



The formation of foraging aggregations in a highly social seabird, the thick-billed murre (*Uria lomvia*), at small and large scales

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Abstract

Analyzing how animals are distributed in space and time is important to understand the behavioural interactions that underlie population dynamics, especially for highly social species. Thick-billed murres (*Uria lomvia*) breed in some of the largest and densest colonies of any seabird. Although this bird is known to aggregate at sea, little is known about when, where, and why the birds form aggregations. We examined the spatial and temporal patterns of foraging aggregations during the breeding season through various scales via (1) measurement of the synchrony of arrivals of adults feeding their chicks at the colony, and (2) use of both GPS and camera loggers attached on the birds to examine the proximity of birds at sea. Adult arrivals at the colony were synchronised when bringing capelin (*Mallotus villosus*), a gregarious pelagic fish, but not when bringing sculpin (primarily *Triglops* spp.), a solitary benthic fish. Camera loggers revealed very close encounters of foraging conspecific (<4 m), much closer than what was predicted by chance, despite low prey densities. GPS loggers also showed diffuse at-sea aggregations with minimal distances closer than expected by chance. However, those study birds did not typically share foraging trajectories. We suggest that, at smaller scales, murres form tight groups to increase searching efficiency underwater. At larger scales, murre aggregations are most likely a result of foraging individuals converging in the more prolific areas, either by independently encountering prey hotspots, or by cueing on other foraging birds.

Introduction

How animals are distributed in space and time when foraging can provide insights about the interactions between individuals and the environment, and between individuals

and other conspecifics (Waters 1959; Spieler 2003; Spiegel et al. 2017). For example, a uniform distribution is often a sign of strong territoriality and interference competition (e.g., Wilschut et al. 2015). On the other hand, an aggregated distribution can reflect clumped resources (e.g., Grant 1993; Schuttler et al. 2015; Halliwell et al. 2017), especially at large scales (Fauchald et al. 2000). At smaller scales, the interaction among individuals is unavoidable, and social foraging often drives the aggregation mechanism (Giraldeau and Caraco 2000). While understanding of the process underlying aggregation patterns—when, why, and at what scale that they are formed—can be difficult to achieve, the subject remains of high importance for conservation, especially for highly social species. The infamous case of the passenger pigeon (*Ectopistes migratorius*), extremely abundant only decades before it disappeared, is just one of the examples of how social behaviour can contribute to rapid declines leading to extinction (Halliday 1980). Furthermore, foraging aggregation patterns must be identified and taken into account when establishing protected areas.

The thick-billed murre (*Uria lomvia*; hereafter “murre”), a deep-diving Arctic seabird, is among the most social birds, breeding in some of the largest and densest colonies in the

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world (Gaston and Nettleship 1981). Some colonies count over 1 million breeding pairs (Brown et al. 1975; Gaston et al. 2012), with most individuals nesting in physical contact with other breeders. At-sea foraging aggregations in this species during the breeding season are observed (Gaston and Nettleship 1981), but, because individuals could not be tracked via observations at sea, some of the factors influencing the formation of these aggregations have not been described in enough depth to infer the underlying mechanisms. Nonetheless, murres usually fly to and from the colony in groups of 4–20 individuals, and there is, consequently, the potential for social information transfer (Gaston and Nettleship 1981). In many seabird species, aggregations are formed at the surface (often in ‘mixed species flocks’) apparently to locate dense forage fish schools that are quickly depleted (Buckley 1997a; Silverman et al. 2004; Thiebault et al. 2014). For example, in the closely related common murre (*Uria aalge*), individuals that successfully located spawning capelin (*Mallotus villosus*) attract other conspecifics (local enhancement), resulting in large aggregations (Burger 1997; Davoren et al. 2003; Bairos-Novak et al. 2015). Thick-billed murres, however, have a more generalist diet and aggregations may be less dense than the other species and local enhancement less important (Cairns and Schneider 1990).

The development of miniature tracking technology, such as GPS and camera loggers, allows researchers to follow individuals at sea, potentially providing insight into the formation of foraging aggregations. Using such approaches, we tried not only to detect the presence of aggregations in thick-billed murres, but also to understand at what scale such aggregations occur and how they are formed. We followed murres spatially and temporally during the breeding season through: (1) measurement of temporal aggregation via synchrony in the arrival of adults when feeding their chicks, (2) observation of small-scale aggregations via camera tracking, and (3) recording of foraging associations using GPS tracks. Synchrony of arrival, such that many individuals arrive in a short time window, is often sign that individuals actively forage in groups (Krebs 1974; Bayer 1981; Burger 1997; Elliott et al. 2009). These groups can be formed via information exchange, with unsuccessful birds following successful ones (information center hypothesis—Ward and Zahavi 1973; Brown 1986; Buckley 1997b; Campobello and Hare 2007), through enhanced detection of prey when in groups (network foraging—Wittenberger and Hunt 1985; Mock et al. 1988) or through synchronised attack on fish schools (cooperative hunting—Bednarz 1988; Ryan et al. 2012, Sutton et al. 2015). Therefore, we hypothesised that individuals feeding on schooling fish would come back to the colony to feed their chick more synchronised in time (i.e., displaying more temporal aggregation) than those feeding on solitary prey. For camera loggers, they have the potential to detect

smaller scale aggregations. In particular, they allow estimation of the short-range encounter rate of conspecifics. Moreover, camera loggers can also be used to look at interactions among clustered foraging individuals (Watanuki et al. 2008; Sutton et al. 2015). Finally, the GPS loggers were used to reveal how aggregations were formed, especially at large scale, therefore, giving insights into the cause of the foraging clusters. More precisely, we assessed if individuals meeting at sea also departed together from the colony or simply met unpredictably using two different foraging paths.

Methodology

Study site

All data were collected at the Coats Island west murre colony (62°56'52.20"N, 82°01'03.70"W) in Hudson Bay, Nunavut, Canada, between 2006 and 2017. The murre colony, situated on cliffs, hosts ~15,000 breeding pairs (Gaston 2002). Murres forage within a semi-arc of 50 km around the colony (Elliott et al. 2008; Gaston et al. 2013). Permits from the Government of Nunavut as well as from the Federal Department of Environment and Climate Change Canada were obtained prior to the beginning of any manipulations. All analyses were conducted using R (R Development Core Team 2018).

Chick-feeding synchrony

We looked at the temporal pattern of adults returning to the colony to feed their offspring. We predicted that murres feeding on prey that form schools, such as capelin (*Mallotus villosus*), would be more synchronised in their arrival time than those preying on solitary prey, such as sculpin (Cottoidea). Other rare fish items (<8%) were ignored for the analyses.

Data for this analysis were collected during “feeding watches” in 2006, 2008, 2009, and 2017, which were the years when the longest periods of feeding watches occurred. In 2008 and 2009, too few sculpin were recorded for the analysis, so only 2006 and 2017 were retained for this prey item. Feeding watches consisted of observing a plot containing around 20 breeding sites, for 12–20 h a day over several days, during the chick-rearing period (Hipfner et al. 2006). Observations were made from a blind located 2–10 m away from birds in the plot, and involved noting when an adult returned to its nest with a prey and what prey type was caught.

For the analysis, we separated the whole feeding watch period during a year into smaller periods of 10 min. We tested for synchronisation of chick feeding at this scale, as murres sometimes circled several times around the colony

with a prey in their beak before deliveries (pers. obs.). Two murrelets from the same foraging group could thus potentially return to their nest within approximately 10 min from each other. For every 10-min interval, we calculated the number of murrelets in the plot returning with capelin or sculpin. For each prey species, and for each year, we then computed a variance-to-mean ratio from the counts made in the 10-min intervals. Using the Poisson distribution as reference to assess homogeneity of temporal point patterns (Dutilleul 2011), a variance-to-mean ratio near to 1.0 would imply that murrelets return at the colony in a completely random pattern, while a ratio above 1.0 would imply that their arrivals are grouped (aggregated pattern) and possibly synchronised. To test for significance, we generated 1000 simulations generated from a Poisson distribution ($P(k) = \frac{m^k e^{-m}}{k!}$, where $P(k)$ is the probability of event k occurring) and took the 95th percentile variance-to-mean ratio as our threshold for significance. For every combination of prey species and year, we recomputed a significance threshold with simulation parameters set according to the observed data (k = number of feeds during an interval and m = observed number of feeds of a prey type during a given time interval). We then redid the analysis previously described, but with periods of 1 h rather than 10 min, to eliminate the possibility that synchronicity was due to a larger scale phenomenon, such as time-of-day effects.

To test the viability of the information center hypothesis through synchrony of departure from the cliff, we recorded when two birds in the plot departed within 1 min of each other. We assumed that, if information exchange happened on the cliff, birds would leave at the most 1 min from each other; otherwise, the extreme density of flying murrelets around the colony would probably make it impossible for one murrelet to follow another.

At-sea distribution with GPS

In 2017, we deployed GPS accelerometers (AxyDepth, 18 g, Technosmart, Rome, Italy, acceleration = 50 Hz; depth and temperature = 1 Hz; GPS point recorded every 5 min) on 93 birds for 2–4 days throughout the season. These birds all resided within 10 m of each other. For the first analysis, only points where the recorded travelling speed was below 10 km/h were retained, as we wanted to select only the points associated with foraging. We also removed all points within 2 km of the colony (the splashdown), as these are associated with social behaviour rather than foraging (Burger 1997; Elliott et al. 2009). Finally, to create temporal snapshots, we retained only points at the time of the day when most equipped murrelets were actively foraging based on preliminary analysis. We chose a window of 30 min to accommodate the sampling rate of GPS while being short enough to be considered a temporal snapshot. We retained

only days when > 3 equipped murrelets were foraging during the snapshot window.

For every snapshot, we calculated the minimum distance observed between two murrelets. To test if these distances were smaller than what would be predicted by chance, we ran 1000 simulations for all possible combinations of equipped murrelets present in the snapshot. Those simulations consisted of redistributing the points from the observed murrelet density map. This density map was made using GPS data for the whole period of study so as to take into account any general habitat preference such as bathymetry or distance from the colony (see suppl. material). We then calculated all minimum and mean distances for these simulations, and used the fifth percentile value as our significance threshold. Finally, when the minimum distance detected in a day was smaller than 2 km, we plotted the individual GPS tracks of those murrelet pairs involved. We used time of departure from the colony and track shape to assess whether the murrelets were travelling together from the colony, or foraged together while having two different initial paths.

At-sea distribution with camera loggers

In 2017, 20 birds were equipped with camera loggers (DVL400M, Little Leonardo, Tokyo, Japan, 15 g), but four cameras were lost during the field season, resulting in data from 16 birds available for the analyses. The cameras recorded for ~ 1–2 h, and all birds were recaptured within 24 h. Because the neck blocked the camera view when the birds were sitting on the water, all analyses were concentrated on the diving phase, when the birds were foraging. We analyzed every video to look for direct evidence of social foraging (coordinated attack, etc.), and we also noted every time that a conspecific or prey item was encountered while diving. We tested if the encounter rate with a conspecific was higher than what would be predicted by chance by calculating the expected encounter rate using the adapted predator–prey encounter rate equation of Gerritsen and Strickler (1977):

$$Z_p = \frac{\pi R^2 N_b}{3} \left(\frac{u^2 + 3v^2}{v} \right) \quad \text{for } v \geq u,$$

where Z_p is the encounter rate, R the encounter radius, N_b the conspecific concentration, u the speed of the subject for which the encounter rate is being calculated, and v the speed of the animals being encountered by the subject. This equation assumes that animals occur following a Poisson distribution in the environment, and an encounter rate much higher than the calculated output would suggest strong aggregation.

To calculate the expected encounter rate, we considered that half of the breeding population at the Coats west colony

was at sea at any moment, for a total of 15,000 foraging individuals. The estimate likely exaggerates the number of individuals at sea, as murres spend some time at the colony with their mates. However, non-breeding birds are also present, which more or less compensates for the previous overestimation. Murres forage within a semi-arc of 50 km around the colony (Elliott et al. 2008; Gaston et al. 2013). However, areas near the colony are seven times denser in murres than those near the 50 km border (suppl. material), so we, therefore, multiplied the calculated concentration by seven, so that the encounter rate would apply to the most murres and be as conservative as possible. The average foraging dive is ~50 m deep (Elliott et al. 2008), making a concentration of 535 murres/km³. However, we considered for our analysis that only birds encountered while diving. Assuming murres at sea spend ~30% of their time underwater (Elliott and Gaston 2014), the actual concentration would be 160 underwater murres/km³. Considering an underwater speed of 7 km/h (Lovvorn et al. 2004; Elliott et al. 2007) and a camera detection range of 4 m at 90°, we expect an encounter rate of ~0.02 murres per hour. We used Fisher's exact test to determine if the observed encounter rate was significantly different from the expected rate.

Results

Chick-feeding synchronisation

We observed 626 capelin feeds and 182 sculpin feeds. During all years, capelin was brought to the chicks at a rate that departed from the expected Poisson distribution at a 10-min scale (Table 1). The distribution of feed counts in the 10-min intervals consisted of more zeros and more high counts than the Poisson distribution, suggesting a clustered, or bimodal, distribution (Fig. 1). We detected no significant synchrony for sculpin at a 10-min scale (Table 1, Fig. 1). No synchrony was detected at the 1-h scale for either prey item, meaning

that the synchrony detected at the 10-min scale for capelin was not caused by a larger scale phenomenon.

For departure from the cliff, a very small proportion of birds departed synchronously (<1%). Furthermore, a few birds faced incoming birds, and adults feeding their chick did not seem to draw the attention of other birds.

At-sea distribution with GPS

Eight snapshots had four or more birds actively foraging (Table 2). Minimal distances observed were smaller than what were produced using simulations for all but two snapshots. Five snapshots recorded a minimum distance that was smaller than 2 km. GPS tracks for those birds showed that, four out of five times, birds near to one another at sea departed from the colony at different times, and often had dissimilar trajectories (Fig. 2b–e). In one case, however, the two birds departed in synchrony, headed in the same direction, stopped at the same patch, and started foraging in the same direction (Fig. 2a). The two birds eventually separated, as one went back to the colony, while the other kept foraging.

At-sea distribution with camera loggers

We recorded a total of 65 h of video, 7.5 h of which were filmed during dives. We did not detect any direct cooperation in the foraging behaviour of murres. We also rarely recorded more than one fish per screen, illustrating that fish (including capelin) did not occur in dense schools in our study site during the camera deployment. Seven of the equipped murres (44%) recorded a conspecific on several occasions while diving, for a total of 19 encounters (Fig. 3). With a predicted 0.02 conspecifics encountered per hour, we did not expect a single murre to encounter a conspecific during the 7.5 h of video recording. The observed proportion (7 out of 16) was, therefore, significantly different than what would be predicted by chance (Fisher's exact test $P=0.006$).

Table 1 Variance-to-mean ratios for prey delivery counts during 10-min intervals and 1-h intervals

Year	Observed variance-to-mean ratio at 10-min scale	Significance threshold at 10-min scale	Observed variance-to-mean ratio at 1-h scale	Significance threshold at 1-h scale
Capelin				
2006	1.58*	1.13	1.17	1.45
2008	1.34*	1.21	0.90	1.85
2009	1.73*	1.22	0.84	1.83
2017	1.20*	1.10	0.97	1.30
Sculpin				
2006	1.23	1.24	1.12	1.41
2017	1.07	1.1	1.13	1.3

*> significant threshold (95% values from simulations)

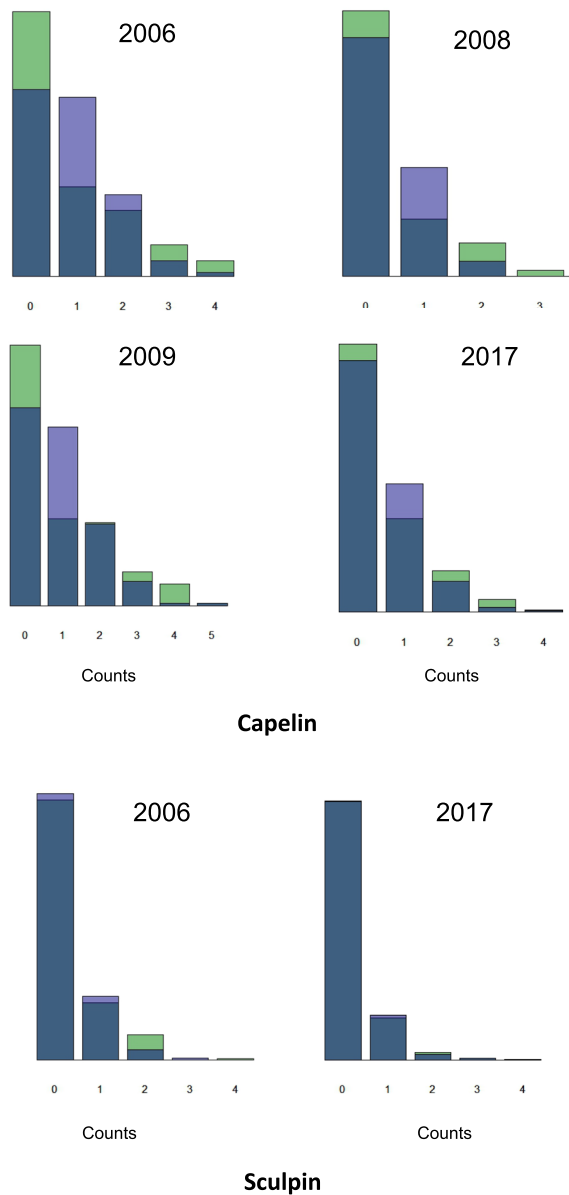


Fig. 1 Observed distribution of the 10-min periods based on the number of feeds of a given prey each contains (green). In purple is the Poisson distribution and in dark blue the overlap between the observed and Poisson distribution

Discussion

The aggregative nature of thick-billed murrelets while foraging is known mostly through boat or aerial surveys (Gaston and Nettleship 1981; Mehlum et al. 1998; Fauchald et al. 2000), which limits the interpretation of the observed aggregations to the time period when an individual can be followed by the observer. On the other hand, our results using camera loggers, GPS, and at-colony observations provide new insights into the temporal and spatial scale

Table 2 Observed minimal nearest-neighbor distance in the eight snapshots compared with the significance threshold from simulation

Day	Number of active GPS	Minimal nearest-neighbor distance (m)	Sig-nificance threshold	Track (Fig. 2)
20-07-17	4	3323*	3699	
22-07-17	4	418*	3699	a
23-07-17	5	277*	3465	b
24-07-17	4	1775*	3699	c
27-07-17	9	1864*	2370	d
28-07-17	7	4517	2934	
31-07-17	10	1498*	2172	e
01-08-17	8	3547	2295	

*< significant threshold (5% values from simulations)

of those aggregations, and more importantly about how they are formed.

Small-scale temporal and spatial aggregations

Synchrony of returning adults to feed their chicks can be an indication that murrelets actively forage in groups (Krebs 1974; Bayer 1981; Burger 1997; Elliott et al. 2009). While Elliott et al. (2009) found little synchrony in the return rate of thick-billed murrelets feeding their chicks, the study did not differentiate among prey taxa, pooling all benthic and pelagic items. In contrast, we found the synchronisation of returning adults feeding their chick with capelin, not sculpin. The fact that this synchrony was discernable at a very small scale (< 10 min) but not at a larger one (> 1 h) suggests that the underlying mechanism is not simply a preference for individuals to forage at a given period in the day. The spatial clumping of resource does not predict such strong temporal synchrony either. Finally, the synchrony of returning adults to avoid predation (Addison et al. 2007) is unlikely at our study site, as adult thick-billed murrelets have no aerial predators at our study site (Gaston and Ouellet 1997). Rather, a more reasonable explanation to the arrival synchrony would be that the birds feeding on capelin were actively foraging in groups.

One weakness of the “synchrony-of-arrival” methodology is that the method cannot confirm that the birds coming back in synchrony were, indeed, coming from the same foraging location. However, we observed synchrony in the arrival of capelin-feeding adults on several days, and a total absence of synchrony of sculpin-feeding adults. This observation fits well with the hypothesis that birds could forage in groups to increase foraging efficiency when preying on schooling fish. Capelin is a pelagic fish forming aggregations, sometimes near the surface (Eschmeyer and Herald 1999). Feeding on this fish species requires more aerial searching than for bottom solitary fish like sculpin (Elliott et al. 2009). Individuals

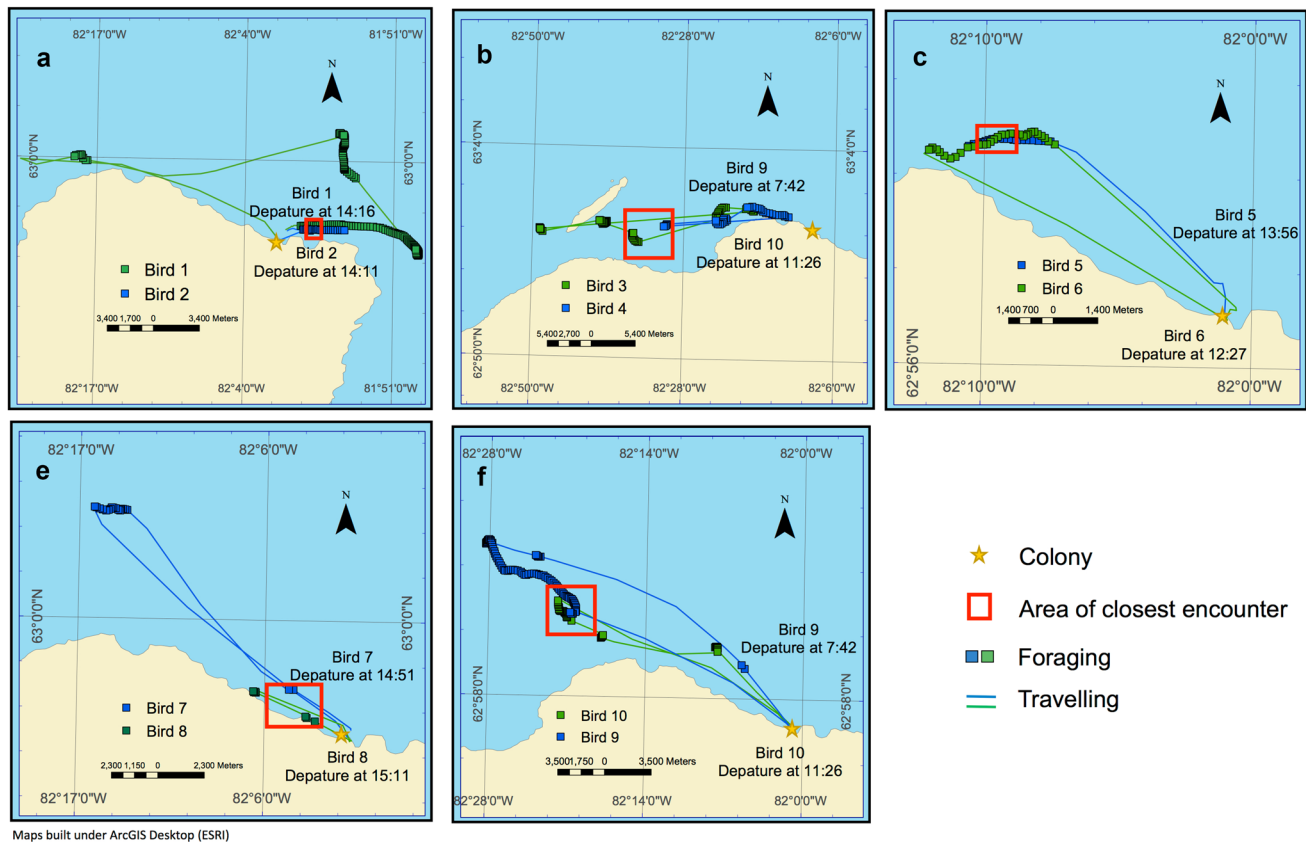


Fig. 2 GPS track of the five closest encounters recorded during the snapshot analysis (see Table 2)

feeding on capelin would, therefore, reduce their searching time when foraging in groups. This strategy, called network foraging (Wittenberger and Hunt 1985; Mock et al. 1988), increases the detection of prey, but also divides the resource among all group members. If fish aggregations are rare, but once they are found, they are large enough to reward all individuals in a group, network foraging becomes a viable strategy. Such conditions could be the case for birds preying on capelin, while providing little to no benefits for those preying on sculpin. Another plausible and not mutually exclusive explanation for the synchrony of arrival is the existence of information exchange among individuals, as proposed by Ward and Zahavi (1973), with naïve birds following those informed on the location of prey hotspots. This strategy also reduces search time per individual, and produces the same predictions about the synchrony of arrival of murres feeding on capelin compared to those feeding on sculpin. If this phenomenon exists in murres, however, the information exchange could not occur directly on the cliff, as initially suggested by Ward and Zahavi (1973). Murres were almost never observed following other murres directly from the colony's cliffs in our study. On the other hand, murres often stop by the water adjacent to the colony, called the splashdown zone, before leaving to forage (Burger 1997;

Elliott et al. 2009). Most birds leave the splashdown zone, and later return to the colony, in groups of 4–20 individuals (Gaston and Nettleship 1981). Any information exchange or group formation—this is true as well for network foraging—will likely be formed at the splashdown. For instance, groups of murres may orient themselves on outgoing trips based on the direction of groups of incoming birds carrying food, which are clearly visible from several hundred meters distant (Gaston and Nettleship 1981).

At a small spatial scale, camera loggers detected several very close encounters of foraging conspecifics (<4 m), more than what would be predicted by chance even in the context of spatial aggregation. However, in 7 h of active foraging over 16 birds, we did not observe cooperative hunting, which is displayed in species like the African penguin (*Eudyptula minor*), where several individuals circle around fish schools to prevent them from fleeing (Ryan et al. 2012). Furthermore, capelin seemed to be loosely aggregated, rather occurring in dense schools. It is unlikely that murres could have surrounded these aggregations efficiently. Following the results on temporal synchrony, those close encounters could have been individuals from a same foraging group formed initially to enhance searching efficiency. However, as the video recordings often started in the middle of the foraging

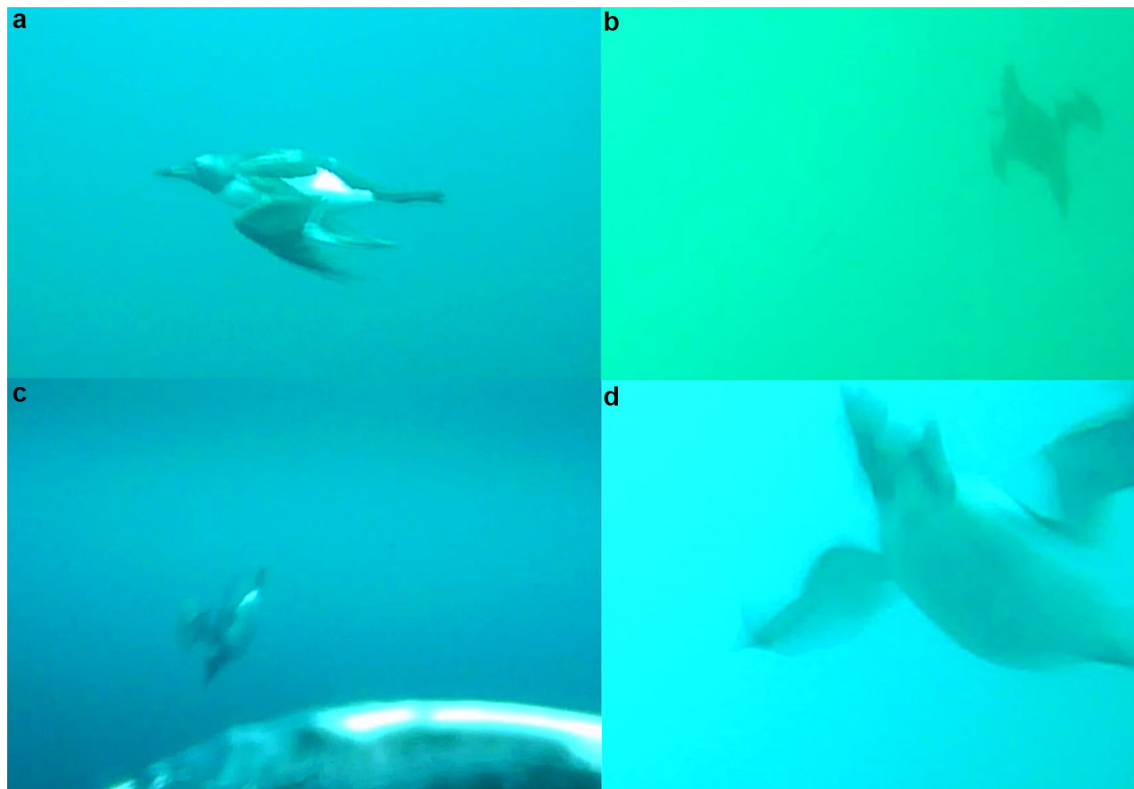


Fig. 3 Examples of conspecific encounters recorded by the camera loggers

trip, it is impossible to confirm that the birds arrived at the foraging spot at the same time.

Large-scale aggregations

GPS loggers also recorded encounters that were closer than what would be predicted by chance, although these encounters were at the scale of hundreds or thousands of meters. Given that there are 30,000 breeding murre, recording individual encounters from GPS loggers placed on a few individuals seems improbable (but see Cook et al. 2017). Among the closest encounters detected, only one consisted of two birds leaving the colony at the same time and heading in the same direction. All other tracks only converged briefly, and the two concerned individuals could not have been part of the same foraging group. This suggests that more than one factor could contribute to aggregations in the thick-billed murre, with some of them influencing different scales of aggregation. While those large-scale encounters could have occurred through a prey-driven behaviour (each individual finding the prey hotspot independently), murre may also have cued on other feeding birds through local enhancement. Gaston and Nettleship (1981) proposed a similar mechanism, with outgoing birds cuing on incoming birds to locate the direction of hotspots. Indeed, foraging murre are much

easier to spot in the open sea than the prey themselves, especially considering that murre are visual predators.

Conclusion

At smaller temporal and spatial scales, we observed close encounters of foraging adults' underwater and high synchrony of arrival at the colony (for adults bringing back capelin to their chicks). One explanation for these observations could be that murre forage in active groups. However, those groups are probably not formed for cooperative hunting, and, consequently, would more likely the result from enhanced searching efficiently (either via network foraging or information exchange). At larger scales, spatial aggregations are also present, but these are not formed by the birds that actively travel together. Convergence of murre occurs at-sea, with individuals being independently attracted either by prey density, or cueing on other foraging conspecifics to locate prey hotspots.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest for any of the authors. All applicable Canadian guidelines for the care and use of animals were followed.

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