

Underwater behaviour of common murres foraging on capelin: influences of prey density and antipredator behaviour

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ABSTRACT: Diving behaviour of seabirds has been studied using data logging devices, but little is known about underwater predator–prey interactions during dives. We used stationary video cameras to investigate how the underwater foraging behaviour of common murres *Uria aalge* was influenced by the density and behaviour of their main prey fish, capelin *Mallotus villosus*, at spawning sites on the northeast Newfoundland coast during July, 2009–2012. From ~720 h of video, we analyzed 99 events where capelin and murres were observed together, ranging from 1–20 s, and 952 events where murres were observed alone, ranging from 1–14 s. Although 91 % of all video footage of capelin was in high density schools, 69 % of active foraging behaviour of murres (i.e. attempted contacts, approaches) was exhibited on individual capelin, compared to 24 % on low density shoals and 7 % on high density schools. Similarly, more murres were observed turning, a proxy of area-restricted search behaviour, when solitary and low density capelin shoals persisted for longer durations relative to when schools persisted for longer. When murres made contact with capelin (n = 16), ~70 % (n = 11) were deemed successful (i.e. resulted in ingestion or ascent with fish in bill). Unsuccessful contacts resulted from fish escaping during beak manipulations to orient the fish head-first. Capelin were 7–11 times more likely to accelerate when murres displayed active versus passive (i.e. search, travel) foraging behaviours and 5–6 times more likely to accelerate in response to murre presence when in schools relative to low density shoals or solitary individuals. Overall, these results suggest that murres may increase their foraging success within areas of high prey density by preferentially searching for and targeting solitary fish that are less responsive to predators.

KEY WORDS: Seabird · Common murre · Capelin · Foraging behaviour · Schooling · Antipredator · Predator–prey

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INTRODUCTION

Animals foraging on patchily distributed prey may maximize prey consumption rates by foraging in areas of high prey density (Holling 1959). Seabirds are major predators of small, pelagic schooling fish around the world (Pikitch et al. 2012) and distributional patterns of seabirds at sea often reveal associations with areas of high prey density (e.g. Piatt 1990, Davoren et al. 2003a). Seabirds appear to minimize

the time and energy spent searching for high prey density areas by cueing to the foraging activities of other marine predators (local enhancement; Davoren et al. 2003b, Grunbaum & Veit 2003), and by returning to areas of predictably high prey density (Irons 1998, Davoren et al. 2003b, Sigler et al. 2012). Seabirds also may decrease search times by employing area-restricted search patterns (Weimerskirch et al. 2007, Paiva et al. 2010, Einoder et al. 2011), characterized by a decrease in travel speed and an increase

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in turning rate (Paiva et al. 2010). Area-restricted searches are often initiated immediately after capturing prey, encountering prey during straight line flight (Weimerskirch et al. 2007) and in areas of high prey density (Einoder et al. 2011). Once an area of high prey density has been located, nested area restricted searches may occur within the larger prey patch to hone in on prey (Hamer et al. 2009).

Within these areas of high prey density, many factors affect the rate at which seabirds capture and consume prey, including prey density (Enstipp et al. 2007), predator density (Götmark et al. 1986), and antipredator behaviour of prey (Wood & Hand 1985). For instance, double-crested cormorants increased consumption rates at higher prey densities in a laboratory setting (Enstipp et al. 2007) and exhibited a typical functional response (Holling 1959). Prey capture rates may also increase with density of conspecifics up to a threshold, above which intraspecific competition decreases consumption rate (Götmark et al. 1986, Shealer & Burger 1993). Schooling behaviour in fish is a particularly important antipredator strategy, due to the reliance of seabirds on schooling forage fish species. Although a school is a high density aggregation of prey, predator consumption rates can be low due to the difficulty of predators to focus on an individual target ('confusion effect'; Pulliam & Caraco 1984) and heightened predator detection and escape responses of schools (Lima & Dill 1990). Previous exposure to predation may cause changes in antipredator behaviour by either increasing the effectiveness of the behaviour (e.g. Wood & Hand 1985) or decreasing the occurrence of the behaviour (e.g. Brown et al. 2006). In the latter case, the behaviour may be too energetically costly to maintain when predation pressure is frequent (Brown et al. 2006). The energetic trade-off associated with antipredator behaviour may be more prevalent when fish are performing other important activities, such as foraging or spawning, where the benefits of these activities outweigh the costs of decreased vigilance (Lima & Dill 1990).

The common murre *Uria aalge* is a pursuit-diving seabird of the family Alcidae. Murres use their wings to propel themselves underwater to capture small schooling fish at depths of over 180 m (Piatt & Nettleship 1985). In the northwest Atlantic, capelin *Mallotus villosus* is the key forage fish species (Carscadden & Vilhjálmsson 2002) and is the primary prey of common murres (Davoren & Montevecchi 2003a, Davoren 2007). Capelin spawn at beach and deep water (<50 m) or 'demersal' sites in coastal Newfoundland during July and August (Davoren et al. 2006). Some

sites are used annually, providing a predictable and highly abundant food source for many predator species (Penton & Davoren 2012), including chick-rearing murres (Davoren 2007). Dive profiles of murres obtained using time-depth recorders in coastal Newfoundland (Hedd et al. 2009) and elsewhere (Elliott et al. 2008) illustrate that murres typically follow a U-shaped dive profile, diving to a particular depth and remaining at that depth throughout the dive before returning to the surface. The duration of the bottom phase of the dive is thought to represent the time available for searching for and capturing prey and the constant depth during this phase corresponds to depths where prey aggregations are found (Hedd et al. 2009). While these dive profiles have been well studied, little is known about how murres search for and capture prey items during this phase of foraging dives and how this is influenced by prey density and behaviour.

The goal of this study was to investigate the underwater behaviour of both common murres and capelin at persistent demersal spawning sites on the northeast Newfoundland coast. Using stationary underwater video cameras, we describe the foraging behaviour of common murres during the bottom-phase of foraging dives, previously described using data loggers in the region (Hedd et al. 2009). In the context of foraging theory, we hypothesized that murres exhibit more active foraging behaviours (e.g. attempt contact) in the presence of high density aggregations of capelin relative to low density aggregations. We also hypothesized that antipredator responses of capelin, specifically accelerations, are influenced by active, relative to passive (e.g. travel), murre foraging behaviours as well as capelin density. Finally, we hypothesized that murres exhibit area-restricted search patterns during the bottom phase of foraging dives and that these patterns intensify when high density capelin schools are observed nearby. Quantifying how predatory behaviour varies with prey density and the factors that affect antipredator responses is critical to increase our understanding of the functional response of pursuit-diving seabirds on forage fish and, thus, predator-prey population dynamics.

MATERIALS AND METHODS

Study area

The study area encompassed a concentration of 4 demersal spawning sites of capelin on the northeast coast of Newfoundland (Gull Island; Fig. 1) that are

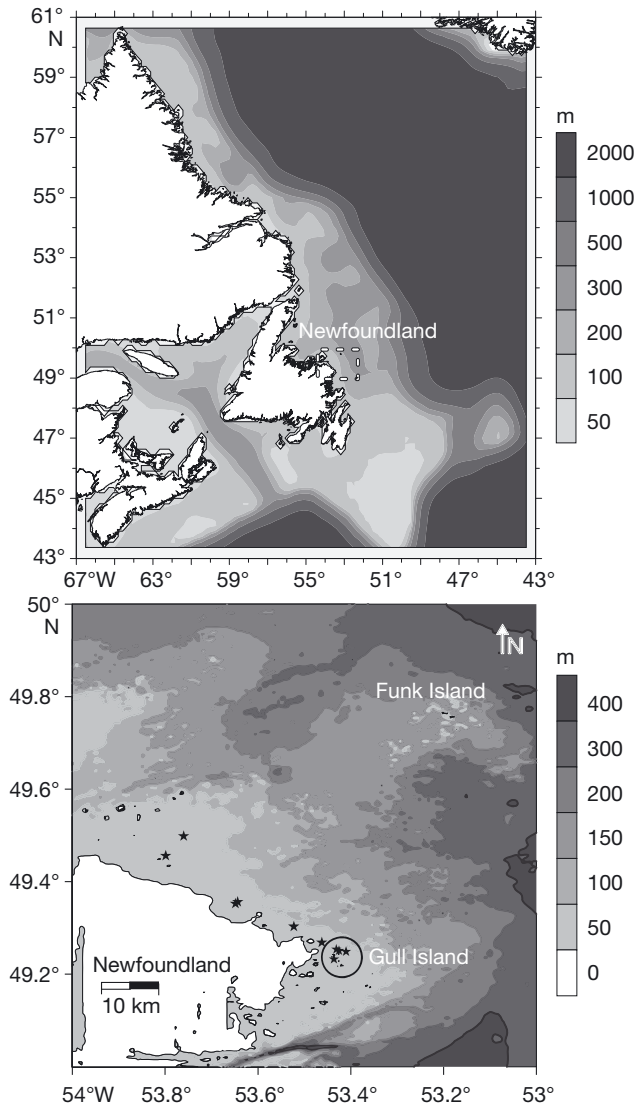


Fig. 1. (a) Location of the study area (square) on the northeast Newfoundland coast, and (b) the study area, indicating all known deep-water, or demersal, spawning sites of capelin (black stars), highlighting the cluster of persistent spawning sites examined in this study ('Gull Island', black circle), and the Funk Island Seabird Ecological Reserve. The gray scale indicates depth contours

used persistently on an annual basis (Penton & Davoren 2012). Capelin do not feed during spawning and, thus, fish are primarily engaged in spawning at these sites (Davoren et al. 2006). The Funk Island Ecological Seabird Reserve (49° 45' N, 53° 11' W; Fig. 1), located 60 km from the coast, harbours the largest common murre breeding colony in the north-west Atlantic (~400 000 breeding pairs; Cairns et al. 1989) and the 4 capelin spawning sites are located within foraging ranges of murre (60–80 km; Burke & Montevecchi 2009).

Video collection

Underwater behaviour and interactions between common murre and capelin were recorded using SeaLife DC1000 digital cameras (SeaLife Cameras, Moorestown, NJ) deployed at the 4 demersal spawning sites of capelin throughout the spawning season (July) from 2009 to 2012. Three cameras were fixed to a heavy metal frame, made of 3 crab pots tied together. A rope and surface float were attached to the frame for easy deployment and retrieval. The metal frame remained stationary on the seabed, immobilizing cameras ~50 cm off the seabed. Each camera faced a different direction to approximate a 360 degree view around the crab pot. The field of view, or observational area of a single camera, was up to a maximum distance of 8 m from the camera, but varied from 5–8 m depending on conditions. Three arrays of 3 cameras each were lowered to the seabed (15–33 m) simultaneously at different sites from 13 m commercial fishing vessels ('Lady Easton II', 'Lady Easton') when capelin were observed on the vessel's echosounder. Each array deployment was given a unique set number. The date, time of day, location (latitude and longitude), and which cameras were deployed on each crab pot were recorded for each set. After deployment, the ship departed the site and cameras were left to record for ~3 h. Upon retrieval, video files were downloaded onto a laptop for later analysis. Camera arrays were retrieved and deployed as often as possible (1–3 times d^{-1}) while capelin were present at spawning sites, typically over 4–8 d per year. Although common murre are known to forage at night within the study area (Hedd et al. 2009), videos were only collected during daylight due to the lack of light available at depth during dark and the likelihood that artificial lighting would alter behaviour.

Video analysis

All videos were initially viewed to bookmark events at 4 times normal speed using Windows Media Player due to the large quantity of video (108–219 h yr^{-1}). An event was classified as any video segment when an organism was observed (capelin, murre, or other). For each event, the year, date, set number, camera number, start and finish time of the event, and a brief description were recorded in a spreadsheet. After initial bookmarking, events containing murre and/or capelin were reviewed to define behaviours and build a list of observed murre

and capelin behavioural categories. Events were divided into 2 types: where one or more murre and one or more capelin were present in the field of view ('murre and capelin') and where only murre were present ('murre only'). Within each event type, the focal animal technique (Martin & Bateson 1993) was used to document the occurrence of defined behaviours.

The densely packed nature of capelin aggregations precluded accurately quantifying the number of fish present from the videos. Therefore, capelin density was categorized by the percent of the total field of view covered by capelin, as well as the behaviour of fish in the aggregation. Density classes were defined as 'individual' when only a single capelin was present in the field of view; 'shoal-low' when >1 capelin were present, covering <50% of the field of view and not all fish were oriented in the same direction; 'shoal-high' when >1 capelin were present, covering >50% of the field of view and not all fish were oriented in the same direction; and 'school' when >1 capelin were present covering >50% of the field of view and all fish were oriented in the same direction and exhibiting coordinated movement. Only 2 events were observed in the shoal-high category, so shoal-high and school were combined for analyses. Capelin density was not categorized unless fish were >0.5 m from the camera because more than one fish would blackout the field of view, precluding observations of murre or fish behaviour.

Within murre and capelin events, murre behaviour was organized into 4 general categories: 'approach', 'attempted contact', 'target search', and 'travel' (Table 1). Murre behaviours were further categorized as 'active' by combining attempted contact and approach as well as 'passive' by combining target search and travel to compare foraging intensity (active versus passive) with capelin density. Events where murre exhibited attempted contact or 'handling' (Table 1) behaviours were used to determine the proportion of attempted contacts that were successful. Contact was deemed successful if the

murre swallowed the capelin ('ingestion'), ascended to the surface carrying a capelin in its bill, or if the murre left the field of view handling a capelin. In addition to successful contact, we also determined the proportion of events where a capelin escaped from a murre and how many attempted contacts resulted in a murre chasing a capelin after missing the capelin or having it escape. The sequence of behaviour exhibited during handling was also determined, by describing the behavioural patterns observed between 'contact' and 'ingestion'.

For all murre and capelin events, we determined whether capelin exhibited an 'acceleration' anti-predator response to murre, defined as an increase in tail beat frequency of one or more capelin resulting in locomotion of stationary fish or altered locomotion of swimming fish in the presence of a murre. Regardless of whether capelin accelerated, the murre orientation with respect to the capelin was recorded as 'behind', 'side', 'head-on', or 'above'. If capelin accelerated just prior (<3 s) to a murre entering the frame, this was considered a response to the murre even though the murre was not present in the frame at the initiation of acceleration.

Within murre-only events, murre were deemed to show area-restricted search patterns when observed performing one or more turn behaviours (Table 2). 'Pause', 'look', and 'wobble' (Table 2) were considered indicators of decreased travel speeds, also characteristic of area-restricted search patterns (Weimerskirch et al. 2007, Paiva et al. 2010).

Data analysis

Murre and capelin events were analyzed to test the hypothesis that murre behaviour was influenced by capelin density using a chi-square test. In addition, chi-square tests were performed for each of the 4 general categories of murre behaviour to determine whether the frequency of each behaviour differed among capelin density categories. A sequential Bon-

Table 1. Behavioural categories of common murre and definitions from 'murre and capelin' events

Behaviour	Definition
Approach	Movement toward a capelin at a constant speed then turning away from capelin
Attempted contact	Acceleration toward capelin, stopping once contact was made or capelin moved away
Handling	Sequence of capture, release, and re-capture prior to ingestion or ascent toward the ocean surface
Target search	Swimming near the seabed, exhibiting head movements, horizontal direction changes, and/or pauses with capelin present
Travel	Swimming with head directed forward, exhibiting no change in horizontal or vertical direction

Table 2. Behavioural categories of common murre and definitions from 'murre only' events

Behaviour category	Behaviour	Definition
Moving	Wobble	Swimming with <45° changes in bird orientation with no changes to horizontal direction vector of movement
Turn	Turn	45–135° change in horizontal direction initiated with a wing flap
	Spin	180° change in horizontal direction with no horizontal displacement
	Loop	135–180° change in horizontal direction resulting in a horizontal displacement
	Drift	A change in the horizontal direction the bird is facing, initiated during a period without wing flapping
	Post-pause	A post-pause (see 'pause') change in the horizontal direction the bird is facing, accompanied by bird acceleration
Pause	Pause	Cessation of all vertical and horizontal motion
Look	Look	Deviation of head direction from straight forward

ferroni correction was applied to adjust significance in these 4 tests to prevent inflation of the experimental error rate above 0.05. To test the hypothesis that antipredator acceleration responses of capelin were influenced by both murre behaviour and capelin density, murre and capelin events were classified as either a presence or absence of acceleration. A logistic regression was performed with capelin acceleration (presence or absence) as the response variable and murre behaviour, capelin density, and murre direction as predictor variables. Odds-ratio tests were performed to determine the likelihood of acceleration occurring within the categories of each predictor variable. Events where a murre was greater than 6 murre lengths (~2 m based on average length of a common murre) away from a capelin were excluded from analysis, as no acceleration responses were observed beyond this distance. Events where a murre entered the frame with a capelin in its bill ('handling') also were excluded as there was no reliable way of determining the presence/absence of acceleration.

Murre-only events were analyzed to test whether murre employ area-restricted search patterns underwater and, if so, whether these patterns intensify with increased duration of high density capelin. The number of murre showing area-restricted search patterns was determined for each camera array set by dividing the number of murre exhibiting area-restricted search by the number of working cameras per set, as some cameras had no usable video or files were corrupted. The number of murre not showing area-restricted search behaviour was similarly quantified and categorized as 'travel'. The proportion of time capelin in each density category, and all categories combined ('total'), was determined by dividing the duration of each capelin density category by the total working camera duration (per set) and were

subsequently categorized into 'zero', 'low', and 'high' duration categories. Although the 3 cameras per array were positioned to cover 360 degrees to observe all capelin in the vicinity of the array, capelin may have been present just out of the field of view (i.e. >5–8 m). For all density and total categories, arrays were classified as 'zero' if no capelin were observed. For individual and shoal-low density categories, 'low' duration was categorized as arrays with <0.1% (mean \pm SE = 0.04 \pm 0.01 and 0.03 \pm 0.01%, respectively) and 'high' as \geq 0.1% of capelin (2.65 \pm 0.78 and 3.21 \pm 1.62%, respectively). For the school category and total capelin, arrays were classified as 'low' if there was <5% (0.78 \pm 0.28 and 0.50 \pm 0.17%, respectively) and 'high' if there was \geq 5% capelin duration (30.69 \pm 5.94 and 33.09 \pm 6.17%, respectively). The categories were defined differently due to the much higher observed duration of schooling capelin and to ensure a similar number of camera array sets within each category. Only array sets where at least one common murre was observed were considered for analysis. Events where the entire murre was not visible (e.g. just a wing) were not included in the analysis as behavioural patterns could not be observed. We compared the mean number of murre exhibiting area-restricted search behaviour per camera among capelin duration categories within each capelin density category and total capelin using Kruskal-Wallis tests with post hoc Dwass-Steel tests, as these data could not be normalized.

RESULTS

A total of 80 camera array sets were deployed from 2009–2012 (23 in 2009, 18 in 2010, 11 in 2011, and 28 in 2012) resulting in ~720 h of video over the 4 yr. Out

of these videos, 178 murre and capelin events were observed, of which 99 were included in the analyses. A total of 1084 murre-only events were observed with 952 used in the analyses. Event durations ranged from 1–20 s for murre and capelin events and 1–14 s for murre-only events. Capelin were observed in all density categories, with 91.3% of all capelin observed on video (~87 h) as schools, 3.3% as shoal-low, and 5.4% as individuals. Out of all murre observed, the majority were solitary (76.8%). Only 23.2% of murre were observed with at least one other murre and group sizes ranged from 2–9 murre. When multiple murre were observed in the same field of view, however, cooperative foraging behaviour (e.g. herding fish schools) was not observed. All murre behaviours were observed in association with most capelin density categories; however, murre did not approach capelin schools.

Attempted contact and handling

Murre attempted contact with capelin in 20 of the 99 murre and capelin events and an additional 12 handling events were observed. When combined, however, only 27 events could be used for analysis due to corruption of a few video files. Of the 27 events, 16 (8 attempted contact, 8 handling) resulted in capture (59.3%), defined as contact of murre beak with capelin. Of these, 11 (68.9%) were considered successful, as indicated by ingestion (n = 5, attempted contact events) or murre exiting the frame while handling the capelin (n = 6, handling events). Five successful events were from attempted contacts, 3 of which were associated with individual capelin and the other 2 with shoal-low; none were associated with schooling capelin. The 3 unsuccessful attempted contact events were due to the capelin escaping from the bill after contact (n = 2) and the murre swimming away from the capelin after making contact (n = 1). Of the 8 handling events, 2 were deemed unsuccessful due to the murre dropping the capelin and not going back to retrieve it. Overall, ingestion of capelin was observed 5 times (3 from attempted

contact and 2 from handling), always with the capelin oriented head first.

Of the 16 capture events, murre exhibited a typical handling sequence after contact, whereby they released and re-captured capelin at a different angle a number of times, moving the fish so it was oriented head-first in the bill (Fig. 2). The entire handling sequence was observed in 5 events, with 1 murre releasing and re-capturing a capelin 6 times before ascending to the surface with the capelin in its bill. In all but 3 capture events (n = 13), murre also manipulated capelin in the bill with rapid opening and closing of the mandibles ($>2 \text{ times s}^{-1}$) until it was oriented head-first. This was observed in addition to the release and re-capture sequence (n = 5) or in the absence of the release and re-capture sequence (n = 8).

In the attempted contact events that did not result in capture (n = 11), murre continued to chase the

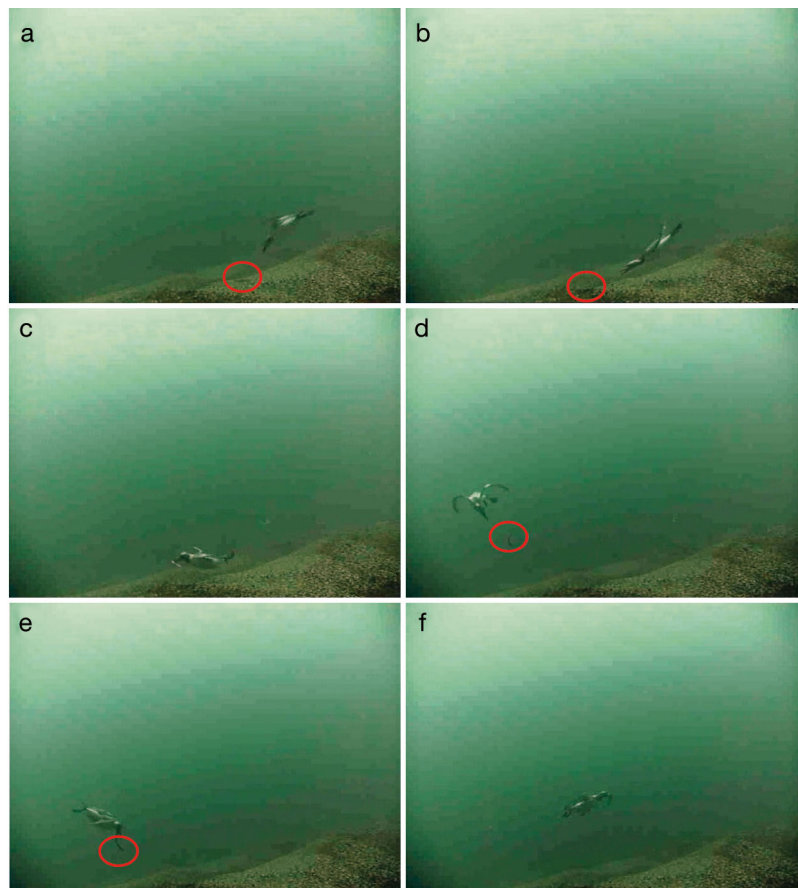


Fig. 2. Example video sequence showing defined common murre behaviours: (a,b) attempted contact, (c) contact, (d) release, (e) recapture, and (f) final position of capelin before ingestion. The red circle indicates the position of the capelin; in (c) and (f), the fish is in the murre's bill

capelin 5 times (45.5%), as revealed by an acceleration in the direction of a capelin after attempting contact. Murres also chased capelin post-contact after the capelin escaped ($n = 3$) and after release ($n = 1$), presumably to reorient the capelin head-first. Only one chase was observed to result in successful contact; however, chases typically continued out of the field of view so the percentage of successful chases could be higher. In the 6 attempted contact events that did not result in capture or chase, murres simply resumed search behaviour. Murres primarily did not attempt contact on dead post-spawning capelin, although this was observed in 5 events. Each involved a brief handling sequence but none resulted in ingestion or ascent carrying the capelin.

Murre behaviour and capelin density

Murre behaviour was not independent of capelin density (G -test: likelihood ratio = 25.936, $p < 0.001$). The frequency of attempted contact did not differ significantly across capelin density categories (chi-square test: $\chi^2_2 = 2.139$, $p = 0.343$; Fig. 3a). In contrast, the frequency of approach and target search differed significantly among capelin densities ($\chi^2_2 = 13.126$, $p = 0.001$; and $\chi^2_2 = 8.915$, $p = 0.012$, respectively), with approach not observed associated with capelin schools and target search observed more often in association with capelin schools (Fig. 3b,c). Travel behaviour was not significantly affected by capelin density after applying a sequential Bonferroni correction ($\chi^2_2 = 6.547$, $p = 0.038$, $\alpha = 0.025$; Fig. 3d). Capelin density had a significant impact on the occurrence of 'active' (i.e. attempted contact, approach) and 'passive' (i.e. target search, travel) foraging ($\chi^2_2 = 17.448$, $p < 0.001$), with more active behaviour on individual capelin (69.4%) relative to shoal-low (23.8%) and schooling capelin (7.1%; Fig. 3).

Acceleration of capelin

An acceleration response of capelin was observed in 48 out of the 99 events and occurred within all murre behaviour, murre direction, and capelin density categories. The logistic regression model considering all 3 variables significantly influenced capelin acceleration ($\chi^2_8 = 33.975$, $p < 0.001$). Murre behaviour and capelin density both had significant effects on acceleration ($\chi^2_3 = 15.169$, $p = 0.004$; and $\chi^2_2 = 7.137$, $p = 0.028$, respectively), whereas murre direc-

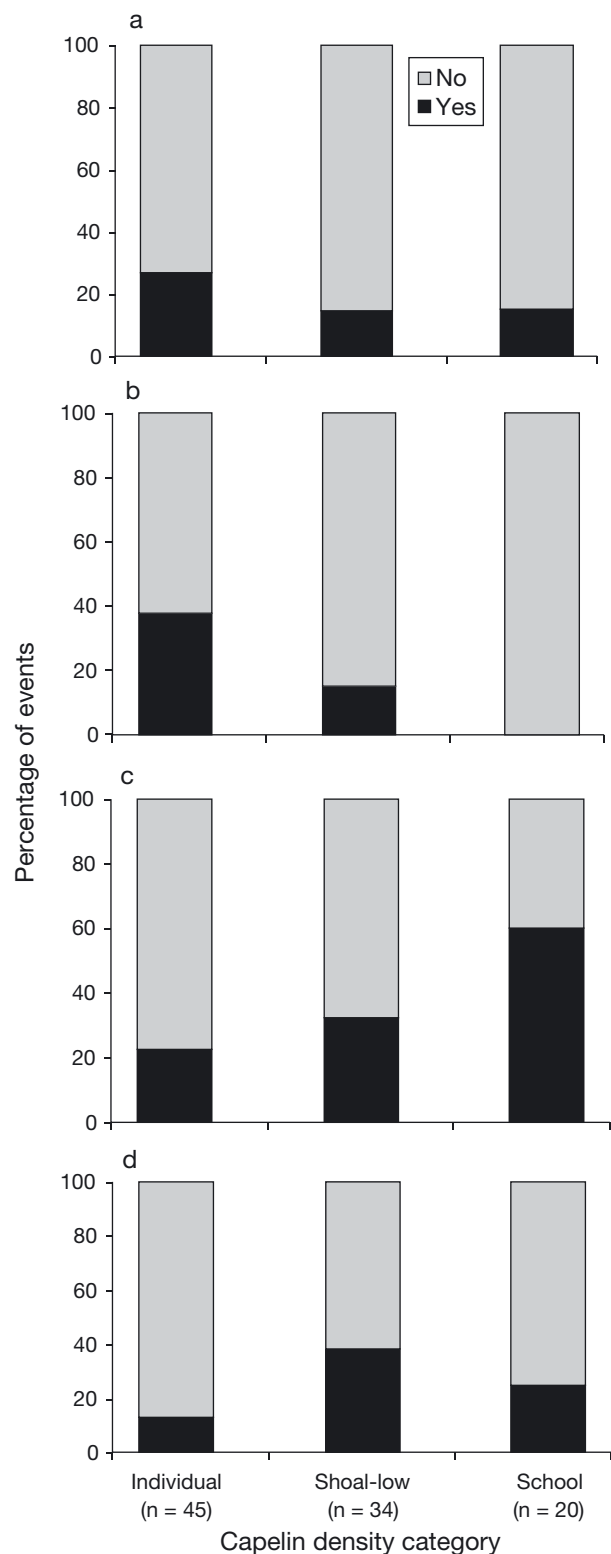


Fig. 3. Percentage of murre and capelin events ($n = 99$) in which each foraging behaviour of common murres occurred (yes) or not (no) within each capelin density category for (a) attempted contact, (b) approach, (c) target search, and (d) travel

tion did not ($\chi^2_3 = 6.445$, $p = 0.092$). Based on the relative odds ratios from the logistic regression, attempted contact was 11.39 (95% CI 2.66, 62.75) and 10.16 (95% CI 2.05, 64.06) times more likely than target search and travel, respectively, to predict acceleration (Fig. 4a). Similarly, approach was 7.61 (95% CI 1.85, 35.91) and 6.79 (95% CI 1.43, 36.80) times more likely to predict acceleration than target search and travel, respectively (Fig. 4a). There was no significant difference between target search and travel in predicting acceleration (1.12 times; 95% CI 0.29, 4.31; Fig. 4a). Within capelin density, there was no significant difference between individual

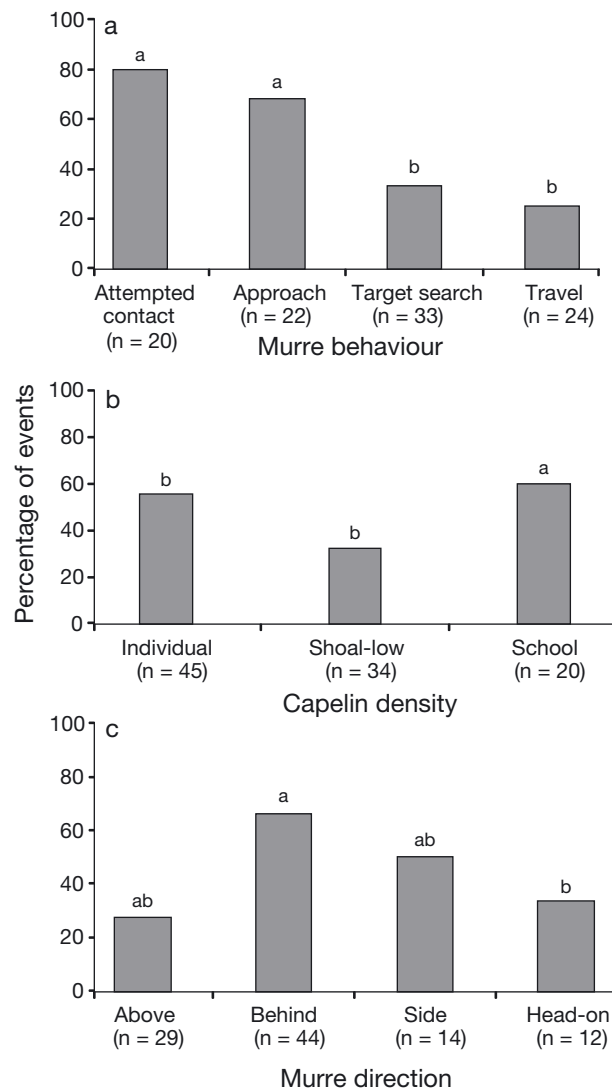


Fig. 4. Percentage of murre and capelin events ($n = 99$) in which capelin acceleration occurred within each of the categories of (a) common murre foraging behaviour, (b) capelin density, and (c) murre attack directions. Categories sharing the same letter do not differ significantly in the likelihood of acceleration occurring (odds-ratio test)

and shoal-low densities in predicting acceleration (1.17 times; 95% CI 0.34, 3.79; Fig. 4b). Alternatively, capelin schools were 5.23 times more likely to accelerate than individual capelin (95% CI 1.26, 25.19) and 6.09 times more likely than shoal-low (95% CI 1.51, 28.21; Fig. 4b). While murre attack direction with respect to the orientation of the capelin was not significant ($\chi^2_3 = 6.445$, $p = 0.092$), if a murre was coming from behind, capelin acceleration was 4.87 times more likely than if it was a head-on encounter (95% CI 1.10, 24.65; Fig. 4c). When acceleration was observed by schooling capelin, all visible capelin in the school were observed accelerating whereas in the shoal-low category, 7 of 10 accelerations were of only a single capelin.

Murre search behaviour

A total of 952 murre-only events were analyzed to determine whether area-restricted search behaviour of murre was observed more frequently when a high duration of capelin were present in the area in high densities. Area-restricted search behaviour was observed in 429 events with a mean observation duration of ~3 s. The remaining 523 events were classified as 'travel' events with a mean duration of ~2 s. One camera array set in 2012 had an unusually high number of murre-only events ($n = 257$) in only one working camera. The Kruskal-Wallis analyses and post hoc Dwass-Steel tests were run on the data both including and excluding this set but no differences were found and, thus, this set was included in the analyses.

The mean number of murre per camera exhibiting area-restricted search behaviour was influenced by the duration that individual capelin were observed (Kruskal-Wallis test: $H = 14.157$, $p < 0.001$) as well as shoal-low ($H = 8.134$, $p = 0.017$) and all density categories combined ('total'; $H = 9.523$, $p = 0.009$; Fig. 5). Despite the positive correlation between the duration of individual capelin and capelin schools (Spearman's $r_s = 0.581$, $p < 0.001$), the duration that schooling capelin were observed did not significantly influence the number of area-restricted searching murre ($H = 4.494$, $p = 0.106$; Fig. 5c). For individual capelin, zero and high durations and low and high durations differed ($p = 0.001$ and $p = 0.042$, respectively), with more searching murre present when high durations of individual capelin were observed (Fig. 5a). For shoal-low, zero and high duration categories differed ($p = 0.021$), with again more searching murre present when high durations of low-density shoals were observed (Fig. 5b). For all capelin density categories

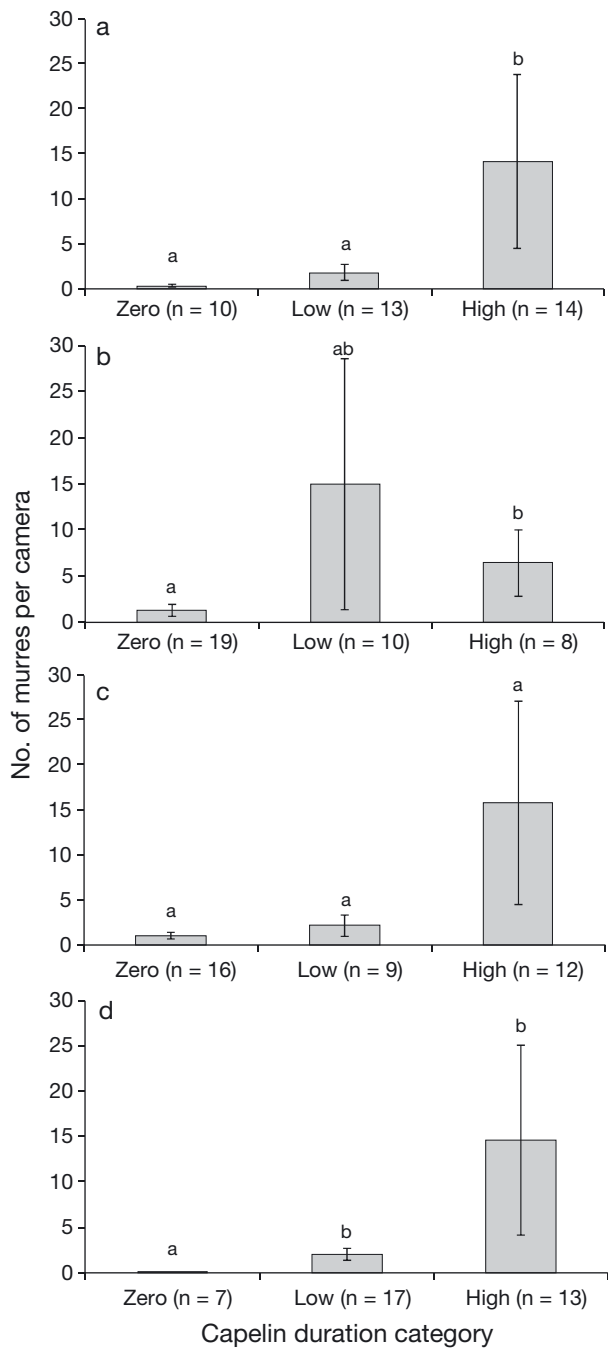


Fig. 5. Mean \pm SE number of common murre exhibiting area-restricted search behaviour per camera in each capelin duration category for (a) individual, (b) shoal-low, (c) school, and (d) total capelin density categories. Categories sharing the same letter are not significantly different (Dwass-Steel test)

combined, zero and high and zero and low categories differed significantly ($p = 0.009$ and $p = 0.037$, respectively), with more searching murre present when capelin were present (Fig. 5d).

DISCUSSION

When capelin were present, they were observed primarily in schools (91%); however, murre primarily approached and attempted to capture solitary capelin (77% and 60%, respectively), rather than capelin in low density shoals or high density schools. Of all attempted contact and handling events, ~60% resulted in murre contacting a capelin and ~70% of contacts were successful (i.e. capelin was ingested or murre ascended to surface with fish in bill). Successful contacts resulted from pursuing capelin that were solitary or in low density shoals, but not schools. Unsuccessful contacts resulted from fish escaping during beak manipulations to orient the fish head-first in the bill. Individual capelin and low density shoals were less likely to show an acceleration response than schools and capelin were also more likely to accelerate in response to active relative to passive foraging behaviours of murre. Similarly, there was a higher number of murre exhibiting area-restricted search behaviour when high durations of individual capelin, low density shoals, and total capelin were present, but this was not the case for schooling capelin. Overall, these findings suggest that murre may preferentially search for and target less responsive solitary capelin and low density shoals and that capelin may associate certain predator behaviour with increased predation risk.

Murre showed more active foraging behaviours and successful pursuits with individual capelin relative to higher density aggregations, including low density shoals and schools. This seems to counter previously observed functional responses of diving birds to fish density (e.g. common mergansers *Mergus merganser*, Wood & Hand 1985; double-crested cormorants *Phalacrocorax auritus*, Enstipp et al. 2007) and aggregative responses of murre to high density capelin schools (Piatt 1990). On a fine-scale during a foraging dive, however, murre may selectively target solitary capelin to counteract the confusion effect, or the difficulty in choosing an individual prey to pursue within an aggregation (Pulliam & Caraco 1984). In support, cormorants tend to target individuals on the periphery of schools or solitary individuals and have higher capture success and lower pursuit times when targeting solitary fish relative to fish in schools, despite exhibiting a typical functional response (Enstipp et al. 2007). Therefore, although murre may target these persistent areas of high capelin density within foraging ranges from the breeding colony in our study area, presumably to minimize search times and increase encounter rates

with prey (e.g. Davoren et al. 2003b, Davoren 2007), they appear to target individual capelin on a small spatial scale during the bottom phase of a dive possibly to decrease handling times.

Seabirds often forage in aggregations (e.g. Camphuysen & Webb 1999), possibly to fragment prey schools to counteract the confusion effect (Götmark et al. 1986, Shealer & Burger 1993) or to cooperatively drive prey schools to the surface (e.g. Grover & Olla 1983). Capelin aggregate near the seabed to spawn within our study area (Davoren et al. 2006), making them more difficult to herd to the surface than in other regions. Murres were observed primarily as solitary individuals underwater and when seen together, murres were not observed cooperatively herding fish to the surface or breaking up fish aggregations. Similarly, birds have been observed foraging in close vicinity to conspecifics in other underwater observational studies, but coordinated group foraging was not observed when targeting solitary, dispersed fish (e.g. penguins, Ponganis et al. 2000; shags, Watanuki et al. 2008). This suggests that group foraging is not beneficial under these circumstances. In addition, murres were observed to capture, release, and re-capture a capelin many times to achieve head-first orientation in the bill, especially when the fish was caught from behind as was primarily observed. This handling sequence may increase the risk of the capelin escaping, as was observed in 3 cases, and also may increase intraspecific competitive interactions, which was previously suggested by scale-dependent aggregative behaviour of murres in the study area (Davoren et al. 2003a).

Murres appeared to assess the quality of capelin and its suitability for consumption or chick provisioning immediately prior to or during capture and handling. This is evidenced by murres abandoning capelin post-capture, especially dead capelin, as well as approaching within contact range of capelin but then turning away. Interestingly, murres captured dead capelin on 5 occasions but none were ingested. Murres are single-prey loaders, and breeders observed foraging in this study would have a 120 km return trip to transport a single fish to their chick at Funk Island multiple times per day (Davoren & Montevecchi 2003b). Likely due to the high cost of flight in murres relative to other birds (Elliott et al. 2013), murres at Funk Island provision their chicks primarily with energy-dense gravid female capelin (Davoren & Montevecchi 2003a, Burke & Montevecchi 2009) rather than lower quality males (Montevecchi & Piatt 1984). Male capelin also experience high physical body damage and often death because they remain at spawning sites to mate with multiple fe-

males (Burton & Flynn 1998). Although murres consume both male and female capelin in the study area (Davoren 2007), they may select higher quality prey for chicks to maximize growth. Unfortunately, the quality of video used here precluded the determination of capelin sex, and higher resolution cameras will be needed to shed light on this in the future.

Not surprisingly, capelin were more likely to accelerate away from murres when aggregated at higher densities. This heightened response of schooling capelin is consistent with the 'many eyes' hypothesis, whereby there is a higher probability of predator detection as the number of vigilant individuals increases (Lima & Dill 1990). This may also explain why murres displayed more active foraging behaviours associated with solitary capelin, as individuals showed less of an acceleration response and presumably required less effort to capture. Interestingly, capelin were more likely to accelerate away from murres exhibiting active relative to passive foraging behaviour, suggesting they may assess predation risk and respond in a way that minimizes this risk while maximizing mating opportunities (Lima & Dill 1990). In support, other fish species respond more intensely to the most immediate threats of predation (e.g. convict cichlids *Archocentrus nigrofasciatus*, Brown et al. 2006), and become more effective in evading capture as experience with the predator increases (e.g. coho salmon *Oncorhynchus kisutch*, Wood & Hand 1985). Antipredator responses of fish also may decrease as predation risk shifts from acute to chronic (risk allocation hypothesis; Lima & Bednekoff 1999). Capelin experience consistently high rates of predation by multiple fish, bird, and mammal predator species near coastal spawning grounds (e.g. Davoren 2007, 2013), as it is the dominant forage fish species in the north-west Atlantic (Carscadden & Vilhjálmsson 2002). These chronically high levels of predation experienced by capelin suggest that individuals could learn to assess the risks posed by murres exhibiting different types of behaviour and may explain a lack of response to the simple presence of murres.

Murres appeared to exhibit area-restricted search patterns underwater during foraging dives, evidenced by increased turning frequency and decreased travel speeds. With the short durations murres were observed (2–3 s) relative to dive durations in the study area (~62 s; Hedd et al. 2009), it is likely that more murres may be performing area-restricted searches than we report here. Area-restricted searching has been documented for seabirds searching for prey patches during flight over a few to tens of kilometers (Weimerskirch et al. 2007, Hamer et al. 2009,

Paiva et al. 2010, Einoder et al. 2011), which may intensify within smaller areas (~1.5 km) nested within larger regions to hone in on prey (Hamer et al. 2009). Due to high energetic costs of flight for murres (Elliott et al. 2013), aerial search over large scales is likely not energetically feasible. Instead, murres in the study area may use memory-based strategies to locate capelin (Davoren et al. 2003b) within these persistent spawning sites (Penton & Davoren 2012), but may increase the probability of prey encounter and capture underwater by employing nested area-restricted searches during foraging dives. In support, area-restricted search behaviour is typically initiated in areas of high prey density (Einoder et al. 2011) to maximize prey encounter rates (Weimerskirch et al. 2007, Hamer et al. 2009). Similarly, murres in this study increased the frequency of area-restricted search patterns when capelin were present nearby, indicated by higher duration of capelin observed on cameras. This pattern was observed across all capelin density categories, with the exception of schooling capelin, suggesting that murres do not actively search for schooling capelin, either because capelin in schools are not being targeted for capture or because schools are more conspicuous and do not require intensive search to locate.

In conclusion, these direct observations shed light on the predator–prey interactions of pursuit-diving seabirds and fish during foraging dives. Although few prey capture events were observed, precluding quantifying the functional response, foraging behaviour was shown to vary with prey density. Likely due to the increased antipredator response (i.e. acceleration) by schooling capelin to murres, murres appeared to preferentially target solitary capelin during foraging dives, possibly requiring area-restricted search patterns. This suggests that shifts in aggregating behaviour of capelin as well as overall density may be important in mediating foraging success of seabirds and other marine predators on key forage fish species.

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