THE AGGREGATIVE RESPONSE OF COMMON MURRES AND ATLANTIC PUFFINS TO SCHOOLS OF CAPELIN

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Abstract. I studied the aggregative responses of Common Murres and Atlantic Puffins to schools of capelin during three summers (1982–1984) at Witless Bay, Newfoundland, by conducting hydroacoustic surveys for capelin in synchrony with seabird censuses. Murres and puffins foraged offshore prior to the arrival inshore of spawning schools of capelin. Both species were abundant during peak periods of capelin abundance from late June to late July, but only puffins continued to forage inshore after capelin schools dispersed in August. On individual surveys, murre and puffin flocks were significantly correlated with capelin schools at fine and coarse spatial scales. Aggregation intensity and spatial correlations peaked at measurement intervals of 2–6 km. At that scale, murres and puffins exhibited sigmoidal (Type III) aggregative responses to capelin schools. Inflection points (thresholds) in sigmoidal aggregative response curves occurred at higher densities of capelin for murres than for puffins and foraging thresholds for both species varied daily with overall capelin abundance in Witless Bay. Murres probably foraged on denser schools of capelin than puffins because of their larger body size and associated higher food demands. The implications of differing foraging thresholds for population ecology of alcids are discussed.

Key Words: Aggregative response; capelin; murre; puffin; hydroacoustics; threshold; foraging; population ecology.

A predator's rate of food intake is limited at low prey densities by how frequently it encounters prey, and at high prey densities by how quickly prey can be captured, eaten, and digested. These constraints determine the form of various biological responses to food dispersion. In particular, the rates at which predators track prey (aggregative response), consume prey (functional response), and reproduce (numerical response), are all non-linear functions of prey density (Holling 1959, 1965; Readshaw 1973; Hassell and May 1974; Murdoch and Oaten 1975).

Predators range in behavior from those that search widely and aggregate at dense concentrations of prey to those that "sit and wait" to forage opportunistically on dispersed prey. Both foraging behaviors are evident in many feeding guilds (e.g., Davidson 1977b, Pianka 1986). Foraging responses are also influenced by such factors as hunger state, learning capacity, and prior experience of the predator, and presence of alternate prey, but, in general, predators exhibit either hyperbolic (Type II) or sigmoidal (Type III) responses to increasing prey density (Holling 1965, 1966; Murdoch and Oaten 1975). Linear (Type I) responses are rare (Hassell et al. 1977, Eveleigh and Chant 1981).

Coexisting predators often forage on different densities of shared prey (Holling 1959, Davidson 1977a). Current theory suggests this would promote the coexistence of competitors for a fluctuating food supply (Abrams 1983). Food is probably the most important resource regulating seabird populations (Birkhead and Furness 1985), and diet overlap between species is often high at seabird colonies (Belopol'skii 1957, Pearson 1968, Diamond 1984). How coexisting Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) respond to variations in the density of capelin (*Mallotus villosus*), their main prey in Newfoundland, is the subject of this paper.

Studies of seabird aggregation behavior have revealed much about how marine predators exploit patchily distributed prey (Brown 1980, Obst 1985, Schneider and Piatt 1986), the oceanographic mechanisms for concentrating prey and predators (Briggs et al. 1984, Brown and Gaskin 1988), and the scales at which these processes occur (Hunt and Schneider 1987). However, we still do not know the minimum densities of prey required for successful foraging (Brown and Nettleship 1984), how and to what degree prey density influences choice of foraging habitats (Brown and Gaskin 1988), how fluctuations in prey abundance affect diet composition (Montevecchi et al. 1988), or why some seabirds exploit prey patches ignored by others (Ashmole 1963). With regard to population biology, Cairns (1987) hypothesized that adult survival, chick growth rates, and breeding success of seabirds are non-linear functions of prey density, but like foraging responses, the forms of these relationships have not been established for any seabird species.

I was able to address some of the foregoing questions by examining the aggregative responses of murres and puffins to schools of capelin. I censused foraging flocks of seabirds around a large breeding colony in Newfoundland while simultaneously conducting hydroacoustic surveys for capelin. Those data allowed me to assess temporal and spatial patterns of association between species, and to characterize the foraging behaviors of murres and puffins. I also consider factors that may influence aggregation behavior
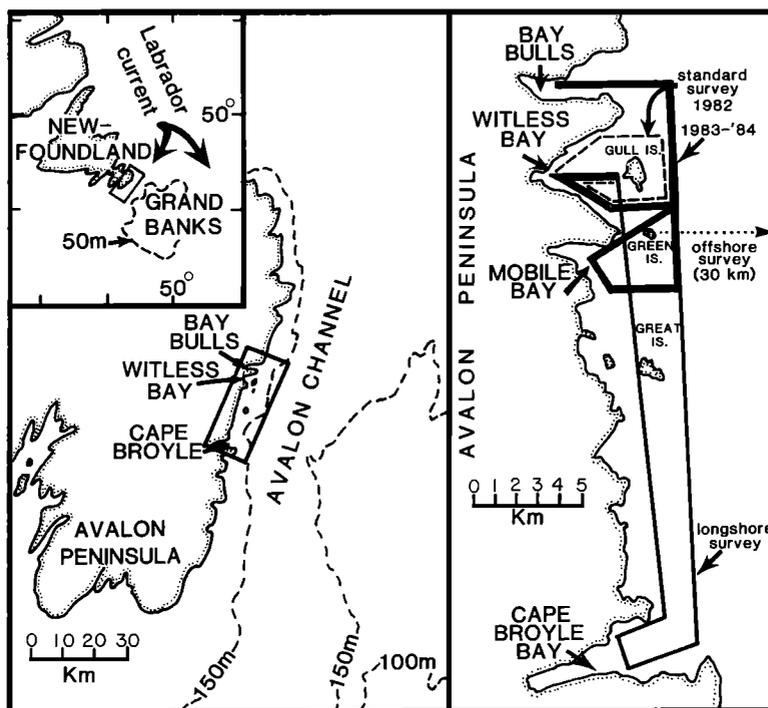
FIGURE 1. Study area in southeastern Newfoundland with survey routes in 1982–1984 indicated.

and its measurement, and discuss some implications of my results for population ecology of seabirds.

STUDY AREA AND METHODS

Data were collected at the Witless Bay Seabird Sanctuary (47°15'N, 52°46'W), which comprises three islands off the eastern edge of the Avalon Peninsula of Newfoundland (Fig. 1). Most seabird and capelin surveys were conducted around Gull and Green islands, which support breeding populations of about 75,000 pairs of murres (>99% Common Murres) and 74,000 pairs of Atlantic Puffins (Brown et al. 1975). Great Island is 10 km southwest of Gull Island and supports about 2800 pairs of murres and 148,000 pairs of puffins.

SEABIRD AND CAPELIN SURVEYS

Surveys were conducted at Witless Bay from May to August in 1982–1984 to record the abundance and local distribution of schooling fish (almost exclusively capelin, Piatt 1987, Methven and Piatt 1989), murres, and puffins. In 1982, surveys were conducted in a 9 m open boat with a side-mounted 38 kHz Skipper 609 echosounder. In 1983–1984, surveys were conducted in a 12 m longliner equipped with a Kelvin-Hughes echosounder (Mark 2, Model 5, 42 kHz), autopilot, and radar. Before starting each survey, the date, time, sea state, cloud cover, visibility, and approximate wind speed and direction, were recorded. Two or more ob-

servers were present on most surveys and exchanged duties at 30 min intervals. Surveys were begun by marking the sounder echogram and starting a stopwatch to synchronize (hr : min : sec) bird and capelin observations. Upon changing course, the echogram was marked and the time recorded to allow synchronization of each survey segment. Time of encounter, number of individuals, and behavior (swimming or flying) were noted on a tape recorder for all seabirds observed within a 50 m radius in front and on either side of the boat. Only birds swimming on the water were used for analyses of bird-capelin associations.

Using these general methods, four different types of surveys were conducted (Fig. 1). Standard surveys (N = 61) followed a fixed route around Gull and Green islands. This route was chosen to survey a variety of habitats: offshore (70–120 m), bays (30–70 m), inshore (5–30 m), submarine ledges, around headlands, and near islands. In 1982, the standard survey consisted of a 12 km circuit of Witless Bay and Gull Island, and in 1983–1984, surveys were extended (ca. 30 km) to include Bay Bulls, Green Island, and Mobile Bay. Standard survey data were used for analyses of seasonal variations in bird and capelin abundance at Witless Bay, and for analyses of aggregative responses.

Other sampling schemes were used to examine diurnal patterns of abundance, and the longshore and offshore distribution of birds and capelin (Fig. 1, Piatt 1987). These data are used here only for examining aggregative responses. On two occasions, standard surveys were conducted repeatedly (N = 4) over a 24-hr
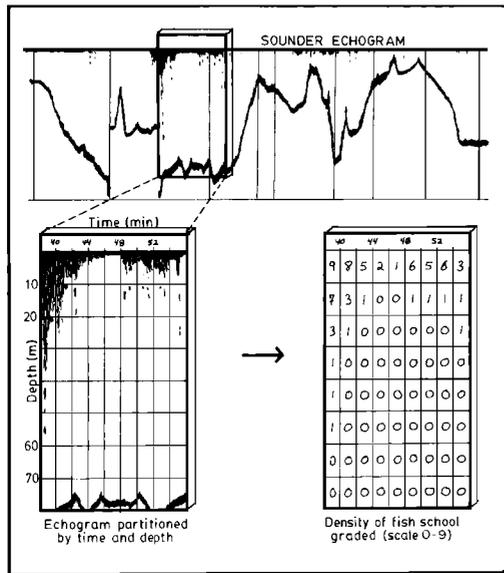
FIGURE 2. Illustration of how acoustic echograms were graded to estimate capelin density (drawn from actual survey echogram).

period to detect diel variations in the abundance of birds and capelin. Offshore surveys (N = 4) originated on the east side of Green Island and ran east-southeast to a point 30 km offshore. Three coastal (longshore) surveys were conducted in 1984 from Witless Bay to Cape Broyle, about 25 km south.

ESTIMATING RELATIVE ABUNDANCE AND DENSITY OF CAPELIN SCHOOLS

The method used to quantify capelin schools on survey echograms is illustrated in Figure 2. Each echogram was partitioned by time (1 min intervals in 1982–1984, and 2 min intervals in 1983) and depth (10 m intervals). The density of capelin registrations appearing in each block was then graded visually on a scale of 0–9 (e.g., Safina and Burger 1985).

Fish abundance is proportional to the square of echo-signal intensity (Forbes and Nakken 1972), and total capelin abundance per survey was therefore calculated as the sum of squared grades on the echogram. Mean abundance of capelin per survey or per minute was estimated by dividing the sum of abundance grades by the number of graded blocks (including zeros) in the survey or minute, respectively. Mean density of capelin schools per survey or per minute was calculated by dividing the sum of abundance grades by the number of non-zero blocks per survey or minute.

Abundance of deep capelin schools may have been underestimated because echo-signal strength attenuates with depth. Time-varied-gain (TVG) adjustments were made to compensate for that effect in 1982 (Forbes and Nakken 1972). Most capelin schools were located within 30 m of the surface, however, so signal attenuation was probably not a large source of error. The spread of acoustic signals with depth tends to overes-timate deep school dimensions, but this was adjusted for in calculating capelin school volumes (Forbes and Nakken 1972).

STATISTICAL ANALYSES

Aggregation intensity was quantified by computing variance-to-mean ratios (I') for bird and capelin abundance on each survey. The dependence on measurement interval (frame size) of I' and correlations between bird and capelin aggregations were determined by computing I' and r^2 over increasing frame sizes for each survey (Schneider and Duffy 1985, Schneider and Piatt 1986). Measurement intervals were scaled in minutes of transect (ca. 250 m traveled per min of transect, or 4 min/km).

Plots of bird versus capelin density at varying frame sizes indicated that the aggregative response of birds to capelin schools was sigmoidal. A simple box model was used to transform sigmoidal curves, locate inflection points (thresholds), and measure the strength of bird-capelin correlations. The model used was:

$$B = k_1F \text{ if } F > F_T, \qquad B = k_2F \text{ if } F < F_T$$

where B = bird density, F = relative capelin density, F_T = test threshold capelin density, and k_1 and k_2 are the mean densities of birds above and below the test threshold F_T. An iterative procedure was used to locate the inflection point. Least squares regression was used to estimate k_1 and k_2.

Using simulated data, an example of this method is shown in Figure 3. The sigmoidal curve is transformed to a linear relationship by dummy coding the independent variable (X) according to whether it is lower (0) or higher (1) than the test threshold X_T (Fig. 3C). Regression of Y on X then reveals (r^2) how well the data fit a linear model. This analysis is performed iteratively for values of X (0, 1, . . . , X_i), which generates a regression coefficient for each test threshold (Fig. 3A). In the example, a test threshold of $X_T = 2$ yields an r^2 value of 0.25; at $X_T = 5$, $r^2 = 0.89$; at $X_T = 8$, $r^2 = 0.18$. Because the relationship between Y and X is sigmoidal, r^2 increases with each iteration up to the inflection point and decreases thereafter. The best fit to the model occurs when X_T equals the true threshold, and r^2 at that point provides the best measure of correlation between X and Y.

When real data were grouped into large measurement intervals to examine the effects of scale, the number of data points available for locating thresholds decreased (e.g., grouping a 128 min survey into 16 min blocks reduced the number of data points from 128 to 8). With bird and capelin density data grouped into a small number of average points, r^2 did not always reach a maximum value and then decline in the iterative threshold test because all the high density data were sometimes grouped into an isolated, terminal data point. In such cases, if a maximum r^2 value occurred just before the terminal data point, a threshold was assumed to occur before that point.

I used Monte Carlo simulations to test the reliability of the above method for measuring correlations and locating thresholds. Two surveys were chosen at random and an International Mathematics and Statistics Library subroutine (GGPER) was used to reassign each 1 min bird count randomly to a new location along the

transect (Schneider and Piatt 1986). One hundred runs were conducted for each survey and bird species. After each run, the iterative threshold test was conducted for the independent variable (relative capelin density). In total, 2400 regressions of randomized data were compared with regressions of original data. Results indicated that significance levels obtained in iterative threshold tests of original data were conservatively estimated by parametric statistics.

To determine if thresholds could occur by chance in plots of original data, the proportion of randomized surveys yielding a simple threshold (maximum r^2 whether significant or not), or a threshold with a significant regression, was determined from 400 Monte Carlo simulations. Because thresholds could also occur before terminal values of capelin density in some cases (see above), and therefore not be located by the iterative threshold test, the probability of obtaining one or two consecutive significant r^2 values anywhere in a plot was also determined from Monte Carlo simulations. The results of these additional simulations are presented and discussed below.

Like spatial correlations, the temporal association between birds and capelin depended on the time scale used in analyzing the data. I used the simple procedure of grouping data over increasing time frames (1–10 d) for the analysis of temporal correlations between birds and capelin at Witless Bay.

RESULTS

TEMPORAL PATTERNS IN ABUNDANCE OF BIRDS AND CAPELIN

In all years, murres and puffins were absent or occurred in low numbers on the water around their breeding colonies in May and early June (Fig. 4). Most breeders attend colonies in Witless Bay by late May (Nettleship 1972, Mahoney 1979), so birds were apparently commuting to foraging areas located farther than about 5 km from the islands. An exception occurred on 9 May 1984, when about 100,000 murres were concentrated inshore by Arctic pack ice. That unique survey was excluded from further analyses.

The abundance of murres and puffins in the survey area increased sharply in late June each year, corresponding to the arrival of spawning schools of capelin inshore (Fig. 4). Thereafter, murre and puffin abundance fluctuated with capelin abundance, although each bird species exhibited different patterns of association. Murres were better correlated with capelin over all time frames examined (1–10 d). Maximal correlations of murres and puffins with capelin were observed when data were grouped over 5-day intervals. At that scale, murre abundance was strongly correlated with capelin abundance in all years (1982: Pearson $r^2 = 0.84$, $P < 0.05$; 1983: $r^2 = 0.83$, $P < 0.0001$; 1984: $r^2 = 0.65$, $P < 0.01$). Murres, like capelin, exhibited one peak of abundance in 1982 and 1984, two peaks in 1983, and were
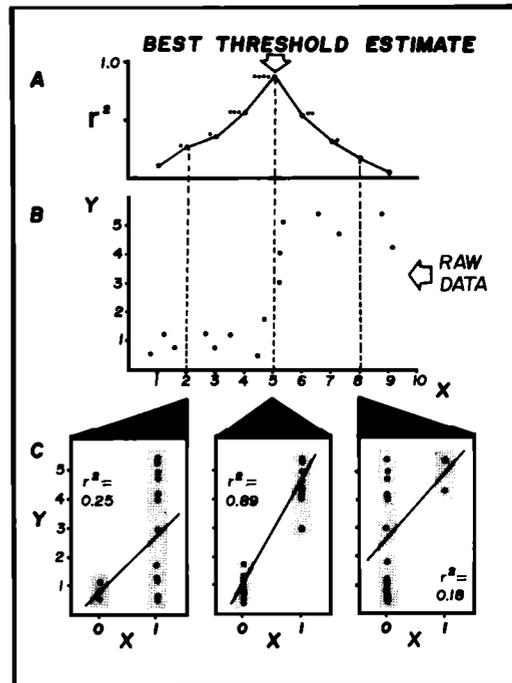
FIGURE 3. Illustration of how sigmoidal curves were transformed with a box model and how thresholds were located using an iterative procedure. Asterisks in panel A indicate significance levels of regressions: *P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001.

scarce in August each year (Fig. 4). Although puffins were also abundant in late June and July, their numbers were poorly correlated with overall capelin abundance in Witless Bay (1982: $r^2 = 0.51$, $P > 0.05$; 1983: $r^2 = 0.11$, $P > 0.05$; 1984: $r^2 = 0.46$, $P > 0.05$) and puffins were often as common in August as they were in July. However, separate analyses revealed that puffins foraged mostly inshore (Piatt 1987), and using only data from inshore habitats, puffin abundance was correlated strongly with capelin abundance in all years (1982: $r^2 = 0.73$, $P > 0.05$, 1983: $r^2 = 0.75$, $P < 0.0001$; 1984: $r^2 = 0.54$, $P < 0.05$).

There was an order of magnitude decline in capelin abundance from 1982 to 1984 (Fig. 4). The mean abundance index for capelin declined from 2.3 (± 0.1 SE) in 1982, to 0.83 (± 0.05) in 1983, and to 0.11 (± 0.02) in 1984. That trend was mirrored by a decline in overall bird abundance in Witless Bay over the same years, although puffins were less affected than murres (Fig. 4).
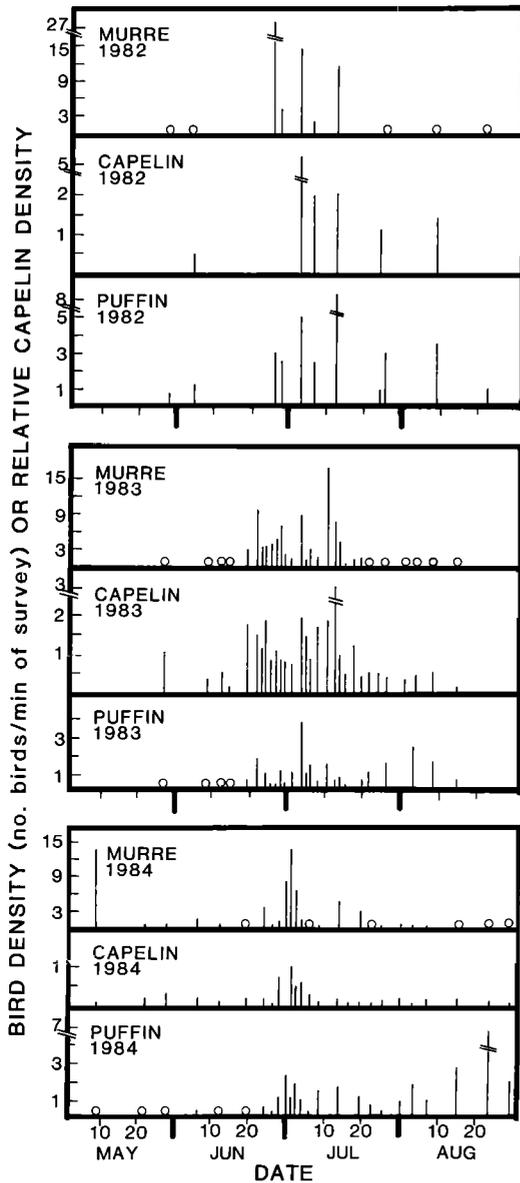
FIGURE 4. Seasonal abundance of Common Murres, Atlantic Puffins, and capelin around the Witless Bay islands, 1982–1984. Data from standard surveys only. Open circles indicate that a survey was conducted, but no birds were observed on the water.

FIGURE 5. Standard survey conducted 13 July 1982, showing Common Murre, Atlantic Puffin, and capelin abundances along the survey route. Note differing scales for murre and puffin abundance.

FINE-SCALE SPATIAL ASSOCIATION BETWEEN BIRDS AND CAPELIN

Some hydroacoustic echograms obtained in 1982 were selected for the quality of capelin school registrations appearing on them, and schools were measured carefully to estimate vol-

umes (Forbes and Nakken 1972, Piatt 1987). This method of measuring capelin abundance was not used for further analyses because it was too time-consuming. In conjunction with bird observations, however, these data illustrate fine-scale associations between birds and capelin (Fig. 5, Table 1).

Between minutes 3–10 (2 km) of a survey conducted on 13 July 1982 (Fig. 5), 24 capelin schools were encountered that had mean and total volumes of 399 and 9575 m^3, respectively (Table 1). The minimum and maximum depths to which capelin schools extended were 0.3 and 16.7 m. The total number of capelin present was estimated at 150,000 individuals, assuming a mean density of 15.7 fish per m^3 (Zaferman 1973). Total biomass was about 3.8 metric tons, assuming the mean weight of individual capelin in the area was 25.3 g (Piatt 1987). Only puffins fed on this shallow aggregation, and most were found over the largest schools of capelin.

Between minutes 37–49 (3.3 km) of the same survey (Fig. 5), 58 capelin schools were recorded that had mean and total volumes of 680 and 39,452 m^3, respectively. The minimum and maximum depths to which schools extended were 0.3 and 42.4 m. The total number of capelin in the aggregation was estimated at 619,000 individuals, with a total biomass of 15.7 metric tons. Both murres and puffins fed on this aggregation, but they were spatially segregated. Murres occurred over large schools concentrated between 10–30 m in the water column, whereas puffins occurred over smaller schools concentrated between 2–15 m. Similarly, most puffins were as-

TABLE 1. FINE-SCALE COMMON MURRE AND ATLANTIC PUFFIN ASSOCIATION WITH SELECTED CAPELIN AGGRE-GATIONS, 3 AND 13 JULY, 1982

Date	Minute	No. of schools	Total[a] school volume (m³)	Mean[b] depth (m)	No. of murres	No. of puffins
13 July	3	2	572	13.3	0	0
	4	4	599	2.5	0	30
	5	3	2213	4.7	0	100
	6	4	2229	3.7	0	75
	7	4	2055	4.2	0	110
	8	2	781	2.3	0	125
	9	4	475	4.7	0	6
	10	1	651	3.1	0	3
	37	7	350	30.1	3	0
	38	8	3698	24.7	25	0
	39	4	222	25.2	4	1
	40	12	1686	24.2	70	5
	41	5	2840	18.6	190	0
	42	4	9026	11.9	300	0
	43	5	723	19.3	201	9
	44	2	68	8.9	1	25
	45	3	7594	13.5	5	85
	46	3	12,355	11.4	15	180
	47	2	620	2.8	2	41
	48	2	254	2.6	2	78
	49	1	16	3.5	0	26
3 July	43	1	46	1.0	0	0
	44	1	743	10.4	1	3
	45	1	45	1.4	0	7
	46	2	369	0.3	0	11
	47	3	1365	4.9	0	35
	48	1	27	4.2	0	19
	49	1	8447	8.3	2	75
	50	2	144	1.4	0	32
	51	1	60	1.0	0	3
	52	1	25	10.4	0	0
	74	3	111	11.9	1	1
	75	10	3905	14.0	0	38
	76	5	3537	18.9	0	15
	77	5	16,472	27.4	50	2
	78	7	5208	22.0	5	0
	79	5	9295	32.0	21	0
	80	11	9043	32.6	6	0
	81	3	1060	12.4	1	0

[a] Total volume of all schools. School volume = $3.14 \, h^2 \, w/4$ (Forbes and Nakken 1972).
[b] Mean depth weighted by volume.

sociated with small, shallow (<20 m) capelin schools, whereas murres were associated with larger, deeper (20–35 m) capelin schools during a survey conducted on 3 July 1982 (Table 1).

Some important features of these and other 1982 surveys were observed also in 1983 and 1984; i.e., the combined distribution of murres and puffins matched the distribution of capelin schools, but murres and puffins were spatially segregated. They either fed in different habitats or fed on different parts of the same capelin aggregations.

SCALE-DEPENDENT AGGREGATIONS AND CORRELATIONS

On most surveys, murre (86%, N = 63 surveys), puffin (76%, N = 70), and capelin (88%, N = 73) aggregation intensity (I') increased with frame size (Fig. 6), yielding significantly higher values of I' at spatial scales of 0.5–15 km than at minimum frame sizes. In most cases, I' increased rapidly over small frame sizes, plateaued or peaked at intermediate frame sizes (2–4 km), and decreased again at large frame sizes (8–16
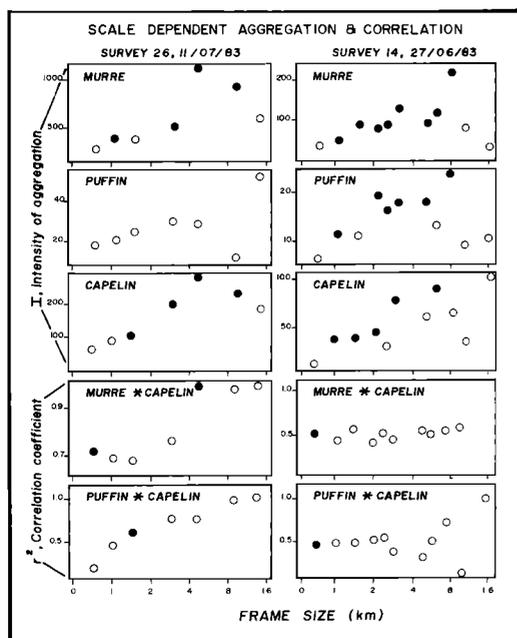
FIGURE 6. Scale dependent aggregation and correlation of Common Murres, Atlantic Puffins, and capelin. Aggregation intensity: closed circles indicate significantly higher I' values than observed at minimum frame size (tested by Monte Carlo analysis). Correlation coefficient: closed circles at minimum frame size indicate significant correlation; at larger frame sizes closed circles indicate that the correlation was significantly higher than that calculated at the minimum frame size (tested by Monte Carlo analysis).

km). Maximal I' values indicate the scale at which aggregations occur (Pielou 1977, Schneider and Piatt 1986) and usually peaked between 2–4 km for puffins, and between 2–6 km for murres and capelin.

Murres (68% of 63 surveys) and puffins (54% of 70 surveys) were significantly correlated with capelin at the minimum scale of measurement on most surveys. Correlations grew significantly stronger with increasing frame size on 35% and 27% of all murre and puffin surveys, respectively (e.g., survey 26, Fig. 6). Spatial correlations between birds and capelin on the remainder of surveys did not improve significantly with increasing frame size, despite significant increases in I' (e.g., survey 14, Fig. 6).

SCALE-DEPENDENT AGGREGATIVE RESPONSE

Because fine-scale associations between birds and capelin were imperfect, plots of bird versus capelin density using fine-scale data gave the impression that large numbers of birds foraged in areas where capelin were scarce or absent (Fig. 7, 2 and 4 min frame sizes). However, when data were grouped into measurement intervals corresponding to the scale of aggregations and replotted, a more realistic picture of murre and puffin foraging behavior emerged (Fig. 7, 8 and 16 min frame sizes).

Using a 10 min frame size to examine all surveys, many plots of bird versus capelin density were sigmoidal (Figs. 7 and 8) indicating Type III aggregative responses to prey density (Holling 1959, Hassell and May 1974). An intermediate
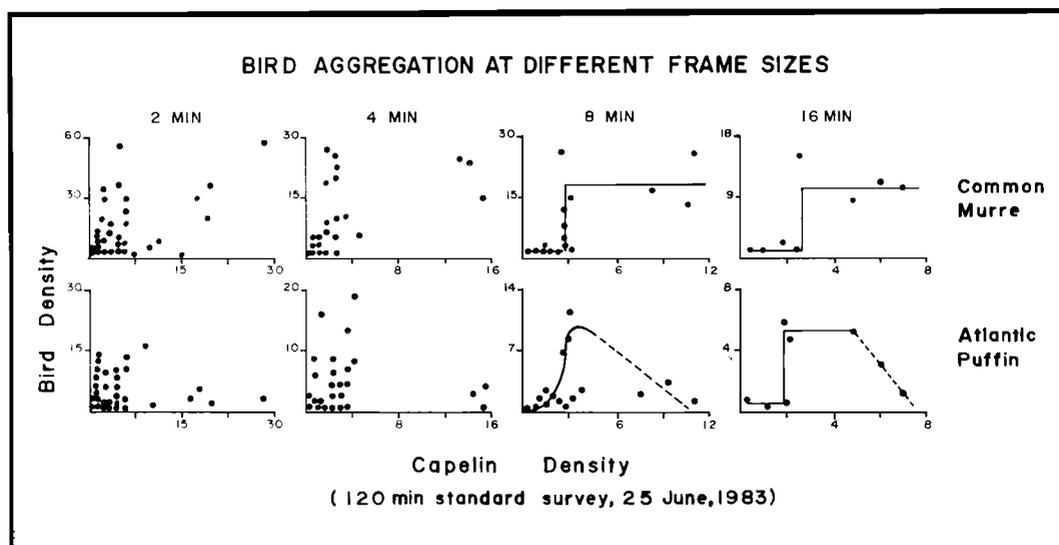
FIGURE 7. Effect of increasing frame size on the form of the aggregative response of birds to capelin.

PREY DENSITY THRESHOLDS
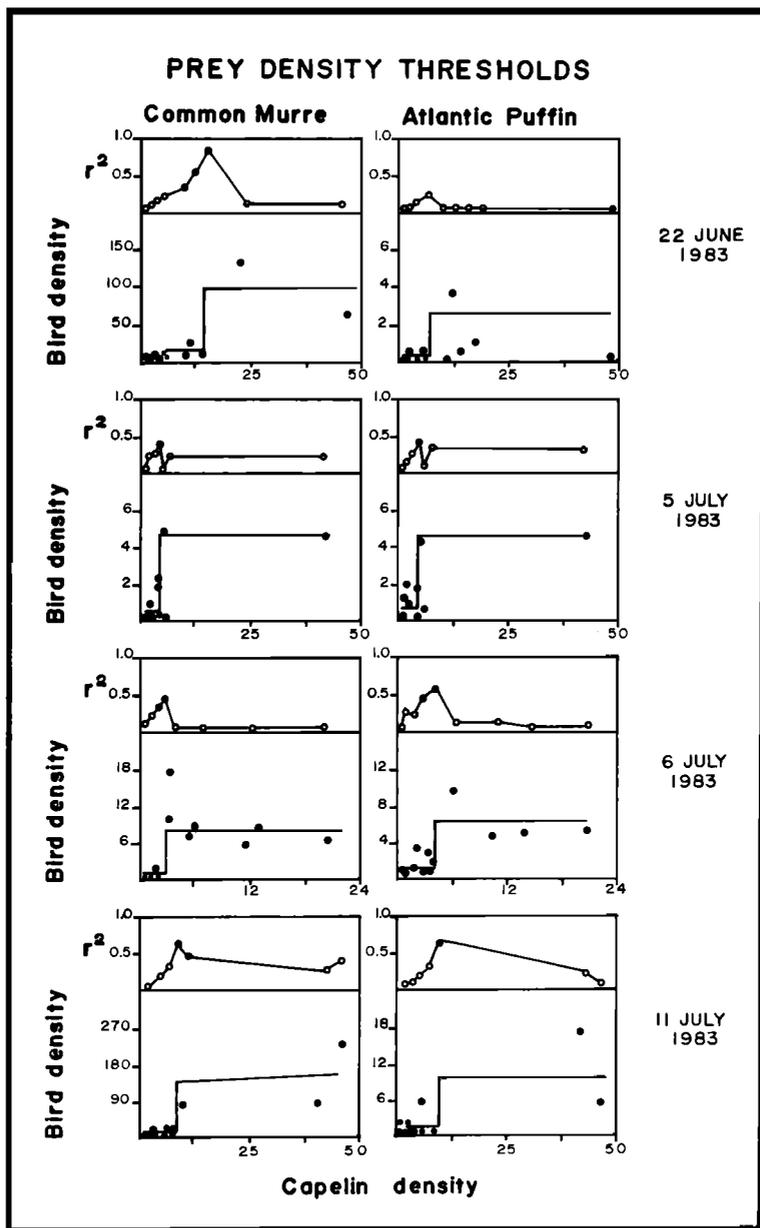
FIGURE 8. Aggregative response of Common Murres and Atlantic Puffins to capelin on four standard surveys in Witless Bay, 1983. Data grouped into 10 min frame sizes. For each date and bird species, the aggregative response is shown in the lower panel, with the estimated threshold indicated by a solid line. Corresponding upper panel shows the result of a threshold location test (closed circle indicates $P < 0.05$ for the corresponding r^2 value).

10 min (2.5 km) frame size was chosen for comparing surveys because aggregation intensity (I′) usually plateaued or peaked at frame sizes greater than about 8 min, the number of data points in an aggregative response plot decreased with increasing frame size (Fig. 7), and seabird census programs often use 10 min observation periods (e.g., Brown et al. 1975).

ESTIMATING THRESHOLDS TO PREY DENSITY

Using the iterative test, most plots exhibited simple thresholds, i.e., a maximum correlation
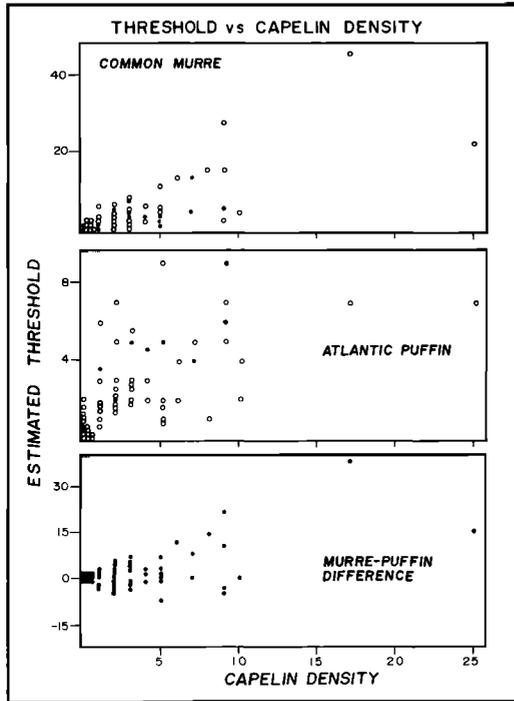
FIGURE 9. Common Murre and Atlantic Puffins prey density thresholds, and the difference between thresholds, in relation to overall capelin density in Witless Bay. Spearman rank correlations calculated using data from all surveys (open and closed circles) or using only surveys with plots exhibiting thresholds with significant regressions (closed circles). Difference plot incorporates all data. Spearman rank correlations: Common Murre—open and closed circles: $r = 0.82$, $P < 0.0001$; closed circles only: $r = 0.58$, $P < 0.05$; Atlantic Puffin—open and closed circles: $r = 0.73$, $P < 0.0001$; closed circles only: $r = 0.89$, $P < 0.001$; murre-puffin difference: $r = 0.33$, $P < 0.05$.

TABLE 3. MONTE CARLO SIMULATIONS: PROBABILITY OF FINDING THRESHOLDS AND SIGNIFICANT REGRESSIONS WHEN CONDUCTING THRESHOLD LOCATION TESTS ON RANDOMIZED SURVEY PLOTS OF BIRD VERSUS CAPELIN DENSITY

Probability[a] of obtaining:	Murre		Puffin	
	A	B	A	B
Simple threshold	0.56	0.58	0.56	0.62
Threshold with significant r^2	0.08	0.07	0.09	0.06
1 Significant r^2	0.15	0.16	0.13	0.17
2 Consecutive significant r^2's	0.02	0.03	0.07	0.05

[a] Based on 100 runs on two different surveys (A, B) for each species (conducted at 10 min frame size).

in the regression of dummy-coded bird and capelin densities occurred at some intermediate density of capelin (Table 2). However, not all regressions were statistically significant and many plots had few high density data points (or one terminal one), making it difficult or impossible to locate a threshold with the iterative test. Monte Carlo simulations revealed that:

1) There was a high probability of finding simple thresholds due to chance alone. The proportion of randomized survey plots with simple thresholds (Table 3) was similar to the proportion of original survey plots with simple thresholds (Table 2).

2) There was a low probability ($P < 0.06$–0.09) of finding a threshold with a significant regression (Table 3), and this was therefore a moderately conservative criterion for identifying true thresholds. Many more survey plots in 1983 and 1984 had thresholds with significant regressions than would be expected by chance (Table 2).

3) The probability of finding at least one significant regression anywhere in a randomized plot

TABLE 2. FREQUENCY OF THRESHOLDS AND SIGNIFICANT REGRESSIONS IN ALL BIRD-CAPELIN PLOTS, 1982–1984 (AT 10 MIN FRAME SIZE)

	1982				1983				1984			
	Murre		Puffin		Murre		Puffin		Murre		Puffin	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
Total no. of surveys	3		5		32		35		26		25	
No. with simple threshold	2	(66)	3	(60)	17	(53)	23	(66)	7	(27)	8	(32)
No. with threshold and significant regression	0	(0)	0	(0)	10	(31)	8	(23)	5	(19)	2	(8)
No. with >2 consecutive significant regressions	1	(33)	1	(20)	19	(56)	10	(38)	8	(31)	6	(24)

TABLE 4. AVERAGE MURRE AND PUFFIN FORAGING THRESHOLDS (THR) TO CAPELIN SCHOOL DENSITY, 1982–1984 (AT 10 MIN FRAME SIZE)

Case	Year	Murre			Puffin			t^a	P
		N	Thr	(SE)	N	Thr	(SE)		
All data	1982	3	9.7	(6.2)	5	3.6	(1.0)	1.2	NS
	1983	32	6.9	(1.6)	35	3.4	(0.3)	2.1	<0.05
	1984	26	1.1	(0.3)	25	1.0	(0.3)	0.7	NS
	Total	61	4.6	(0.9)	65	2.6	(0.3)	2.3	<0.05
If Mt and Pt significant[b]	Total	4	4.1	(3.6)	4	3.4	(2.2)	0.9	NS
If Mr and Pr significant[c]	Total	9	9.5	(2.6)	9	3.7	(0.5)	2.4	<0.05

[a] Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold = 0.
[b] If both murre and puffin plots on the same survey had thresholds with significant regressions.
[c] If both murre and puffin plots on the same survey had ≥2 consecutive significant regressions.

was relatively high (Table 3). However, the probability that two or more significant regressions would occur consecutively in a plot of randomized data was low (P < 0.02–0.07). Consecutive regression coefficients should be high and significant around a true threshold in a sigmoidal curve (Fig. 3) and they could also indicate whether a threshold occurred before an isolated terminal data point. Thus, the existence of consecutive significant regressions was a conservative criterion for identifying true thresholds. A much higher proportion of original survey plots exhibited two or more consecutive significant regressions than would be expected by chance (Table 2).

COMPARISON OF MURRE AND PUFFIN THRESHOLDS TO PREY DENSITY

Murre foraging thresholds were usually higher than puffin thresholds on individual surveys and average murre thresholds were higher than average puffin thresholds in all years (Table 4). Considering only surveys in which murre and puffin plots both exhibited thresholds with significant regressions, the average murre threshold was higher than the average puffin threshold. Finally, considering only surveys in which murre and puffin plots both exhibited two or more consecutive significant regressions (the most conservative analysis), average murre thresholds were significantly higher than average puffin thresholds (Table 4).

The apparent difference between murres and puffins with respect to their prey density thresholds was examined for possible scale-dependency by estimating thresholds at different spatial scales. Grouping the data into larger frames lowered average bird and capelin density values, but at every frame size the average threshold for murres was greater than the average threshold for puffins (Table 5).

THRESHOLD VARIABILITY IN RELATION TO OVERALL CAPELIN DENSITY

Murre and puffin thresholds decreased progressively from 1982 to 1984 corresponding to a decline in capelin abundance (Fig. 4). Murre and puffin thresholds were strongly correlated with overall capelin density at Witless Bay in each year and over all years combined, regardless of the data set used for the analysis (Table 6, Fig. 9). The difference between murre and puffin thresholds was also correlated with overall capelin density. As overall capelin density increased, murre thresholds increased more rapidly than puffin thresholds, and the difference between thresholds widened. Conversely, as overall capelin density declined, murre and puffin thresholds converged.

DISCUSSION

SCALE-DEPENDENT AGGREGATIONS AND CORRELATIONS

In marine systems, biological and physical processes combine to impart spatial structure to plankton and fish communities, and seabird ag-

TABLE 5. EFFECT OF VARYING FRAME SIZE ON AVERAGE FORAGING THRESHOLDS (THR) USING ALL DATA IN 1983 FOR MURRES (N = 32 SURVEYS) AND PUFFINS (N = 35 SURVEYS)

Frame size	Murre		Puffin		t^a	P
	Thr	SE	Thr	SE		
2	7.4	(1.6)	3.2	(0.4)	2.5	0.02
4	7.6	(1.5)	3.1	(0.3)	2.7	0.02
8	7.9	(1.7)	2.6	(0.4)	3.4	0.002
10	6.9	(1.6)	3.4	(0.3)	2.1	0.05
12	6.5	(1.4)	3.6	(0.4)	2.0	NS (0.06)
16	4.9	(0.9)	3.0	(0.4)	2.0	NS (0.05)

[a] Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold = 0.

TABLE 6. SPEARMAN RANK CORRELATIONS BETWEEN MURRE (M) AND PUFFIN (P) THRESHOLDS (THR), THE DIFFERENCE BETWEEN THRESHOLDS (DIFF) AND OVERALL CAPELIN DENSITY (CD), 1982–1984 (AT 10 MIN FRAME SIZE)

Case	Year	MThr × CD			PThr × CD			Diff × CD		
		N	r	P	N	r	P	N	r	P
All data	1982	3	0.99	0.0001	5	0.76	NS	3	0.50	NS
	1983	32	0.66	0.0001	35	0.51	0.01	32	0.38	0.05
	1984	26	0.67	0.001	25	0.76	0.0001	20	−0.09	NS
	Total	61	0.82	0.0001	65	0.73	0.0001	55	0.33	0.05
If Mt and Pt significant[a]		4	0.99	0.01	4	0.80	NS	4	0.80	NS
If Mt or Pt significant[b]		15	0.58	0.05	10	0.89	0.001	—	—	—
If Mr and Pr significant[c]		9	0.75	0.01	9	0.69	0.05	9	0.59	0.05

[a] If both murre and puffin plots had thresholds with significant regressions.
[b] Calculated using all plots in which murre or puffin plots exhibited thresholds with significant regressions. Difference (Diff) cannot be calculated because data for each species taken from different surveys.
[c] If both murre and puffin plots had ≥2 consecutive significant regressions.

gregations reflect the scale at which these processes occur (Schneider 1982). At Witless Bay, the aggregation intensity of birds and capelin varied with measurement interval and peaked at scales of 0.25 to 15 km. Most patches ranged between 2–6 km in horizontal extent. These were small compared to patches reported from other areas (i.e., 5–50 km; Zaferman 1973, Schneider 1982, Briggs et al. 1984, Woodby 1984), but they contained regionally significant concentrations of predators and prey. Thousands of tons of capelin are consumed in summer at Witless Bay by hundreds of thousands of seabirds, cod (*Gadus morhua*), and baleen whales (Brown and Nettleship 1984, Cairns et al. 1987, Methven and Piatt 1989, Piatt et al. 1989).

The present analysis of more than 70 surveys corroborates an earlier finding by Schneider and Piatt (1986) that spatial correlations between birds and capelin in Witless Bay are scale-dependent. Murres and puffins were significantly correlated with capelin on more than half of all surveys before effects of scale were examined, and spatial correlations improved with increasing frame size on about half of those surveys. At measurement intervals of 2.5 km, capelin density frequently explained over 75% of the spatial variation in bird density; it explained over 95% of the variation on nine surveys.

Elsewhere, it has proven difficult to demonstrate significant spatial correlations between seabirds and their prey (e.g., Woodby 1984, Obst 1985, Safina and Burger 1985). Scale-analysis might have been useful in these studies (Schneider and Piatt 1986), although other factors probably contributed more to the difficulty in measuring predator-prey associations. In some situations, seabirds would not be expected to track all prey aggregations, especially at great distances from their colonies or where prey schools greatly outnumber predators (Woodby 1984). Obst (1985) found that aggregations of penguins were reliable predictors of krill (*Euphausia supurba*) schools, but not vice versa. Seabirds may forage selectively in specific habitats or on specific parts of the prey aggregations they encounter (Brown and Gaskin 1988), and interference competition may exclude some species from feeding sites (Piatt 1987). Seabird and prey aggregations may be dispersed by other predators (Safina and Burger 1985) or by the activities of the research vessel or other vessels. Errors also arise from rough sea conditions, poor visibility, weak or spurious signals from the echosounder, and the time lag between bird observations and detection of prey with the echosounder. Finally, seabirds and their prey are patchily distributed and surveys may simply miss significant aggregations.

Despite these potential sources of error, I found strong spatial correlations between birds and capelin in Witless Bay. Presumably, the abundance of breeding birds, close proximity of the survey route to colonies, and the use of Witless Bay for spawning by large numbers of capelin increased the likelihood that capelin schools would be exploited by foraging murres and puffins.

THE AGGREGATIVE RESPONSE

The are many examples of functional, aggregative, and numerical responses in the literature, but most are well-defined curves generated from laboratory experiments (Readshaw 1973, Hassell and May 1974, Hassell et al. 1977). Field

data are more difficult to gather and interpret (Goss-Custard 1970). Response curves must contain an adequate number of high density data points to resolve their shape (Hassell and May 1974), but this requirement was generally not met outside periods of high capelin density in Witless Bay. The same biological and physical sources of error that reduced spatial correlations also affected my ability to resolve aggregative response curves. In addition, the density of puffins was occasionally suppressed at high capelin densities, possibly owing to interference competition from murres (Piatt 1987), and this made it more difficult to characterize puffin response curves.

Despite these limitations, murres and puffins exhibited sigmoidal (Type III) aggregative responses to capelin density on about one-third of the surveys I conducted. Type III responses are typical of higher vertebrates feeding on aggregated prey (Holling 1965, 1966; Goss-Custard 1970, 1977; Hassell and May 1974; Murdoch and Oaten 1975). Aggregative responses were scale-dependent and best resolved at measurement intervals corresponding to the scale of aggregations (ca. 2–4 km). Murres foraged on larger, denser concentrations of capelin than puffins and also formed larger, denser flocks while foraging (Piatt 1987).

BODY SIZE AND FEEDING THRESHOLDS

Both Common Murres (ca. 975 g) and Atlantic Puffins (ca. 475 g) search widely for aggregated prey and dive to pursue their prey underwater. Foraging ranges, diving depths, and dive times are all positively correlated with body size in piscivorous alcids (Piatt and Nettleship 1985, Piatt 1987, Wanless et al. 1988). At Witless Bay, I observed murres and puffins simultaneously as they foraged on the same species of schooling prey. Thus, the difference between species in foraging thresholds must be attributed to biological differences between them (as opposed to differences between their prey or feeding environments), and body size is one obvious difference to consider. The relationship between predator body size and prey density thresholds is predictable from well-known models of foraging behavior.

The principal feature of Holling's (1965) "disc" equation, and many subsequent models of foraging behavior (e.g., Royama 1970, Murdoch and Oaten 1975, Hassell et al. 1977, Werner and Mittelbach 1981) is that:

$$N/T \propto D/(1 + D)$$

i.e., a predator's potential rate of food intake (N/T, where N = the number of prey captured and

T = time spent foraging) is a non-linear function of prey density (D). The major distinction between coexisting predators with similar foraging styles and shared prey is N_{tot}, the amount of food required for daily existence. N_{tot} is the sum of food required for maintenance and foraging, and both are functions of body size (Peters 1983, Werner and Mittelbach 1981).

Optimal foraging theory assumes that predators try to maximize their rate of food intake to allow as much time as possible for other activities (Krebs 1978, Pyke et al. 1977, Pyke 1984). Food intake rates may be maximized by foraging on the biggest or best quality food available (energy maximizer), by minimizing the time spent foraging (time minimizer), or both. To maximize N_{tot}/T, murres and puffins feeding on capelin can only adjust D, T, or the size of capelin consumed, because N_{tot} is a fixed function of body size and time spent foraging (T). Murres require about twice as much food as puffins (Brown and Nettleship 1984) and could therefore obtain their daily ration in the same time (T) as puffins if they foraged on capelin aggregations about $2[D/(1 + D)]$ times as dense as those fed on by puffins. Alternatively, murres could obtain their daily ration by foraging about twice as long on the same prey concentrations used by puffins. However, this would not be optimal behavior for murres, and in any case, evidence suggests that murres spend slightly less time foraging on prey shared with puffins (Pearson 1968). Finally, murres could obtain their daily rations in the same time as puffins if they fed on similar concentrations of much larger capelin. Although murres did take some larger size-classes of capelin than puffins at Witless Bay, the difference was not great enough to compensate for the difference in food demands. Morisita's index of overlap in weights of capelin consumed ranged from 0.82–0.96 in 1982–1984 (Piatt 1987).

Therefore, I postulate that the differing thresholds to capelin density exhibited by murres and puffins result from species-specific behavioral responses to food dispersion that have evolved in concert with metabolic constraints imposed by body size. In other words, puffins choose to exploit lower density prey aggregations than murres—a behavior that: i) is permitted because of lower metabolic demands; ii) is selected for when prey are scarce; and iii) promotes coexistence with murres (see below). An alternative explanation is that puffins were excluded by murres from high density prey patches. There is evidence that asymmetric interference competition for feeding sites occurred at Witless Bay (Piatt 1987). However, this would not explain why the gap between murre and puffin thresholds widened as overall capelin density increased. If

puffins were simply tracking murre thresholds, then the difference between thresholds should have remained constant. Nor would it explain why puffins continued to forage on low density capelin aggregations after murres departed the study area, or why murres formed larger, denser feeding flocks than puffins (Piatt 1987).

VARIABLE THRESHOLDS AND FORAGING EXPECTATIONS

Most foraging models assume that predators change behavior at threshold levels of foraging success (Krebs 1978, Lima 1983), but few predict how thresholds should vary with fluctuations in overall prey density. Such behavior is well simulated in "Foraging by Expectation" models, which assume that a predator will switch patches when its current success rate drops below what it has come to expect from recent experience. As prey density fluctuates, predators should change their expectations and foraging thresholds accordingly (Green 1980, Iwasa et al. 1981, Lima 1983).

Consistent with the above predictions, foraging thresholds of murres and puffins changed from survey to survey and between years in relation to overall capelin density in Witless Bay. Brown and Gaskin (1988) noted similar behavior in phalaropes (*Phalaropus* spp.) foraging on zooplankton in the Bay of Fundy and suggested that phalaropes exploit the densest concentrations of prey available to them at any given time or place.

THRESHOLDS, BODY SIZE AND POPULATION ECOLOGY

Murres and puffins at Witless Bay colonies normally hatch chicks in late June (Nettleship 1972, Mahoney 1979) as capelin arrive inshore for spawning (Templeman 1948, this study). Murre chicks go to sea about 19–25 days after hatching, and because breeding is well synchronized, most adult murres leave the colony within 4–5 weeks after the peak of hatching (Mahoney 1979, Piatt and McLagan 1987). In contrast, puffins take about a month longer to fledge chicks and fledging is less synchronized (45–60 days, Nettleship 1972). Thus, the period of peak food demand by murres in Witless Bay corresponds well with the period of peak capelin density around the colonies (ca. 4 weeks), whereas puffin food demands extend well beyond this period. What accounts for the difference in duration of chick-rearing?

The conventional explanation for timing of reproduction in the Alcidae is that breeding coincides with peak food availability for provisioning chicks (Birkhead and Harris 1985). For murres and puffins, however, which overlap extensively in their choice of prey (Pearson 1968, Piatt 1987), this hypothesis offers little explanation for the marked interspecific difference in duration of chick-rearing. The emphasis on chicks may be misleading because only about 5% of the total food biomass taken by murres and puffins during breeding is fed to chicks (Brown and Nettleship 1984). The bulk of food required for reproduction is used to fuel adult maintenance and foraging activity (Gaston 1985). Therefore, the breeding seasons of murres and puffins may be limited to that portion of the year when local prey densities are sufficient to support adults while they are constrained to forage near their breeding colonies; this period is shorter for murres than for puffins.

Many long-term studies have been conducted on components of Common Murre and Atlantic Puffin population biology (Nettleship and Birkhead 1985) and the results are unequivocal. Where they coexist in the North Atlantic, Common Murres exhibit, on average, higher rates of breeding success (Harris and Birkhead 1985), higher recruitment rates (Hudson 1985), higher rates of adult mortality (Hudson 1985, Evans and Nettleship 1985), and more extreme population fluctuations (Hudson 1985) than Atlantic Puffins. I propose that these differences in population dynamics are related to food thresholds and body size.

At least four factors contribute to this relationship. First, because high density prey offer the greatest rate of energy extraction from the environment, any predator feeding on high density prey should be able to harness more energy for reproduction than any coexisting predator feeding on low density prey (MacArthur 1958). Field measurements of foraging energetics support this hypothesis (Nagy et al. 1984). Second, large animals have lower specific metabolic rates than small animals and can therefore channel a higher proportion of energy into reproduction than small animals feeding on the same food (Peters 1983). Third, predators feeding in dense aggregations face a higher risk of starvation and mortality from competition or stochastic events than dispersed predators feeding in the same environment. Finally, higher reproduction and mortality rates result in larger and more rapid population fluctuations (Utida 1957).

The hypothesis that prey density thresholds are linked to population dynamics in murres and puffins is corroborated by observations on other kinds of animals. Population growth rates are non-linear functions of prey density for most animals that have been studied (Holling 1959, 1965; Readshaw 1973; Murdoch and Oaten 1975), and a few studies have examined how naturally coexisting predators respond numerically to vari-

ations in density of shared prey (Utida 1957, MacArthur 1958, Holling 1959, Taylor 1978, Stemberger and Gilbert 1985). All these studies revealed that predators that could be characterized as low- or high-density foragers also exhibited a suite of population characteristics typical of the prey density to which they were adapted. Specifically, "high-density" predators were found to have higher maximal reproduction rates, higher adult mortality rates, and faster and larger population fluctuations, than coexisting "low-density" predators.

THRESHOLDS, BODY SIZE, AND COEXISTENCE

If food is the most important resource regulating seabird populations (Birkhead and Furness 1985), my hypothesis that murres and puffins specialize on different densities of shared prey offers a plausible mechanism to explain their coexistence. If species have different, non-linear responses to resource density, then coexistence of two or more competitors limited by one resource is possible regardless of the degree of overlap in use of that resource (Abrams 1983). Applying the concept of limiting similarity, it has been proposed that there is a limit to how similar resource density thresholds may be before competitive exclusion occurs (Abrams 1983). In this view, the competitive advantage shifts between high- and low-density adapted predators as resource densities fluctuate, and neither species can exclude the other. For murres and puffins, differing thresholds to prey density may be attributable to differing body sizes. Differential thresholds to food density may also be maintained by marked differences in foraging style, but it appears that animals with the same foraging style and body size do not coexist (Brown 1973; Diamond 1975; Davidson 1977a, b).

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