

RESPONSES OF SYMPATRIC SHEARWATERS TO SUPPLEMENTAL FOOD UNDER VARYING NATURAL PREY AVAILABILITY ON THE WINTERING GROUNDS OF COASTAL NEWFOUNDLAND, CANADA

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ABSTRACT

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Species tend to concentrate in areas with high prey availability, which could lead to competitive interactions within a feeding assemblage as resources become depleted. In coastal Newfoundland, Canada, capelin *Mallotus villosus* is the focal forage fish species that many top predators feed on during the summer; however, inshore availability varies throughout the boreal summer when abundant aggregations migrate inshore to spawn. We investigated the interactions and responses of Great Shearwaters *Ardenna gravis* and Sooty Shearwaters *A. grisea* during their non-breeding season to supplemental food supply under changing natural prey availability (higher and lower capelin availability) by conducting an at-sea experiment during July–August (2015/2016) in coastal Newfoundland. Supplemental food was offered every 30 s over 10 min ('experimental period'), which was preceded and followed by 10-min control periods (i.e., no food provided). The number of both species increased during the experimental periods, indicating that both species were attracted to the food supplementation experiment. Great Shearwaters were 7.6–13.8 times more likely than Sooty Shearwaters to land near the experimental platform and 95.2 times more likely than Sooty Shearwaters to fight over supplemental food items with individuals of the same or different species. These species-specific tendencies remained consistent as prey availability varied within years, but both species increased in their abundance and interactions with other species (including Herring Gulls *Larus argentatus* and Northern Fulmars *Fulmarus glacialis*) during prey capture at lower relative to higher prey availability, as evidenced by lower proportions of flying birds and a greater likelihood of landing on the water. Overall, we suggest that when Great and Sooty shearwaters feed in close association, Great Shearwaters are the more competitively dominant species, which may lead to higher risks of by-catch mortality, especially when the availability of natural prey decreases.

Key words: species interactions, interspecific competition, fisheries discards, prey availability, shearwater, Ardea

INTRODUCTION

In marine systems, mixed-species feeding assemblages of predators tend to concentrate in areas with high food availability (Hunt *et al.* 1999, Worm *et al.* 2003, Davoren 2013, Lewison *et al.* 2014), which may lead to interspecific competition as resources become depleted (Park 1962, Schoener 1983). For seabirds, evidence for interspecific competition is reported in studies examining mixed-species feeding flocks feeding on natural prey, where highly competitive species (i.e., larger and/or more aggressive species) can obstruct access to prey aggregations and reduce foraging success of other predators (Shealer & Burger 1993, Maniscalco *et al.* 2001). Although some pursuit-diving species (e.g., alcids) can enhance foraging efficiency of other species by forcing prey schools to the surface (Hoffman *et al.* 1981, Grover & Olla 1983, Chilton & Sealy 1987, Camphuysen & Webb 1999), other pursuit-plunging (e.g., shearwaters) and plunge-diving (e.g., gannets) species might disperse and force prey to move deeper from the surface, thereby reducing the foraging efficiency of non-diving species (Hoffman *et al.* 1981). Interspecific interactions during prey capture have also been reported when seabird species aggregate to feed on fisheries discards (Hudson & Furness 1988a, Oro & Ruiz 1997, Arcos & Oro 2002, Bugoni *et al.* 2010). When feeding on discards, species composition and behaviour greatly influence feeding success (Garthe & Hüppop 1998, Maynard *et al.* 2020), where larger and more aggressive species have been reported to displace and/or steal

(kleptoparasitism) discards from smaller and less aggressive species (Hudson & Furness 1988b, Jiménez *et al.* 2011). These interactions, however, can also be influenced by the type of discards (e.g., whole fish or offal) and the type of fishery (i.e., species composition and sizes discarded) owing to species-specific prey preferences of predators (González-Zevallos & Yorio 2011).

Two trans-equatorial migrant shearwater species, Great Shearwaters *Ardenna gravis* and Sooty Shearwaters *A. grisea*, aggregate in coastal Newfoundland, Canada, during the boreal summer to feed on a key forage fish species, capelin *Mallotus villosus* (Howell 2010, Carvalho & Davoren 2020). During this time, the two non-breeding shearwater species are known to use the northeast Newfoundland coast to complete their moult (Carvalho 2018) during which they display high dietary overlap (based on stable isotope ratios of carbon and nitrogen; Carvalho & Davoren 2020). Moreover, these species overlap at sea (Carvalho & Davoren 2019) and are often observed foraging together within the same multi-species aggregations (Davoren 2013) with other breeding species, including Herring Gulls *Larus argentatus*, Great Black-backed Gulls *L. marinus*, and Northern Fulmars *Fulmarus glacialis* (Maynard *et al.* 2020). Although such evidence in combination indicated that the benefits of foraging in close association may outweigh the costs (Carvalho & Davoren 2019), the extent of interaction between the two large shearwaters during prey capture is unclear. Fine-scale contests over prey items within a patch are

likely because both shearwater species have similar prey capture behaviour, typically surface-seizing, pursuit-plunging, and pursuit-diving (Ashmole 1971), and both species primarily perform shallow dives when foraging (< 10 m; Raymond *et al.* 2010, Ronconi *et al.* 2010a) despite records of different observed maximum dive depths (Sooty Shearwater: 69 m, Shaffer *et al.* 2009; Great Shearwater: 19 m, Ronconi *et al.* 2010a). These species also appear to vary in temperament (Bugoni *et al.* 2010, Ronconi *et al.* 2010b, Maynard *et al.* 2020), specifically along the shy-bold spectrum (Sih *et al.* 2004). Great Shearwaters display a greater frequency of aggressive behaviours when feeding on offal and are also more abundant in closer proximity to vessels compared with Sooty Shearwaters (Maynard *et al.* 2020). Therefore, behavioural interactions between these shearwaters when foraging in close association may have divergent species-specific costs.

To investigate species interactions between Great and Sooty shearwaters when foraging in close association, we examined their fine-scale foraging behaviour and interactions within mixed-species feeding assemblages under changing natural prey (capelin) availability during their non-breeding season. To do this, we conducted an at-sea experiment off the northeast coast of Newfoundland, by offering supplemental food during periods of lower and higher capelin availability within years. We focused on behaviours indicating the tendency of each species to interact with other bird species within the feeding assemblage (i.e., Herring Gulls, Northern Fulmars, and the other shearwater species; Maynard *et al.* 2020) and whether species-specific tendencies shift under varying prey availability. We predicted that the larger and more bold species (Great Shearwater) would display a higher tendency to interact with

other species during prey capture (e.g., greater likelihood of landing near experimental platform; lower proportion of flying birds) along with more aggressive behaviours (i.e., kleptoparasitism), whereas the smaller and more shy species (Sooty Shearwater) would display a higher tendency to avoid interactions with other bird species (e.g., lesser likelihood of landing; greater proportion of flying birds). We also predicted, however, that both species would be more likely to interact with other seabirds during prey capture under low relative to high prey (capelin) availability. A previous study using the same dataset indicated that Herring Gulls dominated the feeding assemblage (> 70%) throughout the experiment, but that the number of gulls did not affect shearwater attempts to capture supplemental prey (Maynard *et al.* 2020). Therefore, the presence and number of gulls should not affect interactions between the two shearwater species in this study. Understanding species-specific responses and interactions among species under varying natural prey availability will provide insight into niche partitioning and increase our capacity to predict changes in community structure under varying prey regimes.

METHODS

Study area and design

The study was conducted in waters off the northeast coast of Newfoundland during July–August 2015 and 2016. At that time, capelin, a key forage species, migrates from offshore nursery and wintering areas to spawn in this and other coastal regions (Davoren *et al.* 2012), resulting in more than a doubling of the inshore prey biomass (Carvalho & Davoren 2019). The experiment was conducted

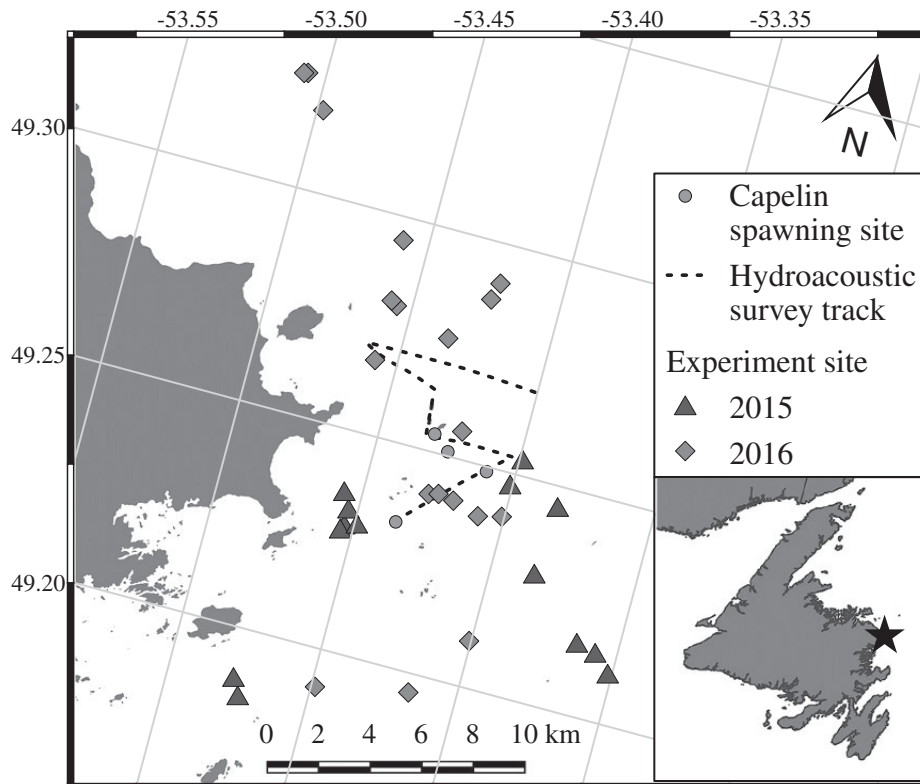


Fig. 1. Map of the study area with the location of the experimental trials conducted during the summers of 2015 (triangle) and 2016 (diamond) in coastal Newfoundland within 1–10 km of the annually persistent capelin spawning sites (circles). Note the route of the weekly survey to quantify capelin biomass and species-specific seabird densities is also indicated.

within 1–10 km of a cluster of four annually persistent, deep-water (15–40 m) spawning sites of capelin (Fig. 1). These sites are known to be frequented by multi-species feeding assemblages of marine predators, including seabirds, predatory fish, and whales (Davoren 2013). Experimental locations varied within and among days (Fig. 1), and we selected locations haphazardly based on the presence of nearby (200–300 m) aggregations of 10–100 shearwaters. Annually persistent capelin spawning sites in the study area (Fig. 1) were monitored to determine the start and duration of capelin spawning, using methods described in Crook *et al.* (2017). Gathered information was then used to define periods of ‘high’ (i.e., during spawning) and ‘low’ prey availability (i.e., during pre- and post-spawning), following Maynard *et al.* (2020). In each year, periods of high and low prey availability were further corroborated during a weekly hydroacoustic survey (Fig. 1), which quantified when capelin biomass peaked during 2015 (0.126 g/m², July 20) and 2016 (0.027 g/m² July 14; see Carvalho & Davoren 2019 for details). Systematic seabird counts collected during these weekly surveys also indicated similar densities in both years for Great Shearwaters (2015: 3.1 ± 1.7 birds/km²; 2016: 3.6 ± 2.8 birds/km²) and Sooty Shearwaters (2015: 9.7 ± 4.2 birds/km²; 2016: 7.4 ± 1.5 birds/km²; unpubl. data). As Atlantic cod *Gadus morhua* is one of the main target species for fisheries in coastal Newfoundland during the summer, we used Atlantic cod offal (liver) as supplemental food in our at-sea experiment.

We conducted 30-min trials, each of which was divided equally in three periods: pre-control, experimental, and post-control. We recorded video during control and experimental periods using a GoPro® (Hero 4) digital video camera attached to a pole on one side of the experimental platform (i.e., 5-m open boat) to record behaviour (Fig. 2). As the recording camera was always placed in the same location at the same height on the experimental platform, the recording area remained a consistent distance (~150 m) away from the experimental platform. Before each trial, the boat motor was turned off to eliminate the influence of motor noise on bird behaviour. During the pre-feeding control period, we did not offer supplemental food so that we could examine species-specific responses to the experimental platform in the absence of the supplemental food. During the experimental period, we offered supplemental food, simulating discards of offal in the Atlantic cod fishery by manually throwing one 30–40 g piece of cod liver

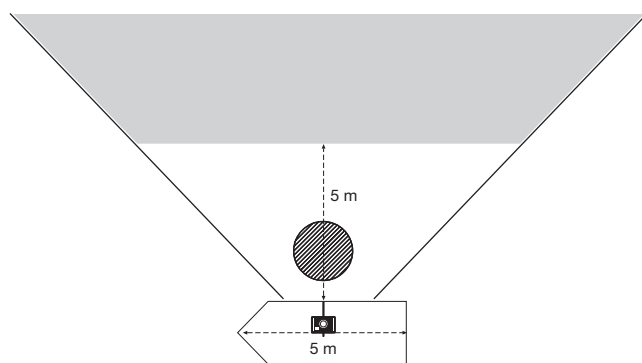


Fig. 2. Experimental design showing the near (< 5 m from the boat; white area) and the far area (> 5 m from the boat; shaded area) where birds were counted on the water and flying. The hatched circle represents the area where the discards were thrown during the experimental period (1–2 m from the boat). The camera (GoPro® Hero 4) was attached to a pole, usually on the right side of the boat.

~1–2 m from the same experimental platform every 30 s for 10 min (Fig. 2). After the experimental period, we conducted a post-feeding control period, where we remained in the same location for another 10 min without providing supplemental food. We conducted up to three trials per day in different locations (~1 km apart) with the time between the beginning and end of each trial varying from 4 min to 2.5 h.

Video and data analysis

All videos were processed to record shearwater numbers by species, both flying and on the water, as well as the number of other seabirds present on the water (i.e., Herring Gulls, Northern Fulmars, and Great Black-backed Gulls). At the beginning of each video and every 30 s until the end of the 30 min trial, the number of birds on the water of each seabird species was recorded in the camera’s field of view. Throughout each trial, we continuously recorded the number of individuals of each shearwater species flying within the camera’s field of view. We used a negative binomial generalized linear model to test whether the species-specific number of shearwaters on the water and flying, separately, differed significantly during the experimental period relative to the two control periods.

Within the experimental period only, we recorded the presence/absence of the following six behaviours for each shearwater species: landing on the water, diving (pursuit or plunge dive), fighting for supplemental food items, consuming a supplemental food item, and presence near (< 5 m) and far (> 5 m) from the experimental platform (Fig. 2). We recorded the duration of dives when possible. We calculated the proportion of birds flying during the experimental period in each trial by dividing the total number of birds flying by the sum of the total number of birds flying and the maximum number of birds recorded on the water during 30 s counts throughout the experimental period. A high proportion of birds flying was used to indicate a lower tendency to interact directly with other species during the capture of a supplemental food item. We used a beta regression model (Ferrari & Cribari-Neto 2004) to test whether the species-specific proportion of flying birds during the experimental period differed between species (Great and Sooty shearwaters), prey availability periods (low and high), years (2015 and 2016), and trials (1 and 2). An interaction term (species × prey availability) was also included to examine whether the species-specific proportion of birds flying changed under varying capelin availability. The number of other seabird species was not included in the model as the composition and relative abundances of bird species remained consistent within capelin availability periods and across years (Maynard *et al.* 2020), resulting in a similar influence of other species (primarily Herring Gulls) on each shearwater species throughout this study. The third trial was omitted from our analyses, as individuals tended to follow the boat after the second trial, resulting in much greater numbers of birds during the third trial, thus biasing the experimental results. Environmental conditions were not included in the analysis, as trials could only be conducted in low wind (< 25 km/hr) and clear conditions (> 10 km visibility). A few trials that were conducted under reduced visibility (< 1 km) or on windy days (> 25 km/hr) were not included in the dataset.

To examine species-specific differences in the likelihood of observing (presence/absence) the six behaviours during the experimental period, we used a generalized linear model with a binomial distribution and logit link function on the presence/absence of each

behaviour in each trial (response variable) with the suite of fixed predictor variables. A greater tendency to interact with other species while capturing supplemental food items was indicated by higher odds of landing on the water, fighting for a supplemental food item, and presence near (relative to far) the experimental platform. In contrast, a lesser tendency to interact with other species during prey capture was indicated by lower odds of landing on the water, fighting for a supplemental food item, presence far (relative to near) from the experimental platform and diving, presumably to capture sinking food items. We evaluated significant differences ($P < 0.05$) in the logistic regressions by calculating odds ratios along with likelihood-based confidence intervals (CI) to indicate the magnitude of different tendencies (odds, or likelihood) of displaying the behaviour. An odds ratio is the ratio of the probability of presence and the probability of absence under different predictor levels, and thus indicates the odds, or likelihood, of the behaviour being present or absent under higher relative to lower prey availability, or in one species relative to another. We report the reduced models, after removing predictors that were not significant ($P < 0.05$) in the full model (i.e., all predictor variables); the top-ranking model was indicated by the lowest Akaike Information Criteria (AIC). Analyses were performed using JMP Pro statistical software version 14.1.0.

RESULTS

Trials where Great and Sooty shearwaters were not observed were deleted from the analysis ($n = 3$). Based on the timing and duration of spawning during 2015 (Carvalho & Davoren 2019), four trials were conducted during high capelin availability (08–09 August) and nine during low capelin availability (02–03 August, 11–18 August). During 2016, trials were conducted between 16 July and 17 August ($n = 12$), with six trials during high capelin availability (25 July–04 August) and six during low capelin availability (16 July, 12–17 August). In total, 438 pieces of cod liver were offered during experimental periods in 2015 and 2016 during low ($n = 229$) and high ($n = 209$) capelin availability. Bird species composition on the water within 150 m of the experimental platform consisted of 71% gull species (56% Herring Gull, 5% Great Black-backed Gull, 10% immature birds of both species), 17% Great Shearwaters, 9% Northern Fulmars, and 2% Sooty Shearwaters. As these percentages were derived from birds on the water only, the percentage of shearwaters within 150 m of the experimental platform was underestimated, especially for Sooty Shearwaters, which were more often recorded flying. Species sighted occasionally flying (i.e., < 5 individuals over all trials) or on the water during the experiment were Common Tern *Sterna hirundo*, Pomarine Jaeger *Stercorarius pomarinus*, and Manx Shearwater *Puffinus puffinus*. Other species common in the area observed passing in flight during the experiment were Common Murre *Uria aalge*, Razorbill *Alca torda*, and Northern Gannet *Morus bassanus*.

The number of birds on the water and flying within ~150 m of the experimental platform was greater during the experimental period (i.e., when cod liver was offered every 30 s) than during the pre-control period for both species (Great Shearwater flying: $X_2^2 = 30.035$, $P < 0.0001$; Great Shearwater water: $X_2^2 = 14.021$, $P = 0.0002$; Sooty Shearwater flying: $X_2^2 = 18.205$, $P < 0.0001$; Fig. 3). The number of birds on the water and flying did not differ between the experimental period and the post-control period for Great Shearwaters (flying: $X_2^2 = 2.311$, $P = 0.129$; water: $X_2^2 = 2.378$, $P = 0.123$), but it did differ for Sooty Shearwaters, with fewer individuals flying in the post-control period ($X_2^2 = 5.331$, $P = 0.021$; Fig. 3). A similar trend

was observed for Sooty Shearwaters on the water, but the numbers of birds did not differ significantly between the experimental period and both the pre-control ($X_2^2 = 2.765$, $P = 0.096$) or the post-control periods ($X_2^2 = 1.904$, $P = 0.168$; Fig. 3). Interestingly, the mean numbers of Great and Sooty shearwaters on the water and flying reached greater maxima earlier in the experimental period (~14–16 min) during low prey availability compared to high prey availability (~17–19 min; Fig. 3).

When examining the influence of year, trial, and the interaction term (species \times prey availability) on the proportion of birds flying and the presence/absence of behaviours, these were not significant ($P > 0.05$) and, thus, we reduced our models to include two predictor variables (i.e., species, prey availability). During the experimental period, the proportions of flying birds differed between species ($X_1^2 = 4.946$, $P = 0.0262$) and between prey availability periods ($X_1^2 = 4.842$, $P = 0.0278$), where there was a higher proportion of Sooty Shearwaters flying ($88.8\% \pm 5.9\%$) than Great Shearwaters ($72.1\% \pm 6.6\%$) and a higher percentage of both species was

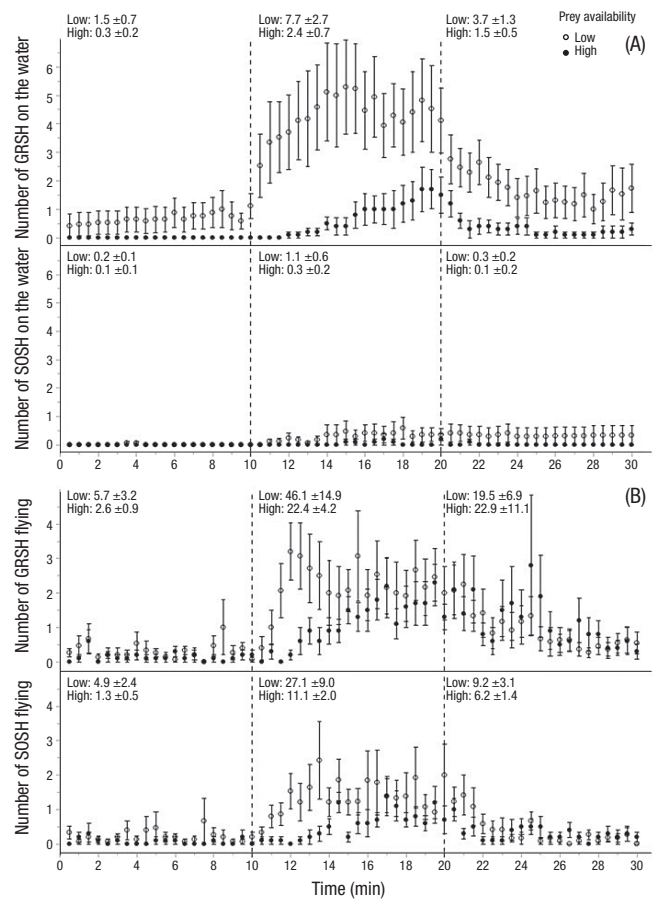


Fig. 3. Mean (\pm standard error, SE) number of birds on the water (A) and flying (B) every 30 s during the 30 min trial for Great Shearwater (top, GRSH) and Sooty Shearwater (bottom, SOSH) during low (open circle) and high (closed circle) prey availability in July–August 2015/2016 on the northeast Newfoundland coast, Canada. Mean (\pm SE) for the 10 min pre- and post-control and experimental periods are indicated for each species. Dashed lines separate the pre-control (0–10 min), experimental (10–20 min), and post-control (20–30 min) periods. Note the different y-axis scale for the number of birds on the water (A) and flying (B).

observed in flight when prey availability was high (Sooty Shearwater: $97.4\% \pm 1.5\%$; Great Shearwater: $92.0\% \pm 2.5\%$) compared with low prey availability (Sooty Shearwater: $96.7\% \pm 1.5\%$; Great Shearwater: $74\% \pm 7\%$). Great Shearwaters were 7.6 times (CI: 1.3–44.0) more likely to land on the water than Sooty Shearwaters (Likelihood Ratio₁ (LR₁) = 6.01, $P = 0.014$; Fig. 4A), and during low prey availability, both species (especially Sooty Shearwaters) were 13.8 times (CI: 2.1–89.9) more likely to land on the water than during high prey availability (LR₁ = 10.029, $P = 0.002$; Fig. 4A). Although the likelihood of diving did not differ between species (LR₁ = 0.219, $P = 0.640$) or according to prey availability periods (LR₁ = 2.525, $P = 0.112$), Sooty Shearwaters tended to dive more often (40% of the trials) than Great Shearwaters (22% of the trials; Fig. 4B). Sooty Shearwaters also had significantly longer dive durations (7.0 ± 5.3 s) than Great Shearwaters (2.2 ± 1.5 s; Wilcoxon test: $Z = 5.18$, $P < 0.001$). When diving, Sooty Shearwaters often traveled underneath the birds fighting for the food item (i.e., hatched circle in Fig. 2). In addition, Sooty Shearwaters did not remain at the surface longer than ~30 s after landing on the water and instead often dove immediately upon landing (pursuit dive) or plunge-dived from the air and took off immediately after surfacing.

When on the water, Great Shearwaters were 48.2 times (CI = 7.1–328.6) more likely to occur close to the experimental platform (i.e., < 5 m; often < 2 m away) than Sooty Shearwaters (LR₁ = 25.425, $P < 0.0001$; see Fig. 5), but the likelihood of both occurring close to the experimental platform did not differ according to prey availability (LR₁ = 1.270, $P = 0.260$; Fig. 4C). Indeed, 97.0% of Great Shearwaters on the water occurred near the experimental platform, while 53.6% of the Sooty Shearwaters on the water remained far (i.e., > 5 m). Great Shearwaters were 95.2 times (CI = 9.3–977.0) more likely to fight over food items than Sooty Shearwaters (LR₁ = 30.118, $P < 0.0001$), but this likelihood did not differ according to prey availability (LR₁ = 0.550, $P = 0.458$; Fig. 4D). Indeed, when present, one or

more Great Shearwaters attempted to catch and consume a food item 91.1% of the times cold liver was thrown during the experimental period, and were successful in 26.0% of these attempts. In contrast, Sooty Shearwaters only attempted to catch and consume a food item 27.4% of the times experimental discards were thrown (mostly one individual, during one trial) when present on the water, and they were successful only once (4.3%).

Interestingly, we observed few aggressive behavioural interactions. Indeed, we observed only one event, when a Great Shearwater stole a supplemental food item from a Northern Fulmar. In two other cases, Herring Gulls stole a food item from a Northern Fulmar and from a Great Shearwater.

DISCUSSION

Not surprisingly, the species-specific number of shearwaters on the water and flying was greater during the experimental period compared with the pre-control period. The use of offal by some species of procellariids as the main or alternative food resource has been observed worldwide in different types of fisheries (Bugoni *et al.* 2010, Bicknell *et al.* 2013). The two shearwater species, however, differed in their behavioural responses when provided with supplemental food. Great Shearwaters, the larger and more aggressive species, showed a greater tendency to interact directly with other species in mixed-species assemblages (gulls and fulmars) to capture supplemental food items. In contrast, Sooty Shearwaters, the less aggressive and smaller species, showed a greater tendency to avoid direct interactions with other seabirds, as indicated by their lower tendency to land on the water and compete for the supplemental food. These species-specific differences remained consistent as prey availability varied within years, but both species increased in number (on the water, flying) and frequency of interactions with other species while capturing prey during low prey availability, as evidenced by disproportionately fewer flying birds and a greater likelihood of landing on the water.

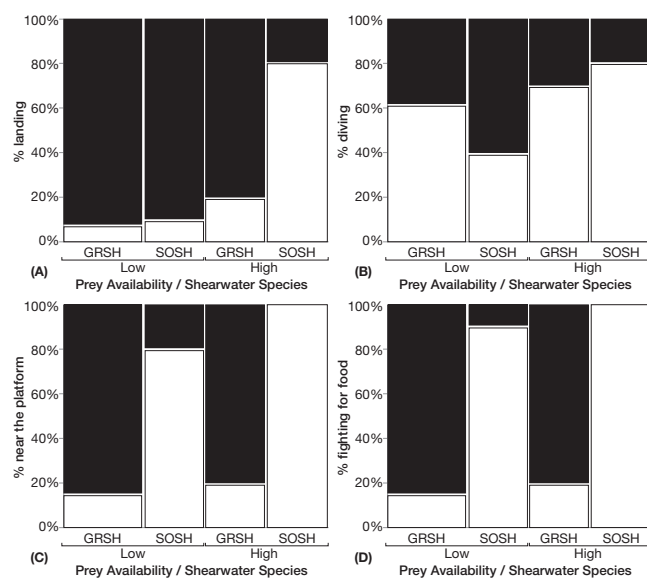


Fig. 4. The percentage of trials during low and high prey availability periods during July–August 2015/2016 where the following behaviours were either present (black) or absent (white) for Great Shearwaters (GRSH) and Sooty Shearwaters (SOSH): landing on the water (A), diving (B), presence near the experimental platform (i.e., < 5 m; C), and fighting for supplemental food items (D).

Great Shearwaters displayed a greater tendency to interact with other species during prey capture than Sooty Shearwaters, as evidenced by a greater proportion of birds on the water, occupation of the proximate (< 5 m) area, and a greater proportion of attempts to capture supplemental food items. These behaviours resulted in more direct interactions, mostly with larger Herring Gulls. Indeed, Great Shearwaters tried to capture supplemental food items during the majority of the times when present within the mixed species feeding assemblage, indicating that they do not appear intimidated by Herring Gulls, as suggested in Maynard *et al.* (2020). However, prey capture success of Great Shearwaters was previously shown to decrease as the number of Herring Gulls increased (Maynard *et al.* 2020), suggesting increasing costs of foraging in association with this and other large gull species. This bold behaviour of Great Shearwaters has been observed in other studies. For instance, Great Shearwaters are frequently observed associated with longline fishing vessels off the Brazilian coast (Bugoni *et al.* 2010) and have been reported to approach larger species (e.g., albatross) by lunging at them and, on a few occasions, were capable of stealing food from Pomarine Jaegers (Olmos 1997). Interestingly, kleptoparasitism events were infrequently observed in this study compared with several others (Hudson & Furness 1988a, Camphuysen & Garthe 1997, Garthe & Hüppop 1998, González-Zevallos & Yorio 2011). Less frequently observed kleptoparasitism may be related to the characteristics of the discarded prey (Camphuysen & Garthe 1997), whereby more kleptoparasitic events may occur when larger prey

is discarded (González-Zevallos & Yorio 2011, Hudson & Furness 1988b). This might be because individuals will usually take longer to manipulate larger prey before swallowing, as previously suggested (Garthe & Hüppop 1998, Spear *et al.* 2007). In contrast, the small, soft food items offered in this study were more easily handled and quickly swallowed.

In contrast to Great Shearwaters, Sooty Shearwaters were less likely to interact with other species during prey capture, as illustrated by the greater proportion of birds flying relative to those on the water, the tendency to occupy the area farther (> 5 m) from the experimental platform, and the tendency to avoid direct interactions with other birds during prey capture, primarily by diving to capture supplemental food items. In support, behavioural tendencies to stay farther from the boat and dive more frequently to capture discards have been documented in other studies (Brown *et al.* 1978, Yorio & Caille 1999, Bugoni *et al.* 2008, Ronconi *et al.* 2010b). For instance, Sooty Shearwaters were observed diving to feed on sinking discards from trawlers in Patagonia (Yorio & Caille 1999), similar to other species (e.g., Balearic Shearwaters *Puffinus mauretanicus*;

Arcos & Oro 2002). Interestingly, similar to dive durations of Sooty Shearwaters in our study, dive durations of other Procellariiformes *Procellaria* petrels feeding on discards averaged 8 s (Olmos 1997). Sooty Shearwaters have been reported to plunge-dive from flight as observed in our experiment and could stay underwater for 15 s or longer while feeding on supplemental food (Brown *et al.* 1978). In our study, diving likely did not increase the capture success of Sooty Shearwaters, because the food item (cod liver) usually floated on the water due to its high lipid content. In other circumstances, however, Sooty Shearwaters might enjoy greater capture success by diving when food items (e.g., dead fish) sink. This would be especially true when Sooty Shearwaters associate with other seabird species with limited or no dive capacity, such as gulls, albatrosses, and fulmars. In contrast to our results, Sooty Shearwaters have been identified as a competitive species in mixed feeding assemblages, especially when feeding on natural prey. For instance, Hoffman *et al.* (1981) classified Sooty Shearwaters as a “suppressor species” in mixed-species seabird flocks in Alaska when feeding on natural prey, as pursuit-diving in groups, leading to prey consumption, compromised the feeding success of other seabirds (exploitation competition; Hoffman *et al.*

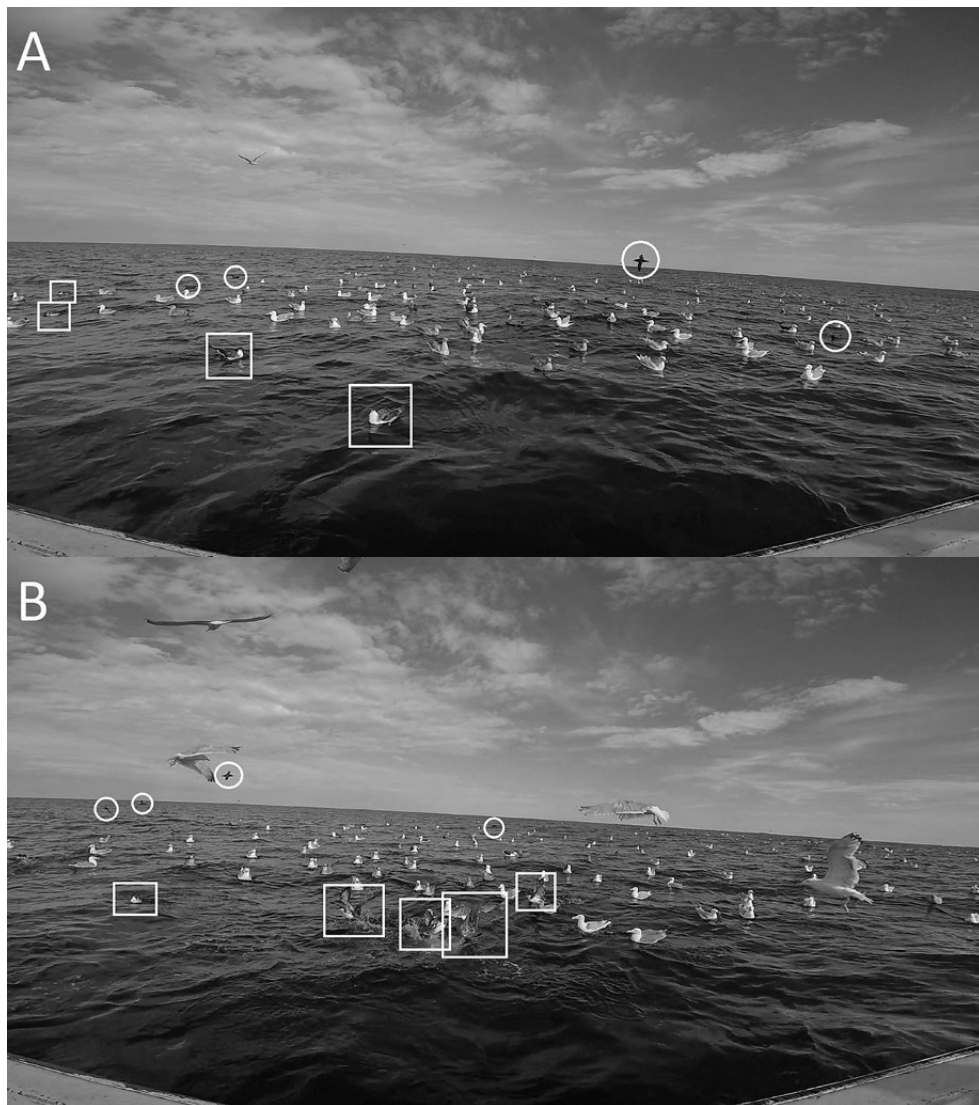


Fig. 5. Video frames from one behavioural experiment conducted in coastal Newfoundland during 2016 before (A) and (B) supplemental food (cod liver) was offered. Sooty Shearwaters flying or on the water far from the experimental platform are highlighted (circles) in both frames, while Great Shearwaters on the water near the experimental platform are highlighted (squares) in both frames.

1981). In addition, Sooty Shearwaters were reported to interfere with the foraging behaviour of surface-feeding Antarctic Terns *S. vittata* by blocking their access to prey (interference competition) when aggregated in large numbers on the surface above prey aggregations (Sagar & Sagar 1989). Differing tendencies of Sooty Shearwaters to interact, mostly indirectly, with other species during prey capture among studies might co-vary according to prey types (natural, discards) and depend to some degree on species composition and the relative abundances of other competing species in mixed-species feeding assemblages.

The species-specific differences in tendency to interact with other species during prey capture were consistent across prey availability periods, but both species displayed greater tendencies to interact with other species during lower prey availability. For instance, the number of shearwaters of both species at the experimental platform reached a greater maximum earlier in the experimental period during lower versus higher prey availability, and we suggest that birds may have been more attentive to the foraging activities of other birds when capelin availability was low. We suggest, therefore, that offal and discarded fish may be an important source of energy when natural prey availability varies. In the study area, capelin is usually readily accessible to most sub-surface predators when high-abundance aggregations of capelin form in shallow areas (< 40 m) to spawn (Davoren *et al.* 2008). Therefore, the use of alternative food resources by shearwaters, such as fishery discards, may not be as important during these periods. On the other hand, when prey availability is low, shearwaters might use other methods to find prey, such as visual cueing to the foraging activities of other seabirds (local enhancement; Thiebault *et al.* 2014, Bairos-Novak *et al.* 2015). In support, both species of shearwaters show high spatial overlap in the study area, with the primary factor underlying the presence and density of each species within the meso-scale study area being the presence of the other shearwater species (Carvalho & Davoren 2019). Shifting between natural prey and discards under varying natural prey availability has been shown in other procellariid species. For instance, Balearic Shearwaters shifted their diet during the breeding season from demersal fish derived from trawling discards to pelagic fish (anchovies) due to the reduced availability of demersal fish throughout their breeding season and the higher energy value of the anchovies (Navarro *et al.* 2009). Overall, the attraction and use of fisheries discards as a food resource may reduce energy expenditure by scavenger procellariid species during the non-breeding season when searching for patches of natural prey that are in low abundance.

In conclusion, when Great and Sooty shearwaters feed in multi-species flocks, Great Shearwaters appear to be more competitively dominant, likely due to their propensity for interacting with other species during capture of offal. Although this may ultimately be energetically beneficial to Great Shearwaters, attraction to fisheries discards results in a high risk of by-catch mortality in different fisheries and has become one of the major concerns for seabird conservation (Croxall *et al.* 2012, Lewison & Crowder 2003). Additionally, because both shearwater species increased their tendency to use supplemental food during periods of low natural prey (capelin) availability, we suggest that by-catch mortality of both species would be more likely during periods of lower prey availability. Forage fish currently contribute 37% of the global fish catch (Pikitch *et al.* 2014), and shearwaters and other seabird species likely will rely more on fisheries discards as a main food resource if forage fish availability is reduced. We expect that species-specific responses to discards among procellariids experiencing varying prey availability will likely result in varied and

episodic by-catch mortality in certain regions and at certain times of year. However, the response to discards among shearwaters is complex and will also likely vary with changes in seabird species composition and relative abundance.

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