 2 km of the nest), and trips of less than 5 km from the colony to account for rafting (Bodey *et al.*, 2014). We calculated the foraging trip duration, the foraging range as the maximum distance reached from the colony, and the total distance as the summed distance between each successive GPS location. We then compared trip duration, as a proxy for food availability, in relation to the square root of colony size with the data for other colonies published in Lewis *et al.* (2001).

Co-occurrence of gannets and fishing vessels

To assess co-occurrence with tracked gannets, we used time-matched fishing vessel locations and vessel speeds at approximately 10-min frequency. We obtained vessel locations from the Icelandic Directorate of Fisheries recorded by either satellite-based Vessel Monitoring Systems (VMS) or radio-based Automatic Identification Systems (AIS) for fishing vessels of all sizes (Geirsson, 2011). This covered the two study periods (29 June 2016 to 12 July 2016 and 29 June 2017 to 12 July 2017) across the gannet foraging areas for Skrúður (64°N to 66°N, 15.5°W to 11.5°W) and Hellisey (62.5°N to 64°N, 23.1°W to 19°W). We excluded records for which a vessel ID could not be obtained (~7% of records), with 245 731 vessel locations remaining for analysis. Gear type was obtained for 77% of vessels by cross-referencing with the Icelandic Directorate of Fisheries Logbook database (Geirsson, 2011). For 4% of records, the gear type was known for 1 d, but unknown for the previous or next day and the vessel remained within the study area for a 30-min window around midnight, so we relabelled these records with the previous or next gear type. We classified vessel activity as "steaming", "drifting", and "fishing" using gear-specific speed thresholds (Supplementary Table S1; Gerritsen and Lordan, 2011; Bodey *et al.*, 2014).

For each trip, we recorded the presence of vessels and vessels travelling at fishing speed within the foraging range during the trip duration. We classified bird behaviour into "travelling", "resting", and "foraging" states based on step length and turning angle with a three-state Hidden Markov Model implemented using the "moveHMM" R package (Michelot *et al.*, 2016), using linear interpolation to regularize the GPS data to sampling frequency (1 or 2 min). Distributions of step length and turning angle for each state, and model checks were typical for the method (Supplementary Figures S1–S3), which has been tested for northern gannet foraging behaviour using dive loggers to ground-truth foraging behaviour (Bennison *et al.*, 2018). Hidden Markov Models proved more successful than *k*-means clustering, first passage time, speed/tortuosity thresholds, kernel density, effective maximization binary clustering, and machine learning (Bennison *et al.*, 2018). We recorded the instances of each behaviour occurring within 1, 2, and 11 km of the nearest vessel; 1 and 2 km indicate potential scavenging, and gannets respond to vessels at 11 km away (Bodey *et al.*, 2014). These distance categories are not mutually exclusive, such that if a vessel is within 1 km, it is also within 2 km.

Behavioural response to fishing vessels

To quantify behavioural responses to nearby vessels, we investigated the effect of vessel distance on the probability of switching from travelling to foraging behaviour (see Figure 1 for the modelling process). We choose to model the probability of switching to foraging rather than the probability of foraging because this is more likely to represent a direct response to the vessel. On the other hand, if a bird is already foraging while a vessel approaches (perhaps even using the foraging gannets as a cue for locating fish), the foraging behaviour may be unrelated to the proximity of the vessel.

We used the behavioural classifications from the Hidden Markov Models detailed above to identify instances where gannets switched between the behavioural states of travel, foraging and rest. We then modelled state-switching probability using multi-state Markov models implemented in the "msm" R package (Jackson, 2011; Bodey *et al.*, 2014). We did not use more recently developed packages, as these interpolate covariates where data are unavailable, which is inappropriate for distance to the nearest vessel. We extracted the location of each vessel before and after each regularized bird location and linearly interpolated vessel tracks to the time of the bird record. We calculated distances to the nearest: (i) vessel, (ii) trawler (Danish seine, pelagic trawl, otter trawl, and Nephrops trawl) that may provide scavenging opportunities during net hauling, (iii) demersal trawler (Nephrops and otter trawls) that have high historical discard rates indicating a higher probability of illegal discarding, and (iv) vessel travelling at fishing speed, as intermediate speeds may reflect hauling or sorting and so relate to higher potential food availability for scavenging seabirds. We modelled state (travel, forage, or rest) in relation to time, with the distance to the nearest vessel, trawler, demersal trawler, and vessel travelling at fishing speed fitted as a binary covariate for each 1 km interval up to 25 km (Bodey *et al.*, 2014).

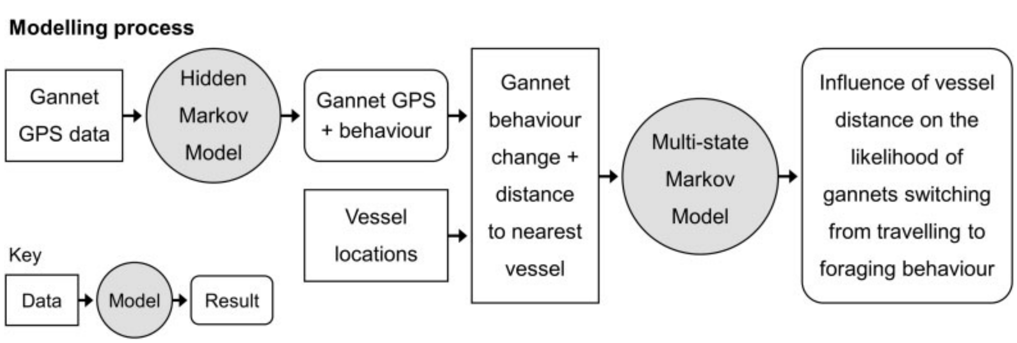

Figure 1. An outline of the two-stage modelling process for investigating the influence of fishing vessel proximity on northern gannet *M. bassanus* foraging behaviour.

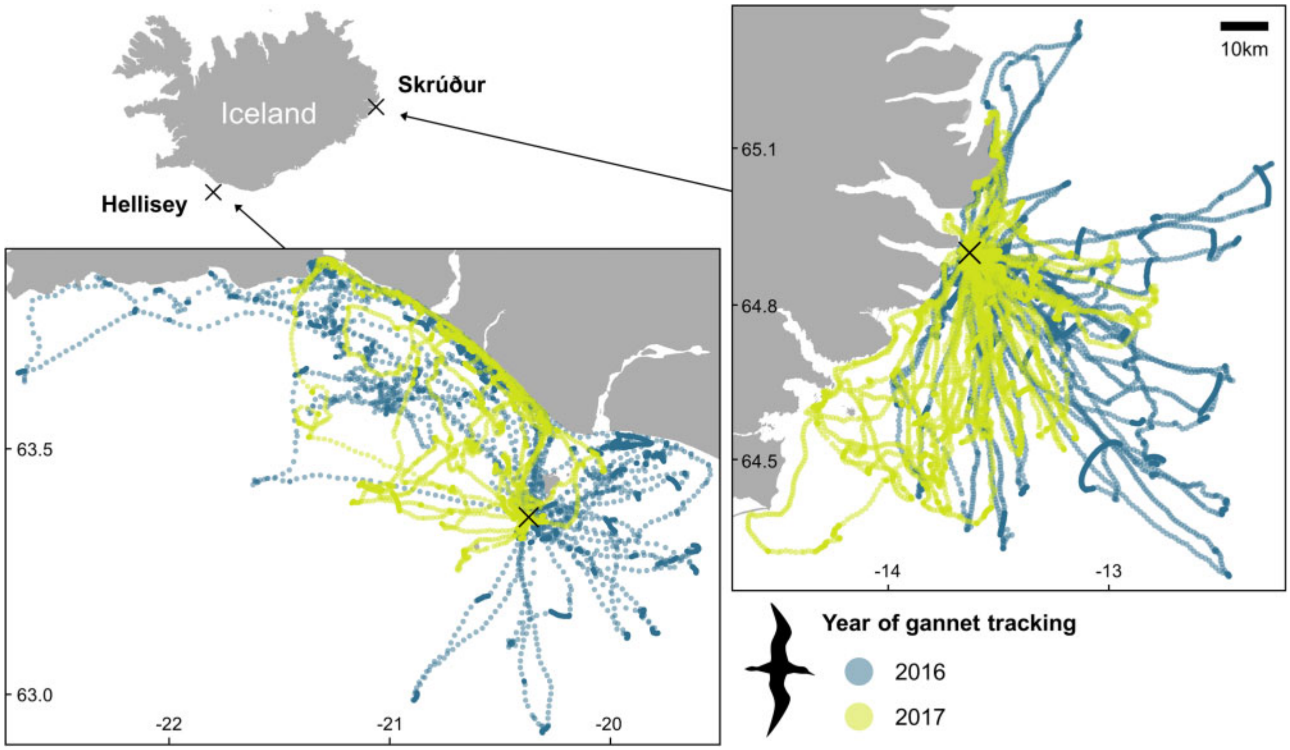

Figure 2. Foraging trips for chick-rearing northern gannets *M. bassanus*, from Hellisey and Skrúður, Iceland, coloured by sampling year. Map adapted from tiles by Stamen Design, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

Results

Gannet foraging trips

We recorded 82 complete foraging trips for 36 individuals (Figure 2)—30 trips for nine birds from Hellisey and 52 trips for 27 birds from Skrúður. For Hellisey and Skrúður, respectively, the mean ± standard deviation trip durations were 10.23 ± 7.41 and 4.81 ± 4.53 h, foraging ranges were 42.95 ± 27.04 and 29.19 ± 24.16 km from the colony and total distances travelled were 150.16 ± 127.93 and 93.55 ± 85.52 km. The mean foraging trip durations for each colony were lower than expected for the colony size, particularly for Skrúður (Figure 3).

Co-occurrence of gannets and fishing vessels

Fishing vessels were present in the spatial and temporal range of 94% of gannet foraging trips ($n = 77$) and were travelling at fishing speeds for 76% of the trips ($n = 62$). The nearest vessel to each gannet location used mainly handlines or longlines but 24% of the nearest vessels were trawlers (Table 1). Hidden Markov Models assigned behaviours to all 33 323 regularized bird locations, with 27% labelled as foraging. Gannets rarely foraged close to vessels, with only 1.9% of foraging locations occurring within 1 km of a vessel, despite 38% occurring within 11 km (Table 2). Visual inspection of the tracks coded by behaviour and by time confirmed that gannets generally continued travelling when encountering a vessel (Figure 4).

Behavioural response to fishing vessels

We recorded 691 transitions from travelling to foraging states. Multi-state Markov models show no significant effect of the distance to the nearest vessel, demersal trawler, or vessel travelling at fishing speed on gannets switching from travelling to foraging. Gannets were slightly more likely to switch to foraging within 4 km of the nearest trawler, but we did not detect an effect for any other distance (Figure 5; Supplementary Table S2).

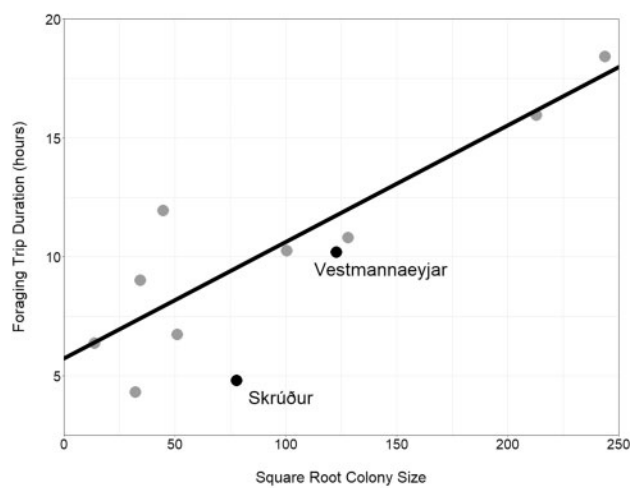

Figure 3. Mean foraging trip durations for northern gannet *M. bassanus* colonies in relation to the square root of colony size. Grey circles indicate trip durations from Lewis *et al.* (2001), and the black line shows a linear relationship for just these nine colonies observed in 2000. Black circles indicate the colonies in this study.

Table 1. Number of vessel records within the study area encompassing the foraging ranges for each colony (Skrúður: 64–66°N, 15.5–11.5°W and Hellisey: 62.5–64°N, 23.1–19°W) and time window during which gannets were tracked (29 June 2016 to 12 July 2016 and 29 June 2017 to 12 July 2017) with each gear type or category, and the number of regularized northern gannet *M. bassanus* locations where the nearest vessel at the time has that gear type or category.

		Vessel records in study window		Gannet locations	
Category	**Gear types**	**Number of vessel records**	**Percentage**	**Nearest vessel gear type frequency**	**Percentage**
Total	All gears	245 731	100	33 323	100
Single gear	Longline	39 007	15.9	9 514	28.6
	Gillnet	1 319	0.5	0	0
	Handline	119 411	48.6	9 744	29.2
	Danish Seine	6 618	2.7	2 475	7.4
	Otter trawl	13 375	5.4	2 179	6.5
	Pelagic trawl	12 238	5.0	2 562	7.7
	Nephrops trawl	6 975	2.8	902	2.7
	Unknown	46 788	19.0	5 947	17.8
Trawler	Danish seine, pelagic/ otter/ Nephrops trawl	39 206	16.0	8 118	24.4
Demersal trawlers	Otter trawl, Nephrops trawl	20 350	8.3	3 081	9.2
Fishing speed	All gear types	113 308	46.1	12 333	37.0

Table 2. Number of northern gannet *M. bassanus* locations for each behaviour occurring within specified distances of the nearest fishing vessel.

		Distance to vessel, *n* (%)		
Behaviour	**Total**	**<11 km**	**<2 km**	**<1 km**
All	33 323	12 797 (38)	1 150 (3.5)	472 (1.4)
Foraging	9 029	3 444 (38)	337 (3.7)	175 (1.9)
Resting	15 635	5 426 (35)	547 (6.3)	227 (2.6)
Travelling	8 659	3 927 (45)	266 (1.7)	70 (0.4)

Diet

We examined regurgitates from three tracked adults, all of which contained mackerel *Scomber scombrus*. Concurrent sampling of 159 chick regurgitates from Hellisey and Skrúður for 2016 and 2017 revealed 49.4% herring *Clupea harengus*, 44.4% mackerel, 2.5% Capelin *Mallotus villosus*, or similar, 1.2% gadoid and 2.5% unidentified fish (Supplementary Table S3).

Discussion

We investigated interactions between foraging gannets and fisheries in Icelandic waters, where discarding is banned. Fishing vessels were abundant within the gannets' foraging range, but there was little evidence of attraction to vessels—the distance to the nearest vessel did not influence the probability of gannets switching from travelling to foraging, regardless of gear type and fishing activity. Gannet diet samples were dominated by naturally occurring pelagic fishes, and short trip durations implied this prey was plentiful. The potential reasons for gannets ignoring fishing vessels in Iceland, and the wider implications of this behaviour, are discussed below.

Variation in behavioural response to fishing vessels

Icelandic gannets largely ignore vessels even though fish are available during net hauling (Petyt, 1995). Our findings contrast with the strong behavioural response of gannets to fishing activity in the Celtic Sea where discarding is common (Votier *et al.*, 2013, 2010; Bodey *et al.*, 2014; Patrick *et al.*, 2015). Bodey *et al.* (2014) found that gannets were more likely to switch from travelling to foraging when closer to a vessel and the response was stronger for vessels travelling at fishing or catch sorting speed. This comparison contributes to a growing literature showing that attraction to vessels varies not only among species (Collet *et al.*, 2017) but also within species in different regions (Soriano-Redondo *et al.*, 2016; Cianchetti-Benedetti *et al.*, 2018). Such differences likely relate to variation in discard rates. For instance, long-term variation in discard consumption by great skuas *Stercorarius skua* is closely correlated with changes in discard rates (Votier *et al.*, 2004; Church *et al.*, 2018). Moreover, seabird bycatch rates can be higher during discarding and offal dumping (Watkins *et al.*, 2008; Pierre *et al.*, 2010; Maree *et al.*, 2014). This evidence suggests that discarding is important in determining the extent to which seabirds are attracted to fishing vessels (Wahl and Heinemann, 1979).

Food availability may also contribute to regional variation in seabird–fisheries interactions. Scavenging is less likely when natural food is plentiful (Hamer *et al.*, 1991; Skov and Durinck, 2001; Tew Kai *et al.*, 2013; Church *et al.*, 2018), partly because scavenged foods can have lower nutritional quality compared to natural prey (Grémillet *et al.*, 2008). Conditions in Iceland seem to be favourable for gannets—there is likely to be ample natural prey, as evidenced by shorter foraging trips than expected given the respective sizes of the two colonies studied here (Figure 3). Recent influxes of pelagic fish linked to climate warming (Vigfúsdóttir *et al.*, 2009; Astthorsson *et al.*, 2012), and a relatively small gannet population compared to the Celtic Sea may have resulted in little competition for resources (Murray *et al.*, 2015; Garðarsson, 2019). We found that most gannet diet samples were pelagic fishes (94% herring or mackerel, consistent with surveys of gannet chick diet in 2006, 2007, 2011, and 2013; Vigfúsdóttir *et al.*, 2009; Vigfúsdóttir, unpublished data). These species are not only the subject of commercial fisheries but also available as natural caught prey. Therefore, while the evidence is only circumstantial, Icelandic gannets may be ignoring fishing vessels because pelagic prey is plentiful.

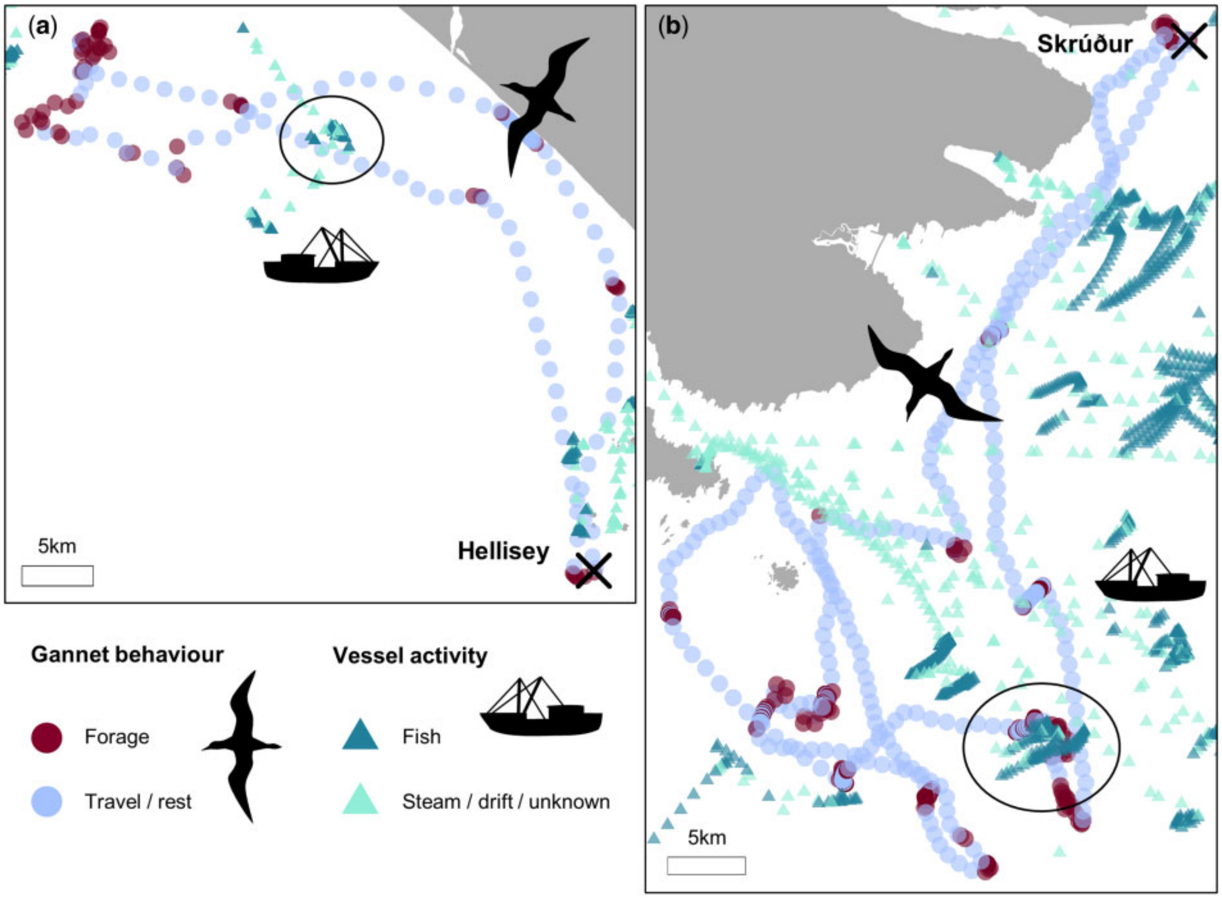

Figure 4. Examples of one foraging trip for a northern gannet *M. bassanus* from (a) Hellisey and (b) Skrúður with regularized GPS locations coloured by behaviours (circles) and fishing vessel locations from the duration of the foraging trip coloured by activity (triangles). Black ovals indicate that the gannet is near to vessels in space and time. In (a), the bird travels past a vessel travelling at fishing speed without switching behavioural state. In (b), the bird forages within 1 km of a vessel, which occurred rarely (<2% of gannet foraging locations). Map adapted from tiles by Stamen Design, under Creative Commons (CC BY 3.0) using data by OpenStreetMap, under the Open Database Licence.

Implications for impacts of discard bans

Discard bans are being introduced in the European Union, Norway, Chile, and New Zealand to improve the sustainability of the fishing industry (Marchal *et al.*, 2016). Our results suggest that in areas with low discard rates and apparently sufficient natural prey, seabird scavenging is likely to be limited, and so populations may be little affected. However, we can be less certain of the response of seabirds to discard bans in waters with historically high discard rates, where they may have become dependent on subsidies (Oro *et al.*, 2008; Bicknell *et al.*, 2013; Sherley *et al.*, 2019). Gannets show repeatable responses to fisheries (Votier *et al.*, 2010; Patrick *et al.*, 2015; Bodey *et al.*, 2018), and such individual behaviours are likely to be learned (Votier *et al.*, 2017). Gannets and other seabirds also use social information and follow conspecifics to prey patches (Weimerskirch *et al.*, 2010; Thiebault *et al.*, 2014; Jones *et al.*, 2018), with large aggregations often forming at fishing vessels (Wahl and Heinemann, 1979; Camphuysen *et al.*, 1995a). This combination of individual learning and social information is likely to enhance regional variation in attraction to vessels by encouraging individuals to become specialist scavengers. Our findings also highlight the importance of maintaining healthy stocks of alternative foods for scavenging species, which may be able to switch back to a more natural diet in the face of discard bans (Bicknell *et al.*, 2013).

Implications for bycatch

Fishing gear kills very large numbers of seabirds (Lewison *et al.*, 2004; Anderson *et al.*, 2011), yet factors influencing bycatch rates are not fully understood. However, variation in discarding is likely to be important. Boat-based studies reveal increased bycatch during discarding or offal dumping (Watkins *et al.*, 2008; Maree *et al.*, 2014) and bycatch reductions when discarding is delayed until gear is out of the water (Pierre *et al.*, 2010). Gannets are consistently bycaught by fisheries in the north Atlantic (García Barcelona *et al.*, 2010; Žydelis *et al.*, 2013; Oliveira *et al.*, 2015), although they are rarely recorded as bycatch in Icelandic waters (Anderson *et al.*, 2011). An assessment of seabird bycatch in relation to spatial and temporal variation in rates of discarding would provide much-needed information on the risks of fisheries management to seabirds.

Methods for assessing seabird–fishery interactions

Simultaneously tracking seabirds and fishing vessels have provided important insights into seabird–fisheries interactions

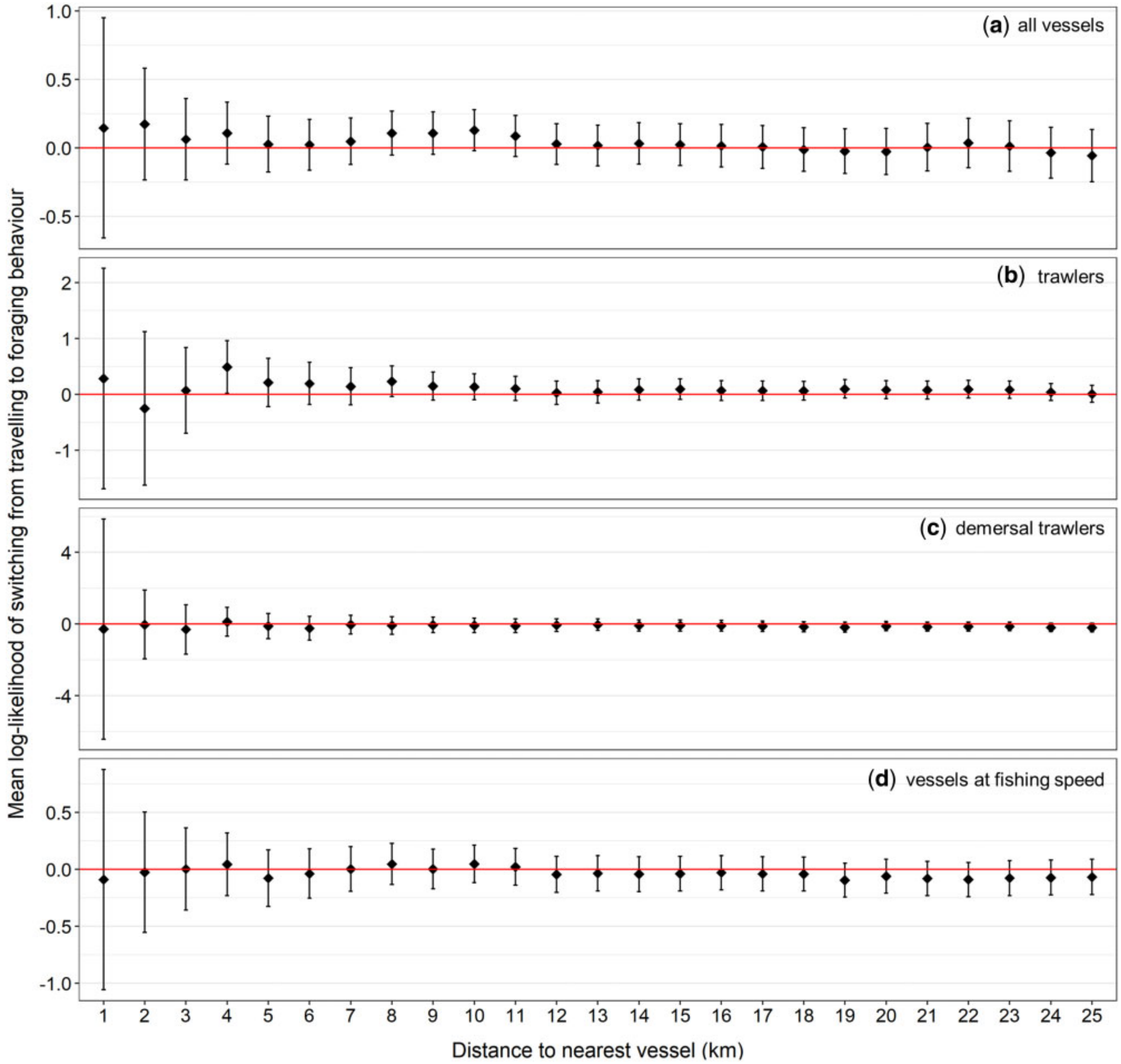

Figure 5. Mean log-likelihood of northern gannets *M. bassanus* switching from travelling to foraging behaviour (±95% *CI*s) in relation to different distances to the nearest: (a) vessel, (b) trawler (otter/Nephrops/pelagic/Danish seine), (c) demersal trawler (otter/Nephrops), and (d) vessel travelling at fishing speed. *CI*s crossing 0 (red line) indicate that the covariate does not have a significant effect.

(Votier *et al.*, 2010; Granadeiro *et al.*, 2011; Soriano-Redondo *et al.*, 2016; Collet *et al.*, 2017; Sztukowski *et al.*, 2017; Cianchetti-Benedetti *et al.*, 2018). This approach has some advantages over boat-based observations (Watkins *et al.*, 2008) that cannot determine the origin and status of seabirds that follow vessels or the repeatability of their behaviours, and dietary analysis (Votier *et al.*, 2004) that cannot always distinguish between scavenged and natural prey, and does not provide information about the availability of vessels. Crucially, neither method can provide information on birds that ignore all available fishing vessels. However, tracking may fail to establish whether interactions represent scavenging, or fishers and birds targeting the same prey. To achieve this requires more detailed information such as from bird-borne cameras (Votier *et al.*, 2013) or very high-resolution tracking. Moreover, VMS and AIS used to track vessel movements may be limited to large vessels. This was not a concern in Iceland because locations were available for all vessel sizes. Studying seabird–fishery interactions is best understood using a range of different approaches.

Conclusion

To conclude, we show that, despite foraging in waters with abundant fishing activity, Icelandic gannets did not respond to nearby vessels. This is likely explained by the low levels of discarding from these vessels and high availability of natural foods. We, therefore, believe it is important to consider regional variation in behaviour, particularly when predicting bycatch mortality and the impacts of large-scale changes in fisheries practice or policy.

Supplementary data

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

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Author contributions

BLC, SCV, and FV designed the study. BLC and FV collected the bird tracking and diet data. JMB accessed and processed the vessel data. BLC, MJJ, and TWB planned and performed the analysis. BLC and SCV drafted the manuscript. All authors commented on the manuscript.

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