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RESEARCH ARTICLE

Seabirds vary responses to supplemental food under dynamic natural prey availability and feeding aggregation composition

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ABSTRACT

While foraging, a predator can feed solitarily or in a group. The net energy gain of joining a group is predicted to vary with prey patch quality, species-specific prey capture behavior, and the size and species composition of the predator group. In coastal Newfoundland, Canada, capelin (*Mallotus villosus*), a key forage fish, migrates inshore to spawn during the summer, resulting in a dramatic shift in prey availability. During July–August 2015–2017, we examined the numerical and behavioral responses of procellarid (Great Shearwater [*Ardenna gravis*], Sooty Shearwater [*A. grisea*], Northern Fulmar [*Fulmarus glacialis*]), and gull species (Herring Gull [*Larus argentatus*], Great Black-backed Gull [*L. marinus*]) to fish offal under varying capelin availability as well as flock size and composition using an at-sea experiment on the northeast Newfoundland coast. The experiment consisted of providing offal every 30 s (10-min experimental period), along with 10-min control periods before and after. We recorded the species-specific number of birds on the water, the number of birds simultaneously attempting to capture offal, and the number of successful attempts ("foraging success"). The number of birds on the water was lower during high capelin availability for all species, except for Northern Fulmar. The number of conspecifics simultaneously attempting to capture offal increased with the number of conspecifics on the water, but plateaued at different numbers (4–17) for most species. The species-specific proportion of successful attempts (i.e. foraging success) varied with flock size and composition (i.e. number of conspecifics, heterospecifics, species). Foraging success of Herring Gulls and fulmars were moderately affected by flock size and composition, suggesting that they may be dominant competitors. Findings suggest that seabirds rely more heavily on supplemental food sources, such as fisheries discards and offal, when natural prey availability declines, potentially resulting in a higher risk of by-catch during fisheries activities as forage fish stocks decline.

Keywords: capelin, fisheries discards and offal, foraging success, gull, *Mallotus villosus*, mixed-species feeding assemblage, optimal group size, procellarid

Les oiseaux marins varient leurs réponses numériques et comportementales à des abats de pêche selon la disponibilité en proie naturelle et la composition du groupe d'alimentation

RÉSUMÉ

Lors de l'alimentation, un prédateur se nourrit solitairement ou en groupe. En joignant un groupe, les gains énergétiques nets peuvent varier avec la qualité des sites, les techniques de capture du prédateur et la taille et la composition du groupe d'alimentation. À Terre-Neuve, Canada, le capelan (*Mallotus villosus*), un poisson de fourrage, migre vers les côtes durant l'été pour frayer, résultant en un changement radical de la disponibilité côtière en capelan. Par l'intermédiaire d'une expérience en mer montée au nord-est de Terre-Neuve, les réponses numériques et comportementales des procellariidés (Puffin majeur *Ardenna gravis*, Puffin fuligineux *A. grisea*, Fulmar boréal *Fulmarus glacialis*) et des goélands (Goéland argenté *Larus argentatus*, Goéland marin *L. marinus*) à des abats de poissons ont été examinées sous différentes disponibilités en capelan et compositions du groupe d'alimentation, durant Juillet-Août 2015–2017. L'expérience constituait à fournir des abats tous les 30 s (période expérimentale de 10-min), en plus de périodes contrôles de 10-min avant et après la période expérimentale. Le nombre maximal d'oiseaux sur l'eau par espèce a été enregistré tous les 30 s, en plus du nombre d'oiseaux tentant simultanément de capturer l'abat et la somme des tentatives fructueuses de capture (c.-à-d. succès d'alimentation) par espèce. Le nombre d'oiseaux sur l'eau était plus bas lorsque la disponibilité en capelan était élevée, à l'exception du fulmar boréal. Le nombre d'oiseaux tentant simultanément de capturer l'abat augmente avec le nombre de conspécifiques, mais plafonne à des nombres différents (4–17) selon l'espèce. La proportion de succès d'alimentation varie selon la taille et la composition du groupe d'alimentation (c.-à-d., nombre de conspécifiques, d'hétérospecifiques, d'espèces). Le succès d'alimentation des goélands argentés et des fulmars étaient modérément affectés par la taille et la composition du groupe, suggérant qu'ils sont potentiellement des compétiteurs dominants. Les résultats indiquent que les oiseaux marins s'appuient sur des proies artificielles, telles que les abats de pêche, lorsque la disponibilité en proie naturelle est basse. Avec le déclin des stocks de poissons, les risques de captures accidentelles pourraient ainsi augmentées lors des activités de pêche.

Mots-clés: abats et rejets de pêche, capelan, goéland, groupe d'alimentation mixte, *Mallotus villosus*, procellariidé, succès d'alimentation, taille de groupe optimale

INTRODUCTION

While foraging, a predator will try to maximize its net energy gain by deciding what prey to consume as well as how and where to forage (Stephens and Krebs 1986). One important decision is whether to feed in a group or solitarily. Seabirds often feed in mixed-species flocks on natural prey (Hoffman et al. 1981, Camphuysen and Webb 1999). As prey are patchily distributed in the marine environment, seabirds can benefit from group foraging by finding prey patches more efficiently, for example by cueing to the foraging activities of others ("local enhancement"; Bairos-Novak et al. 2015), as well as increasing prey capture efficiency, by causing aggregated prey to become more dispersed and easier to capture (Gotmark et al. 1986, Thiebault et al. 2016). When prey densities decrease within a patch, however, group foraging may result in predators competing for food resources (Beauchamp 2011). This competition would reduce or eliminate the benefits of group foraging (Beauchamp 2011), especially for mixed-species assemblages, where some species are expected to have higher foraging success than others (Hoffman et al. 1981). Overall, the net energy gain of joining a feeding group is predicted to vary with the number and quality of the patches in the region, as well as the diversity of competitors encountered at prey patches.

When whole fish or offal (internal organs) is discarded at sea during fisheries activities, the benefits of group foraging related to prey capture efficiency are presumably absent. Therefore, as the number of competitors increases, the probability of successfully capturing prey decreases, whereby this probability is likely dependent on the prey capture behavior of both conspecific and heterospecific competitors (Furness et al. 1992, Garthe and Hüppop 1998). Indeed, aggressive species are often the most successful and their presence may affect the behavioral responses and negatively influence the foraging success of other seabird species within a flock (Furness et al. 1992, Garthe and Hüppop 1998). Despite high densities of competitors and minimal benefits of group foraging, seabirds may continue to aggregate in response to fisheries discards and offal, especially under low natural prey availability when search costs for prey patches are high. Species-specific foraging success at fishing vessels may also vary according to whether whole fish or offal is discarded (Furness et al. 1992). For instance, prey capture success of Northern Fulmars (*Fulmarus glacialis*) is greater for offal than whole fish (Furness et al. 1992, Camphuysen et al. 1995). During discard and offal experiments, however, larger species, such as gulls, are often the most abundant and successful at capturing food items (Furness et al. 1992, Walter and Becker 1997, Garthe and Scherp 2003). Indeed, fisheries discards and offal can be an important food source for gulls (Furness et al. 1992, Walter and Becker 1997), and closures of local fisheries have been followed by declines in gull populations (Chapdelaine and Rail 1997). The suppressing behavior of gulls at these mixed-species feeding assemblages can affect the foraging success of other pelagic species present, such as other gulls (Walter and Becker 1997) or procellarids (e.g., shearwaters, fulmars; Garthe and Hüppop 1998). Altogether, flock size and composition strongly affect behavioral responses and species interactions for fisheries discards and offal.

In coastal Newfoundland, Canada, an important natural prey for seabirds and other marine predators is capelin (*Mallotus villosus*), a small pelagic forage fish (Carscadden et al. 2002). Capelin migrate from offshore to coastal regions during the summer to spawn, resulting in a dramatic increase in inshore prey availability for seabirds (Davoren et al. 2012). This seasonal event causes shifts in the diet of several breeding seabird species, including gulls (Pierotti and Annett 1987, Gulka et al. 2017) and alcids (Carscadden et al. 2002, Gulka et al. 2017). Additionally, the arrival of trans-equatorial migrating Great Shearwaters (*Ardenna gravis*) and Sooty Shearwaters (*A. grisea*) in coastal Newfoundland also corresponds with the inshore arrival of spawning capelin (Davoren 2013).

The objective of this study was to investigate seabird responses to offal discarding within mixed-species foraging assemblages under varying natural prey availability. We conducted an at-sea experiment, whereby the responses of seabirds, primarily nonbreeding shearwaters and breeding gulls, to fish offal discards were quantified as natural capelin availability and seabird flock size and composition varied. We hypothesized that capelin availability would affect both the species-specific numerical response (i.e. number of each species present) and behavioral response (i.e. foraging attempts and success) to supplemental food items. We also hypothesized that flock size and composition would affect the species-specific behavioral response to supplemental food items. We predicted that fewer seabirds would be present during supplemental food delivery when capelin availability was higher (i.e. spawning) relative to lower (i.e. pre- and post-spawning), owing to an increased number of high-quality natural prey patches in the region. We also predicted that the species-specific number of food capture attempts and successes would increase with the number of conspecifics until a particular group size is reached, which would differ among seabird species. Finally, given the suppressing behavior of gulls, we predicted that the presence of gulls would reduce the number of food capture attempts and successes of procellarids during the experiment, while the opposite would not be true.

METHODS

Experimental Design

The at-sea experiment was performed from July to mid-August during 2015, 2016, and 2017 on the northeast Newfoundland coast, Canada. The experiment was conducted near a cluster of deep-water capelin spawning sites (Appendix Figure 7), which represents a multi-year hotspot for many marine apex predators (Davoren 2013). Capelin presence and abundance ("availability") within the study area was evaluated throughout July and August by monitoring known and persistently used capelin spawning sites (Penton and Davoren 2012). Following Crook et al. (2017), beach spawning sites were monitored every second day for evidence of spawning (e.g., presence of capelin eggs, dead capelin) and deeper water (15–40 m) spawning sites were monitored by examining bottom sediment for evidence of spawning on a weekly basis (Appendix Figure 7). Capelin availability was considered "high" when capelin spawning was initiated in the study area until capelin spawning had finished and was considered "low" outside of this period.

Thirteen experimental trials were performed in 2015, 14 trials in 2016, and 15 trials in 2017, with up to 3 trials conducted per day. Time between the end of one trial and the beginning of the next trial when conducted on the same day varied from 4 min to 2.5 hr. Each trial consisted of 3 periods: pre-control, experimental, and post-control. To mimic local summer fisheries activities in our study, to which seabirds were presumably accustomed, we used a 5-m open boat, designed for inshore fishing of Atlantic cod, crab, and lobster, as our experimental platform. Additionally, the boat motor was turned off prior to beginning a trial. During the experimental period, a piece of fish liver (30–40 g; Atlantic cod [*Gadus morhua*]) was thrown ("supplemental food") every 30 s from the same experimental platform over a 10-min period. This was meant to resemble smaller-scale recreational cod fishing, where cod offal is discarded from small boats at a similar rate. A 10-min control period before and after the experimental period was conducted, where no supplemental food was provided, resulting in a 30-min trial. A GoPro Hero4 digital video camera attached to a pole recorded throughout each trial and was angled to ensure an optimal view of birds in the area where the supplemental food was delivered (i.e. 2–5 m from the experimental platform) and the larger experimental area (~150 m on starboard side). We recorded environmental conditions (i.e. sea state, wind speed, visibility) and the location (latitude, longitude) at the start of each trial. Estimated wind speeds were confirmed by obtaining wind speeds from Environment Canada (climate.weather.gc.ca) at Pools Island Station, Newfoundland (49.1122°N, 53.5811°W). During 2015 and 2016, trial location was chosen by finding seabird aggregations within the cluster of beach and deep-water spawning sites, whereas in 2017, trial location was fixed within this same area to reduce the effect of spatial variation among trials (Sotillo et al. 2014; Appendix Figure 7).

Data Analysis

From the recorded videos for each trial, at 30-s intervals we quantified (1) the number of birds per species on the water within the experimental area (~150 m from the boat), (2) the number of birds per species trying to capture each supplemental food item either by active flying or swimming toward the supplemental food item ("attempting"), and (3) the species that successfully captured each supplemental food item ("success"). For each trial, we determined the maximum number of birds of each species per period and summed the number of successful captures per species. Birds were counted only if they could be identified to species. Variation in identification ranges occurred during trials with high-speed winds (i.e. >25 km h^{-1}) as gulls remained in flight and could not be reliably counted within the experimental area. Therefore, trials conducted in high winds were removed from the analysis. Visibility was always high (>5 km); thus, trials were not eliminated from analysis due to variation in detection ranges. Video analyses were performed by the same person to prevent variation and biases during data collection.

Statistical analyses were performed using R 3.4.4 software (R Core Team 2018) with the *MASS* (Brian et al. 2018) or *mgcv* (Wood 2018) packages. To evaluate whether seabirds were responding to the supplemental food and not simply the experimental platform, a generalized linear model with a negative binomial distribution was used to compare the maximum number of birds between the experimental and control periods within trials. To evaluate whether the numerical response of each species to the supplemental food changed between low and high capelin availability periods, we used a similar model with the maximum number of birds on the water during the experimental period only as the response variable. Predictor variables for this model were capelin availability (i.e. low and high), species, and the interaction between capelin availability and species. To account for variation between trial and years, we also included trial (i.e. first, second) and year (i.e. 2015–2017) as predictor variables. The third trial during a day was omitted from this analysis to minimize autocorrelation from birds following the experimental platform among trials and because a third trial was not performed consistently across each summer. When a predictor was statistically significant ($\alpha = 0.05$), post hoc Tukey tests were used to examine differences among factor levels for predictors with >2 factor levels using the *multcomp* package in R (Hothorn et al. 2017).

To evaluate factors influencing each species' attempt to capture supplemental food items, generalized additive models were developed for each species. The response variable was the maximum number of birds of each species within a trial simultaneously attempting to capture supplemental food items. Considering the nature of the response variable, we used a negative binomial distribution (Wood 2006). Smoothed predictors included the maximum number of conspecifics on the water, the maximum number of procellarids (when modelling for gull species) or gulls (when modelling for procellarid species) that were on the water, and the maximum number of species present on the water (range: 1–6 species). Capelin availability (i.e. low, high) was also included as a parametric predictor.

To evaluate factors influencing each species' success at capturing supplemental food items, generalized additive models with a binomial distribution were developed for each species. Individual birds could not be identified and followed, precluding measures of individual-level foraging success. The datasets used for these species-specific models were restricted to experimental periods where at least one individual of the focal species attempted to capture a supplemental food item. The response variable was the number of successful and failed attempts per species within a trial, including only the supplemental food item deliveries when at least one individual from that species attempted to retrieve the food item. Within the analysis using a binomial distribution, the response variable is represented by the proportion of attempts that were successful per species within a trial (i.e. foraging success). Smoothed predictors included the maximum number of conspecifics within a trial simultaneously attempting to capture supplemental food items, the maximum number of procellarids (when modelling for gull species) or gulls (when modelling for procellarid species) within a trial simultaneously attempting to capture supplemental food items, and the maximum number of species simultaneously attempting to capture food items. Capelin availability (i.e. low, high) was also included as a parametric predictor. For all models, smoothed predictors were smoothed using thin plate regression splines and if the estimated degree of freedom (edf) equaled 1, suggesting that the relationship is linear (Wood 2006), the predictor was converted to parametric and the model was run again. Means and standard error are presented as mean ± SE.

RESULTS

Species observed regularly during trials across years were Herring Gulls (*Larus argentatus*), Great Black-backed Gulls (*L. marinus*), Northern Fulmars, Great Shearwaters, and Sooty Shearwaters (Appendix Figure 8). Considering age can affect foraging behavior (Burger and Gochfeld 1981, Bertellotti and Yorio 2001, Steenweg et al. 2011), immature gulls (*Larus* spp.) were separated into their own category for analyses. Great Shearwaters and Northern Fulmars were primarily located near the experimental platform (<2 m; i.e. where the supplemental food was delivered), whereas immature and Herring Gulls were typically located 2–5 m from the experimental platform. Sooty Shearwaters and Great Black-backed Gulls usually were located farther away (>5 m). Gulls were the most abundant taxon (>70%), except when there were fewer than 10 seabirds present (Appendix Figure 8).

A generalized linear model revealed that the maximum number of seabirds on the water differed between experimental and control periods (likelihood ratio $LR_2 = 90.5$, $P < 0.001$), with the pre-control period having a significantly lower number of birds relative to both the experimental ($P < 0.001$) and post-control periods ($P = 0.001$). The number of birds in the post-control period, however, did not differ from the experimental period ($P = 0.98$). A generalized linear model revealed that the maximum number of seabirds during the experimental period was lower during high relative to low capelin availability ($LR_1 = 39.21$, $P < 0.001$), but the interaction between capelin availability and species/age was significant ($LR_5 = 65.61$, $P < 0.001$). Indeed, the maximum number of birds on the water was lower during high capelin availability for most species, but the number of Northern Fulmars was higher during high capelin availability ($P < 0.001$; Figure 1).

The number of attempts to capture supplemental food items was high across most species. When Herring Gulls were present, they attempted to capture supplemental food items 94.9% of the time food items were offered, whereas immature gulls attempted 82.7% and Great Black-backed Gulls only attempted 38.9% of the time. For the procellarid species, Northern Fulmars attempted to capture supplemental food items 72.1% of time food items were offered, whereas Great Shearwaters and Sooty Shearwaters attempted 89.0% and 32.7% of the time, respectively. The low percentage of attempts (i.e. <50%) by Great Black-backed Gulls and Sooty Shearwaters resulted in low sample sizes for the generalized additive models and, thus, both species were omitted from further analysis.

Species-specific generalized additive models of the maximum number of birds per species that simultaneously attempted to capture a food item revealed that the maximum number of conspecifics on the water was an important predictor for all species/age groups (Figure 2 and Table 1). The maximum number of individuals simultaneously attempting food capture significantly increased with the number of conspecifics but eventually plateaued despite further increases of conspecifics on the water (Figure 2).

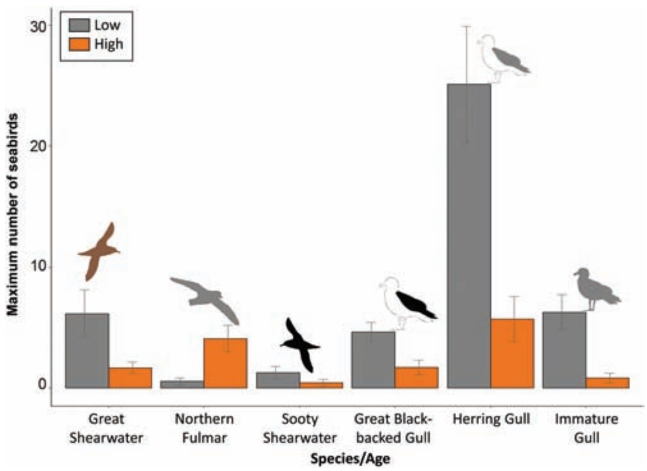

FIGURE 1. Mean (±SE) maximum number of birds per species/age, including Great Shearwater, Northern Fulmar, Sooty Shearwater, Great Black-backed Gull, Herring Gull, and immature gulls on the water during the experimental period at low and high capelin availability in coastal Newfoundland.

Herring Gulls plateaued at ~15 individuals simultaneously attempting food capture (12 at low capelin availability, 17 at high capelin availability), which was reached when ≥30 conspecifics were present on the water (Figure 2A). Immature gulls plateaued at ~4 individuals simultaneously attempting food capture when ≥7 conspecifics were present on the water (Figure 2B). Plateaus for procellarids were absent for Great Shearwaters or less pronounced for Northern Fulmars, plateauing at ~5 individuals when ≥9 conspecifics were present (Figure 2C, D). Among the species-specific models, no other predictor significantly influenced the number of birds attempting food capture, except for the negative effect of the number of procellarids on the water on the number of immature gulls simultaneously attempting food capture (Figure 3). Capelin availability also significantly influenced the number of Herring Gulls simultaneously attempting food capture (Figure 2A).

Capture success varied across species and was affected by the number of individuals attempting to catch the food item. When examining successful attempts at capturing

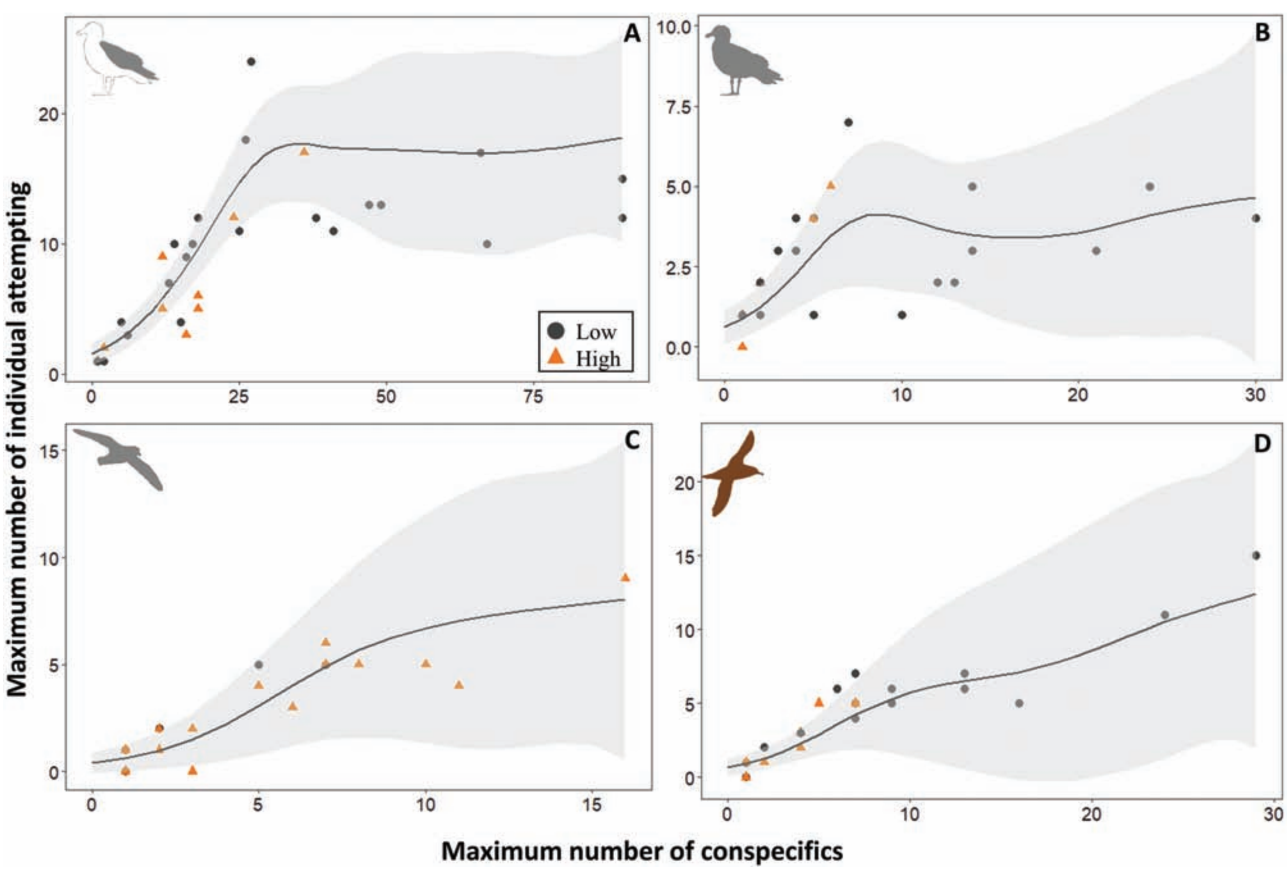

FIGURE 2. Maximum number of conspecifics that simultaneously attempted to capture a supplemental prey item within a trial relative to the maximum number of conspecifics on the water for Herring Gull (**A**), immature gull (**B**), Northern Fulmar (**C**), and Great Shearwater (**D**) in coastal Newfoundland. Gray area represents 95% confidence intervals. Note the different *x*- and *y*-axis scales. Circles represent period of low capelin availability and triangles represent period of high capelin availability.

TABLE 1. Generalized additive models with negative binomial distribution of the maximum number of birds simultaneously attempting to capture a supplemental prey item within a trial for Herring Gulls, immature gulls, Northern Fulmars, and Great Shearwaters in coastal Newfoundland. Predictors are the maximum number of conspecifics on the water, maximum number of heterospecifics on the water (procellarids, when modelling for gull species; gulls, when modelling for procellarid species), capelin availability, and maximum number of species present. SE = standard error. edf = estimated degree of freedom. Ref.df = reference degree of freedom

Models	Parametric fixed effect					Approximate significance of smooth terms					*n*	Variance explained
		Estimate	SE	χ^2	*P* value		edf	Ref.df	χ^2	*P* value		
Herring Gull	Intercept	2.71	0.3		<0.001	Number of conspecifics	4.21	5.04	75.8	<0.001	34	88.0%
	Number of Procellarids	−0.001	0.01	0.01	0.908							
	Capelin availability	−0.34	0.16	4.47	0.035							
	Number of species	−0.17	0.09	3.46	0.063							
Immature gull	Intercept	1.57	0.33		<0.001	Number of conspecifics	3.54	4.25	15.62	0.004	28	82.2%
	Number of Procellarids	−0.09	0.04	5.26	0.022	Number of species	1.52	1.83	2.96	0.246		
	Capelin availability	−0.01	0.34	0.03	0.978							
Northern Fulmar	Intercept	1.61	0.67		0.016	Number of conspecifics	2.46	2.97	26.54	<0.001	23	79.7%
	Capelin availability	−0.33	0.65	0.27	0.605	Number of gulls	1.241	1.44	0.09	0.824		
	Number of species	−0.18	0.15	1.43	0.232							
Great Shearwater	Intercept	0.72	0.69		0.299	Number of conspecifics	3.17	3.98	26.61	<0.001	29	90.3%
	Number of gulls	−0.005	0.001	0.79	0.376							
	Capelin availability	−0.16	0.3	0.27	0.604							
	Number of species	0.11	0.15	0.54	0.463							

food items, Herring Gulls were successful in 68.4% of supplement food offerings where at least one individual attempted, whereas Great Black-backed Gulls were successful in 11.7% of the attempts and immature gulls in 32.7% of the attempts. Northern Fulmars were successful in 81.1% of the attempts, whereas Great Shearwaters and Sooty Shearwaters were successful in 32.2% and 18.8% of the attempts, respectively. Species-specific generalized additive models of success revealed that the proportion of successes increased significantly with the number of conspecifics simultaneously attempting for all species, but this relationship eventually plateaued (Figure 4 and Table 2). Therefore, as the number of conspecifics on the water of a particular species increased, this species was the primary or only species that was successful at catching supplemental food items. Herring Gulls and Northern Fulmars reached >95% success at ~15 and ~6 individuals attempting, respectively (Figure 4A, C), meaning that each species was the primary or only species that was successful at capturing supplemental prey items beyond these numbers of conspecifics on the water. Immature Gulls only reached a plateau of 50% success (at ~6 individuals attempting), and Great Shearwaters only reached 64% success (at ~11 individuals attempting; Figure 4B, D).

The capture success of supplemental food items was also affected by the number of heterospecific competitors attempting for all species except Northern Fulmars, whereby success was lower when the number of heterospecific competitors attempting was higher (Figure 5 and Table 2). The effect of heterospecific competitors attempting was more important for Great Shearwaters and immature gulls, whereby success was <10% after 12 and 10 competitors attempting simultaneously, respectively (Figure 5B, D). Although the raw data do not fit the modelled curve well for Great Shearwaters, likely due the effects of other predictor variables, proportions decreased with an increase in the number of heterospecific competitors attempting to capture supplemental food items (Figure 5D). In contrast, Herring Gull success did not decrease below 47%, despite increases in procellarids attempting simultaneously (Figure 5A). Finally, the success for all species was significantly lowered by the number of species present (Figure 6).

DISCUSSION

Seabirds appeared to primarily respond to the supplemental food, rather than simply the experimental platform, as evidenced by higher numbers of birds present during the experimental period relative to the pre-control period. As hypothesized, seabird numerical responses to the supplemental food varied with capelin availability, whereby the number of birds on the water was lower during high

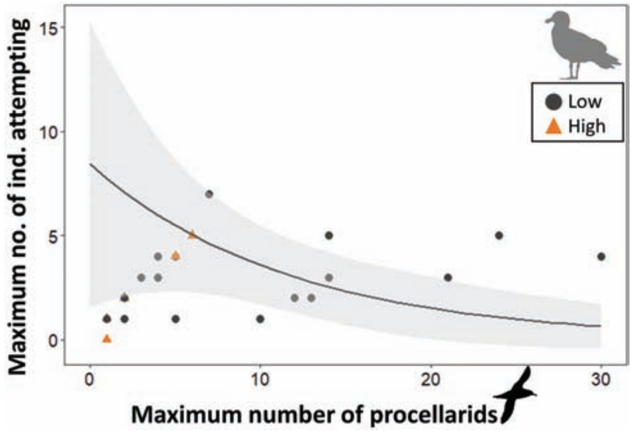

FIGURE 3. Maximum number of immature gulls that simultaneously attempted to capture a supplementary prey item within a trial relative to the maximum number of procellarids on the water in coastal Newfoundland. Gray area represents 95% confidence intervals. Circles represent period of low capelin availability and triangles represent period of high capelin availability.

capelin availability for most species as predicted. We also hypothesized that flock size and composition would affect species-specific behavioral responses. Indeed, the number of birds simultaneously attempting to capture supplemental food items increased with the number of conspecifics until a plateau was reached, but the plateau varied among species. Additionally, food capture success was affected by the number and/or the presence of heterospecific competitors for all species. The food capture success of Northern Fulmars and Herring Gulls, however, was much less affected by heterospecifics, which supports our prediction that gull capture success would not be influenced by the presence of procellarids. The success of immature gulls, however, was negatively affected by an increase in the number of species and procellarids attempting food capture, suggesting an impact of procellarids as well as adult gulls. Overall, the abundance and foraging success of seabird species varied during supplemental food offerings under dynamic natural prey availability and seabird abundance and composition.

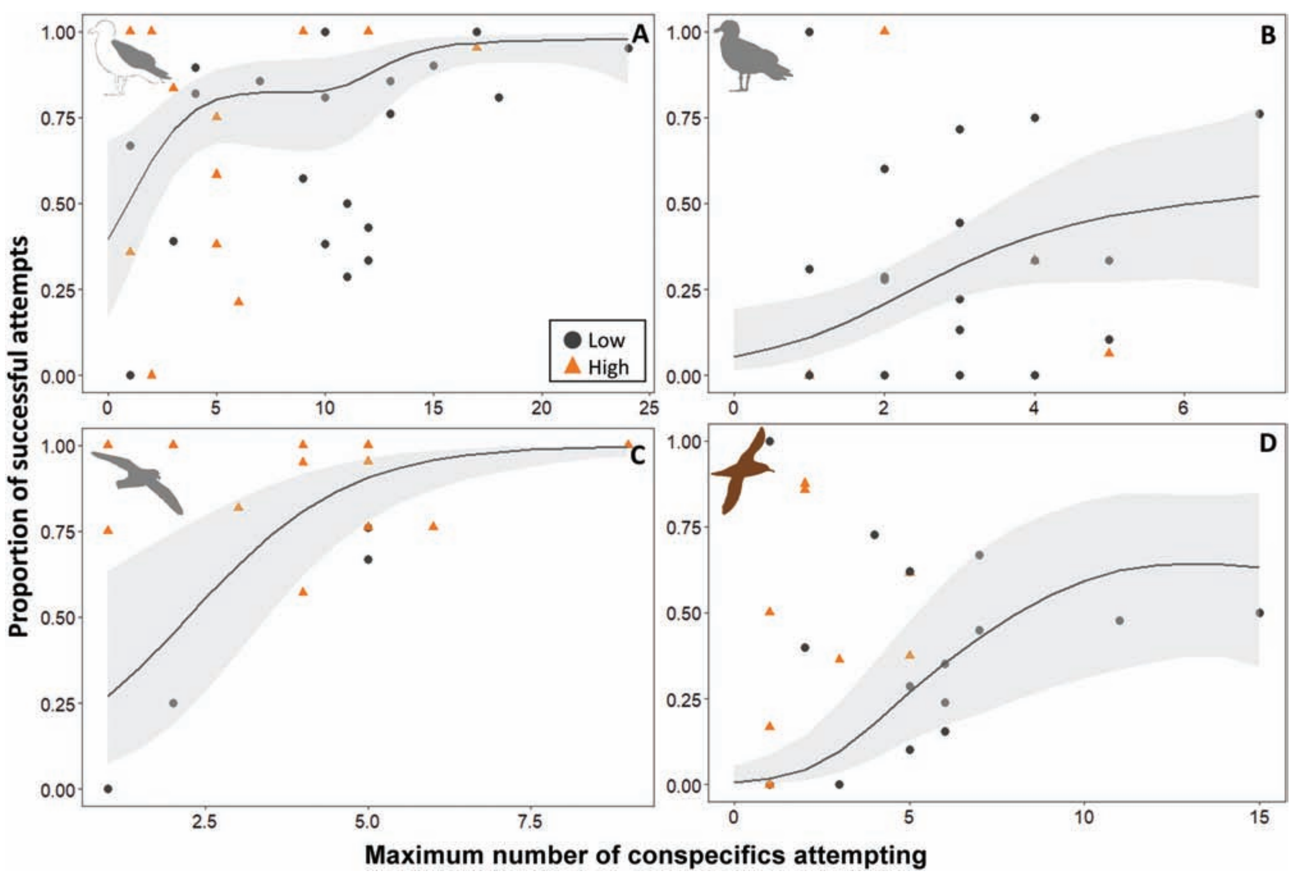

FIGURE 4. Proportion of successful attempts where at least one individual attempted within a trial relative to the maximum number of conspecifics simultaneously attempting to capture a supplemental prey item, for Herring Gull (**A**), immature gull (**B**), Northern Fulmar (**C**), and Great Shearwater (**D**) in coastal Newfoundland. Gray area represents 95% confidence intervals. Note the different *x*-axis scales. Circles represent period of low capelin availability and triangles represent period of high capelin availability.

TABLE 2. Parameters of generalized additive models with binomial distribution of the proportion of successful prey capture attempts within a trial for Herring Gulls, immature gulls, Northern Fulmars, and Great Shearwaters in coastal Newfoundland. Predictors are the maximum number of conspecifics simultaneously attempting to capture a supplementary prey item, maximum number of heterospecifics (procellarids, when modelling for gull species; gulls, when modelling for procellarid species) simultaneously attempting to capture a prey item, capelin availability, and the maximum number of species attempting prey capture. SE = standard error. edf = estimated degree of freedom. Ref.df = reference degree of freedom

Model	Parametric fixed effect					Approximate significance of smooth terms					*n*	Variance explained
		Estimate	SE	χ^2	*P* value		edf	Ref.df	χ^2	*P* value		
Herring Gull	Intercept	0.91	0.17		<0.001	Number species	1.81	2.24	10.65	0.007	34	56.4%
	Capelin availability	0.13	0.33		0.69	Number of Procellarids	4.05	4.85	22.91	< 0.001		
						Number of conspecifics	4.12	4.96	34.66	< 0.001		
Immature gull	Intercept	−0.92	0.54		0.09	Number of conspecifics	1.92	2.31	13.65	0.002	27	80.9%
	Number of Procellarids	−0.32	0.09	12.04	<0.001	Number of species	3.75	3.96	16.3	0.003		
	Capelin availability	1.31	0.57	5.22	0.02							
Northern Fulmar	Intercept	0.61	1.11		0.59	Number of species	2.52	3.02	13.24	0.004	18	94.1%
	Capelin availability	−0.72	0.79	0.84	0.36							
	Number of conspecifics	0.82	0.20	17.39	<0.001							
	Number of gulls	−0.13	0.11	1.49	0.22							
Great Shearwater	Intercept	−0.94	0.31		0.003	Number of conspecifics	2.90	3.42	26.14	<0.001	27	66.5%
	Capelin availability	0.44	0.47	0.88	0.35	Number of gulls	2.81	3.31	22.76	<0.001		
						Number of species	2.42	2.88	10.91	0.02		

The lower number of birds on the water during high capelin availability suggests that birds may have dispersed to natural prey patches in the region when capelin availability was higher. This contrasted with the period of low capelin availability, when predators aggregated nearby the experimental platform despite high densities of competitors. This result suggests that natural prey availability is an important factor explaining variation in seabird abundance at vessels discarding whole fish and offal. This numerical response to supplemental food under varying capelin availability was the same for all species, except Northern Fulmars, for which higher numbers at the experimental platform were observed during high relative to low capelin availability. As shallow divers (Garthe and Furness 2001), fulmars might rely less on capelin (Lilliendahl and Solmundsson 1997) and more on discards and offal (Phillips et al. 1999) relative to other species in the study area. Indeed, fulmars participate less in multi-species feeding flocks associated with natural prey (Camphuysen and Webb 1999) and usually have high success capturing offal discarded from fishing boats despite the presence of other species (Camphuysen et al. 1995). This is supported by only a slightly lower foraging success of Northern Fulmars when heterospecific competitors were present. Northern Fulmars remain closer to fishing boats than other species, possibly providing opportunities to obtain offal before other species (Furness et al. 1992). Overall, fulmars appeared to benefit from foraging on offal despite natural prey conditions and flock composition.

The number of individuals attempting to simultaneously capture supplemental food items increased up to a maximum number of conspecifics, suggesting that there is a number of conspecifics beyond which individuals will not attempt prey capture and that capture efficiency does not increase beyond this group size. Indeed, larger conspecific flocks reduce individual-level foraging success due to the accumulation of competitors with similar prey capture techniques for a single prey item (Gotmark et al. 1986). Interestingly, the maximum group size varied among species, suggesting that species differ in their propensity to compete with conspecifics for offal discards. The maximum number of conspecifics simultaneously attempting food capture was much higher for Herring Gulls than for immature gulls and Northern Fulmars. This higher maximum number for Herring Gulls may be due to their prey capture techniques compared to other species. As gulls are surface feeders (Hoffman et al. 1981), they have a limited capacity to capture underwater prey relative to diving shearwaters (Ronconi et al. 2010), making our floating supplemental food items more valuable to gulls than other species. In support, fisheries discards and offal are known to be an important food source for gulls (Walter and Becker 1997, Sotillo et al. 2014), possibly making them more inclined to compete with the high number of competitors. Individual-level prey capture success, however, likely decreases with

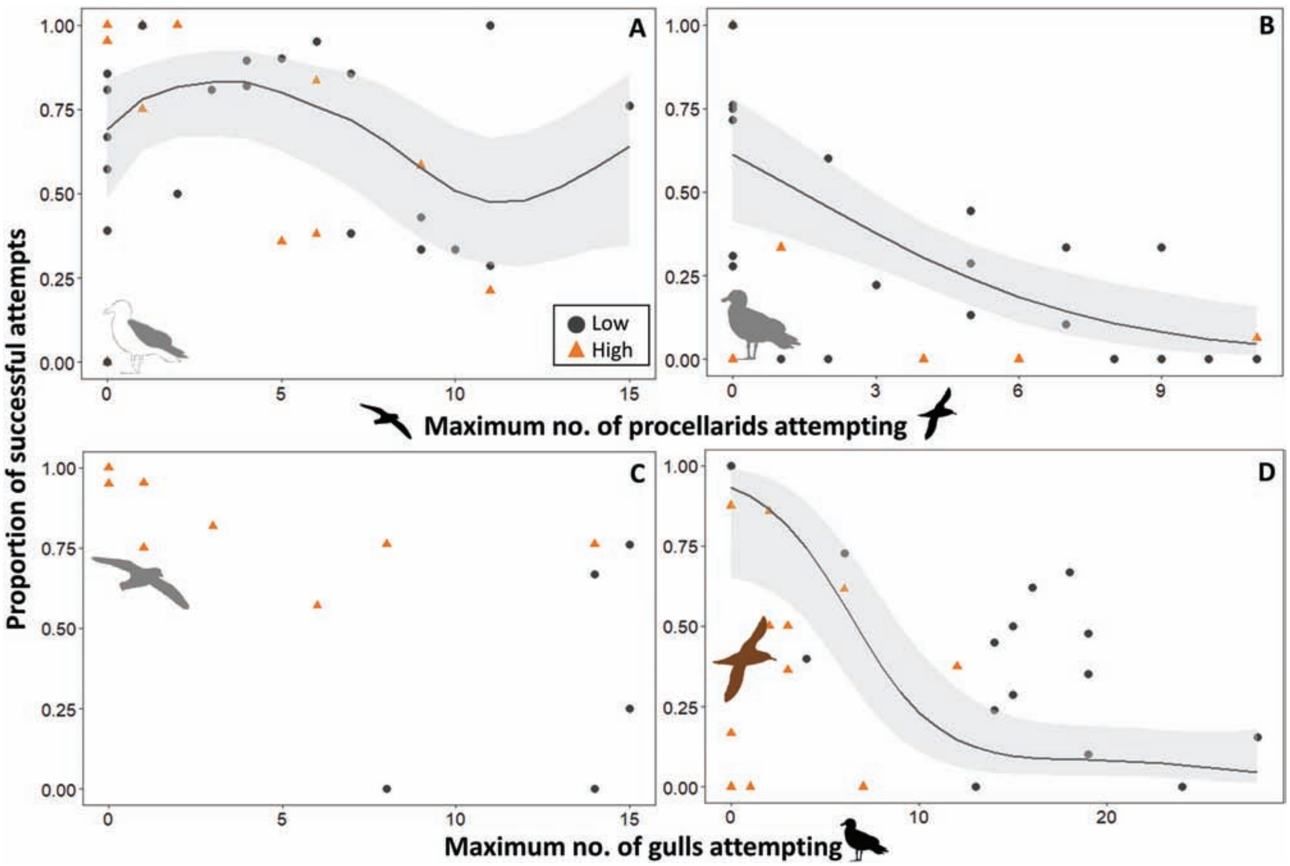

FIGURE 5. Proportion of successful attempts where at least one individual attempted within a trial relative to the maximum number of heterospecifics (procellarids or gulls) simultaneously attempting to capture a supplemental prey item for Herring Gull (**A**), immature gull (**B**), Northern Fulmar (**C**), and Great Shearwater (**D**) in coastal Newfoundland. Gray area represents 95% confidence intervals. Note the different *x*-axis scales. Circles represent period of low capelin availability and triangles represent period of high capelin availability.

more conspecifics (Gotmark et al. 1986). In contrast, immature gulls appeared to have the lowest propensity to compete, possibly due to a lack of experience and the possibility of being displaced by more experienced adult gulls (Greig et al. 1983). The maximum number of Herring Gulls simultaneously attempting food capture was 2 individuals lower during high capelin availability, suggesting a lower motivation to compete for the supplemental food items when capelin, another preferred prey type (Pierotti and Annett 1987), was highly available.

For all species, foraging success was influenced by flock size and composition, but Northern Fulmars were the least affected. As mentioned previously, fulmars have higher success capturing offal discarded from fishing boats than other species despite heterospecific presence (Camphuysen et al. 1995). Herring Gull foraging success was also affected to a lesser degree than both immature gulls and Great Shearwaters. This suggests that Northern Fulmars and Herring Gulls were the dominant competitors under our experimental conditions, which is supported by their high success rate. In contrast to fulmars, Herring Gulls were the numerically dominant species, which could increase species-specific success, but not necessarily individual-level success. Other discard and offal experiments have shown similar relationships, where the success of Herring Gulls as a species was primarily determined by their abundance within feeding flocks (Furness et al. 1992). Herring Gulls likely show low individual-level success with increasing numbers of conspecifics attempting prey capture, similar to Gotmark et al. (1986), despite increasing success of the species when more are present, as shown here. Despite the presence of both numerically dominant and highly successful species (i.e. Herring Gulls and Northern Fulmars), immature gulls and Great Shearwaters were typically present throughout our experiment even though their capture success was reduced by the presence of these species. For instance, the success of Great Shearwaters declined with increasing numbers of gulls. To compete with gulls, different behavioral strategies may be necessary. Like Northern Fulmars, Great Shearwaters typically remained close (<2 m) to the boat during our experiment (Carvalho 2018) as well as in other discard and offal experiments (Furness et al. 1992, Camphuysen and Webb 1999), whereas adult and immature gulls often stay farther

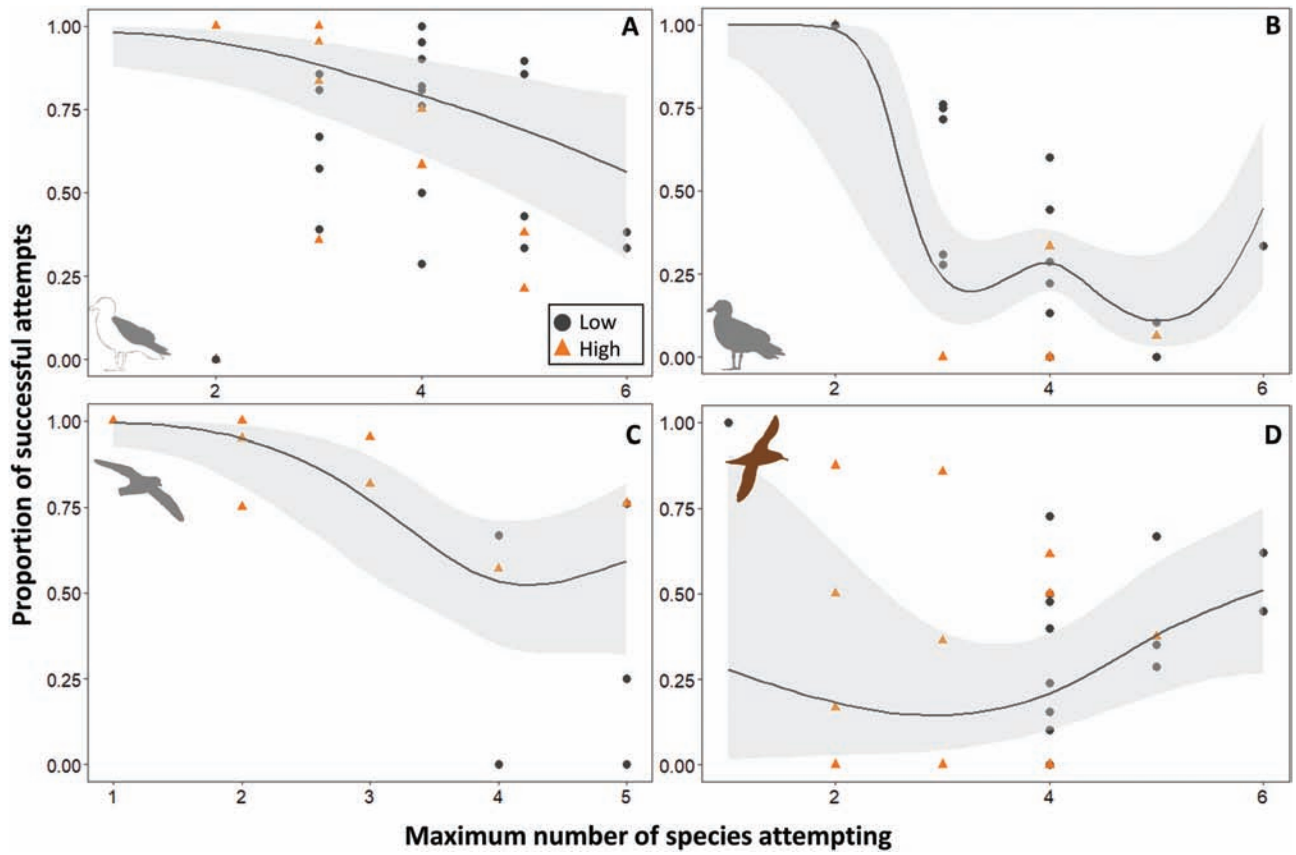

FIGURE 6. Proportion of successful attempts where at least one individual attempted within a trial relative to the maximum number of species simultaneously attempting to capture a supplemental prey item for Herring Gull (**A**), immature gull (**B**), Northern Fulmar (**C**), and Great Shearwater (**D**) in coastal Newfoundland. Gray area represents 95% confidence intervals. Note the different *x*-axis scales. Circles represent period of low capelin availability and triangles represent period of high capelin availability.

(>5 m) from the boat (Furness et al. 1992, Camphuysen and Webb 1999) and, thus, have a greater distance to cover to retrieve discarded food items. This strategy, however, only worked occasionally for Great Shearwaters. As Great Shearwaters are capable of diving deeper to capture their prey (Ronconi et al. 2010), they may be less motivated to compete for and, thus, successfully capture prey items under our experimental conditions, relative to fulmars that are restricted to capturing prey at surface or during shallow dives (Garthe and Furness 2001). Finally, the success of immature gulls decreased with an increase in the number of procellarids and species simultaneously attempting capture of supplemental food. Immature gulls are less successful than adult gulls when using a kleptoparasitic strategy (Steele and Hockey 2010, Sotillo et al. 2014) and when competing against adult gulls and other species (Greig et al. 1983, González-Zevallos and Yorio 2011). This reduced success may have resulted in the lower willingness to compete with adult gulls or procellarids for supplemental prey items in our experiment, which is supported by the lower number of immature gulls attempting when there was a higher number of procellarids.

Given that Great Black-backed Gulls are the largest gulls in the study area, we expected them to be more aggressive than the smaller Herring Gulls, as has been shown in other studies (Cotton 2009, Steenweg et al. 2011, Ronconi et al. 2014). Indeed, most studies examining interactions between these 2 large gull species during discard and offal experiments showed that Great Black-backed Gulls usually outcompete Herring Gulls, unless the latter are numerically dominant (Furness et al. 1992, Cotton 2009). During our experiment, Great Black-backed Gulls were never more abundant than Herring Gulls, which could explain this lack of dominance. Additionally, Great Black-backed Gulls often steal prey from other species (Garthe and Hüppop 1998, Cotton 2009) and, thus, may be attracted to the bird assemblage nearby the experimental platform for this purpose. Great Black-backed Gulls were not observed to kleptoparasitize other species, however, and rarely attempted to capture supplemental food items, often remaining much farther (>10 m) from the experimental platform. The experimental platform may have only been used as an at-sea roosting site, where they could still benefit from increased predator detection (e.g., Bald Eagles [*Haliaeetus* *leucocephalus*]) by joining the group (Bijleveld et al. 2010). In Newfoundland, Great Black-backed Gulls are known to forage more at seabird colonies (i.e. eggs and chicks or stolen fish from breeding alcids) than Herring Gulls (Regehr and Rodway 1999, Veitch et al. 2016) and, thus, might not rely on fisheries discards and offal to a great extent.

CONCLUSION

Multiple factors influenced the species-specific numerical and behavioral responses and foraging success of seabirds within mixed-species seabird flocks during offal discarding. Gulls and most procellarids shifted their foraging behavior to rely on this supplemental food source when natural prey availability was low, which resulted in shifting interactions among species. These findings suggest that net energy gain during fisheries discarding of whole fish and offal varies with natural prey availability, highlighting the importance of monitoring local prey availability when studying species interactions, particularly in the context of discarding. Indeed, natural prey availability may explain variations in seabird abundance during other discard and offal experiments. Prey capture attempts and success of Herring Gulls and Northern Fulmars were moderately affected by flock composition or relative abundances of other species, suggesting that they may be dominant competitors on fisheries offal in coastal Newfoundland. Despite the presumably minimal benefits of group foraging during offal discarding, birds continued to aggregate to forage, suggesting that benefits of group foraging, such as reduced search costs for prey patches ("local enhancement"), outweigh the costs, especially under low natural prey availability. Future experiments are need to quantify the energetic benefits of local enhancement relative to costs of competitive interactions to understand shifts in net energy gain of seabirds with natural prey availability and flock size and composition during fisheries discarding. These studies will be important as the increase in global catches of forage fish species continues (Smith et al. 2011), because this reduction in natural prey availability may lead to a higher reliance on fisheries discards by seabirds, ultimately resulting in higher risks of seabird mortality through by-catch (Lewison and Crowder 2003, Croxall et al. 2012). Additionally, a further understanding of divergent tendencies to capture offal and discards among similar species will be an important avenue of future research.

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Ethics statement: The experimental protocol (F16-017) was approved by the University of Manitoba, Fort Garry Campus Animal Care Committee in accordance with the Canadian Council of Animal Care.

Author contributions: All authors formulated the questions and designed the methods; G.K.D. supervised research; all authors collected data; L.D.M. analyzed the data and wrote the paper.

Data depository: Analyses reported in this article can be reproduced using the data provided by Maynard et al. (2019).

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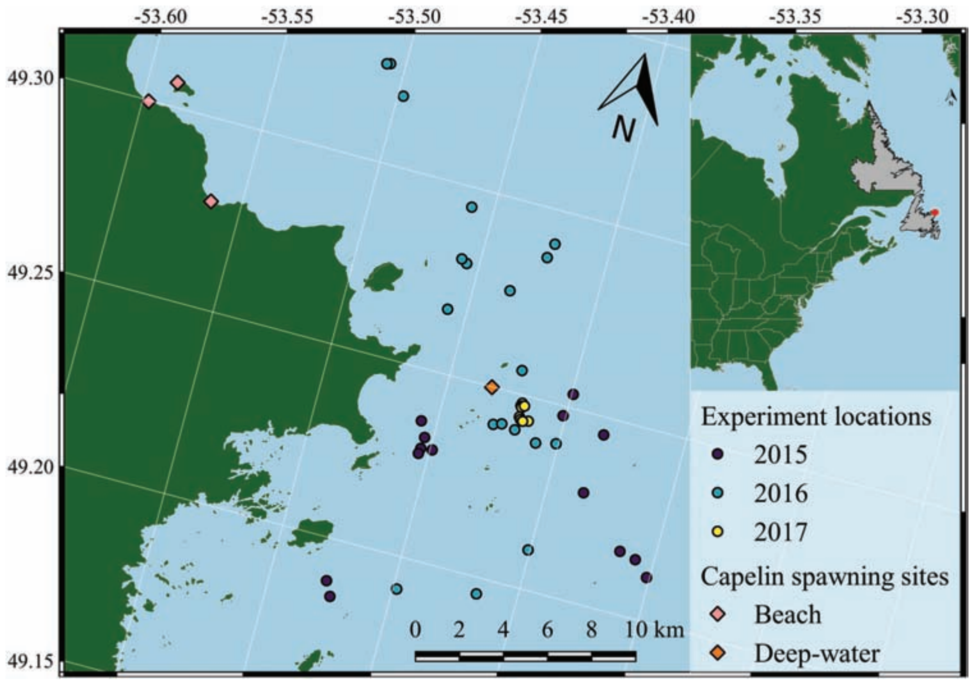
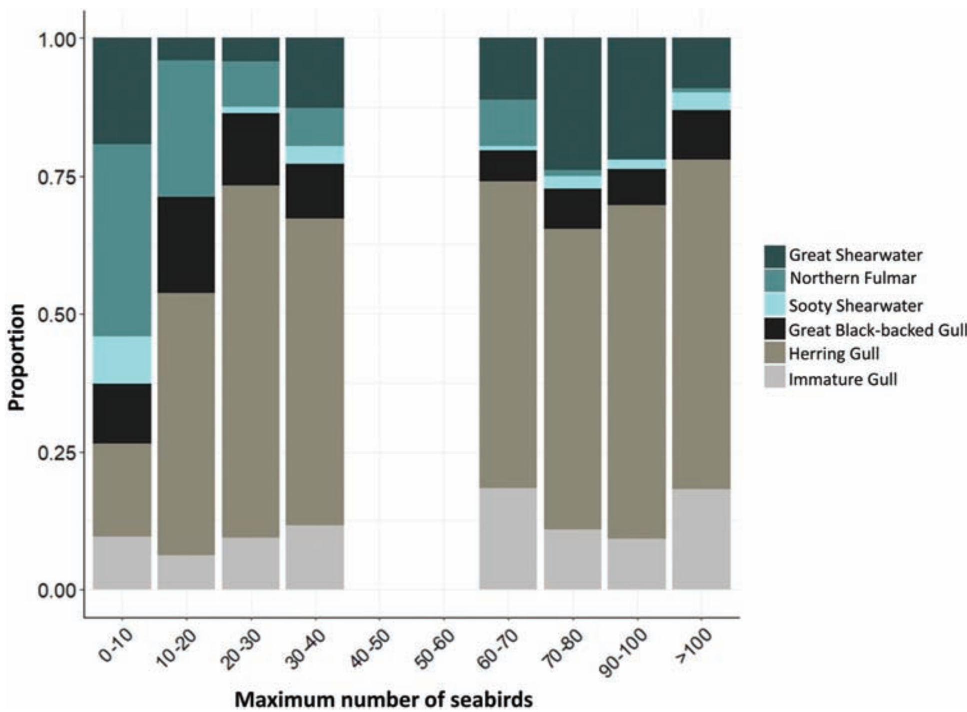


APPENDIX FIGURE 7. Locations of supplemental food experiments by year relative to capelin spawning sites on the northeast Newfoundland coast.



APPENDIX FIGURE 8. Proportion of each species across varying maximum numbers of seabirds on the water during the experimental period in the coastal Newfoundland study area.