Predator Stomachs as Sampling Tools for Prey Distribution: Atlantic Cod (*Gadus morhua*) and Capelin (*Mallotus villosus*)

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We demonstrate a direct relationship between the amount of prey (capelin, *Mallotus villosus*) in its predators' stomachs (Atlantic cod, *Gadus morhua*) and the biomass of the prey in the same localities. The relationship at a local scale implies that predator stomach contents can be used to estimate prey distribution. There is no evidence for either (1) a negative effect of local predator abundance on stomach contents (expected if local prey depletion and/or feeding interference occurs when predator density is high) or (2) a negative effect of the amount of other food in cod stomachs on the amount of capelin in the stomachs (expected if prey switching occurs). There is a negative effect of bottom depth on amount of capelin in cod stomachs as expected, since capelin are pelagic and cod are primarily bottom-dwelling, resulting in less vertical overlap between the species in deep water. This type of analysis may be useful in other predator–prey systems. Simultaneous stomach samples and independent biomass estimates of the prey are required, but once the model is built, it permits estimation of prey distribution in places and times when no direct survey of the prey can be done.

Nous établissons un rapport direct entre l'abondance d'une proie (capelan, *Mallotus villosus*) dans le contenu stomacal de son prédateur (morue franche, *Gadus morhua*) et la biomasse de la proie aux mêmes endroits. Ce rapport, à échelle locale, signifie que le contenu stomacal du prédateur peut servir à estimer la distribution de la proie. Rien n'indique 1) un effet négatif de l'abondance locale du prédateur sur le contenu stomacal (sauf en cas d'épuisement local du stock des proies ou d'une interférence dans l'alimentation lorsque la densité des prédateurs est élevée) ni 2) qu'il existe un effet négatif exercé par l'abondance d'autres sources alimentaires dans le contenu stomacal de la morue sur l'importance du capelan trouvé dans le contenu stomacal (sauf si le prédateur passe à une autre proie). La profondeur du fond exerce un effet négatif sur l'abondance du capelan dans l'estomac des morues, comme il fallait s'y attendre, puisque le capelan est pélagique et que la morue est benthique, par conséquent, que les aires des deux espèces coïncident moins sur le plan vertical. Ce type d'analyse peut se révéler utile pour l'étude d'autres systèmes prédateurs-proies. Des échantillons simultanés des estomacs et des estimations indépendantes de la biomasse des proies sont nécessaires, mais une fois que le modèle est construit, il permet l'estimation de la distribution d'une proie à différents endroits et différents moments sans devoir procéder à un recensement direct des proies.

One of the common methods of surveying marine fish stocks is the trawl survey in which trawl samples are taken over the area of the stock, usually in either a grid pattern or a random or stratified random pattern. These surveys often include subsampling of the fish for later analysis of stomach contents (e.g., Daan 1987; Livingston 1989; Magnusson and Palsson 1989; Mehl 1989; Lilly 1991). Since for some types of prey the stomach contents can be identified to species, the question arises whether the predators can be viewed as a sampling tool for the quantitative distribution of the prey species, at least within the stock area of the predator. In other words, is the amount of prey in predator stomachs an indication of local prey biomass?

The use of stomach contents of predators as an inexpensive way to obtain useful information about prey has been promoted by Gotshall (1969) and Saville (1977). There are some instances of rare species that are known largely or entirely from their occurrence in the stomachs of predators (Rofen 1966; Temple-

man 1970). Predators have also served as collectors of prey in those size ranges that are not readily collected with regular sampling tools. For example, juvenile shrimp found in the stomachs of cod off eastern Newfoundland proved to be helpful in the construction of a growth curve for shrimp (Parsons et al. 1986). Gotshall (1969) and Parsons et al. (1986) illustrated the use of the prey size frequency distribution and the number of prey per stomach to infer age distribution and relative strength of year-classes. Similar analyses have been conducted using stomach contents of marine birds (e.g., Hatch and Sanger 1992 and references therein).

Use of predator stomach contents to indicate distribution of prey has to date been qualitative (e.g., Kovalyov and Kudrin 1973; Livingston 1989). This is because the first step in constructing a quantitative method for inferring prey distribution from stomach data is the acquisition of independent quantitative data on prey distribution, coincident in time and space with the stomach samples. Since stomach data have typically been used for information about prey only when direct sampling of prey is lacking, such analyses have not been conducted. The present study demonstrates the potential use of stomach content data

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as a quantitative indicator of local abundance (i.e., distribution) of prey, using coincident data from predator stomachs and direct sampling for the prey.

Two major factors are expected to affect the relationship between the amount of a prey species in a predator's stomach and the biomass of the prey in the environment. First, the amount of prey in the stomach may not be independent of the local abundance of the predator. It is possible that large numbers of predators in an area result in lower mean prey abundance per unit predator stomach, either because of intraspecific feeding interference among the predators or because of localized prey depletion due to the predator feeding. Second, prey switching may complicate the relationship between prey biomass and amount of prey in predator stomachs.

We present analyses of the relationship between local biomass (i.e., distribution) of a prey species, capelin (*Mallotus villosus*), and the amount of capelin in the stomachs of its predator, Atlantic cod (*Gadus morhua*), in the same local areas. Our analyses demonstrate that there is a strong relationship between stomach contents and prey biomass at the local scale.

Methods and Results

Data

The data were collected during the spring (April-June) of 1985-89 in an area of approximately 70 000 km² on the northwestern part of Grand Bank off Newfoundland. This area is in Northwest Atlantic Fisheries Organization (NAFO) division 3L, which is the southern (approximately) one third of the area occupied by the "Northern cod" stock. Two datasets were used in the analyses. The first was data of capelin content in cod stomachs. The cod stomachs were collected during bottom trawl surveys (Doubleday 1981). Trawl stations were selected in a stratified random design, where stratification was by bottom depth. Stomachs were collected, as permitted by the catch, from a sample of five fish per 9-cm length group at each trawl station. Fish showing signs of regurgitation were not selected. If there were more than five fish in a 9-cm length group, then five fish were selected at random; otherwise, all fish were included in the sample. Only stomachs of cod in the appropriate length range for predation on capelin (36-71 cm) (Lilly and Fleming 1981; Turuk 1968) were included in our analyses. The average amount of capelin per unit of cod per sampling location (Lilly 1991) was calculated as F, the "partial stomach fullness index" (Lilly and Fleming 1981):

$$(1) \quad F = \frac{1}{n} \sum_{j=1}^{n} \frac{W_j}{L_j^3} \times 10^4$$

where W_j is the weight of capelin in cod stomach j, L_j is the length of cod j, and n is the number of cod in the sample. This index is based on the assumption that stomach capacity is a power function of length. Length is used in preference to weight as a measure of predator size because length is not influenced by changes in the weight of liver, gonads and stomach contents. This index is analogous to Fulton's condition factor (weight per length³); see, for example, Ricker (1975).

In the second dataset, biomass of capelin was estimated along acoustic survey transects in a systematic zigzag pattern. Details of the acoustic survey method are given in Miller et al. (1982) and Miller and Carscadden (1984). We averaged the capelin biomass estimates over 10-min periods, producing a capelin
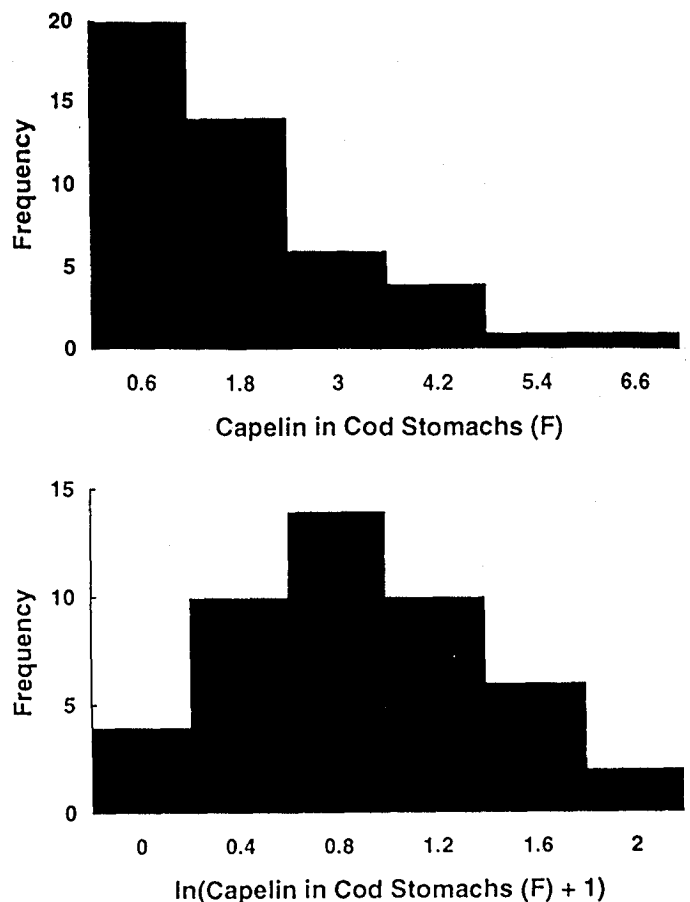

FIG. 1. Frequency histograms of capelin content in cod stomachs (F; see text) and $\ln(F + 1)$. Data shown are the 46 points used in the analyses, i.e., maximum time difference and maximum distance permitted between the stomach and acoustic points were 48 h and 40 km, respectively.

biomass (grams per square metre) estimate for every 3.1 km of the transects.

To determine whether the amount of capelin measured in cod stomachs was a measure of the capelin biomass in the local area, one would ideally like to have an estimate of the capelin biomass from the acoustic survey to match with each point estimate of capelin in cod stomachs from the bottom trawl survey. However, the two surveys were conducted using different vessels and although they were both conducted in the spring and in NAFO division 3L, they followed different courses through the area. The subset of the data that is useful for our purposes is therefore the data from those points in time and space at which the two vessels passed near to each other.

Since we did not have a priori criteria for "nearness" of the two vessels, we conducted a series of correlations between the capelin in cod stomachs (from the trawl survey) and the capelin density estimate (from the acoustic survey), for varying maximum time and space differences between the two. For each stomach content point, we determined whether there were any capelin biomass points within the selected time–space window. If there were more than one capelin biomass point in the window, the points were averaged. In all cases, only capelin biomass points that occurred before the stomach content point were considered, since the stomach contents reflect the capelin biomass when the capelin were consumed. The maximum time
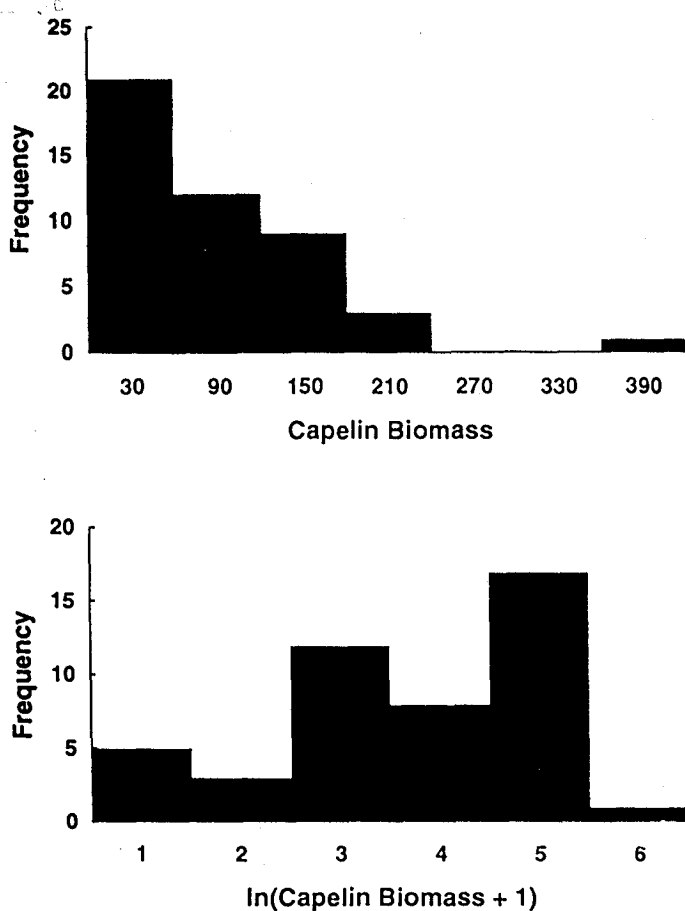
FIG. 2. Frequency histograms of acoustic estimates of capelin biomass and ln(biomass + 1). Data shown are the 46 points used in the analyses, i.e., maximum time difference and maximum distance permitted between the stomach and acoustic points were 48 h and 40 km, respectively. Biomass values were averaged within the time–distance windows (see text).
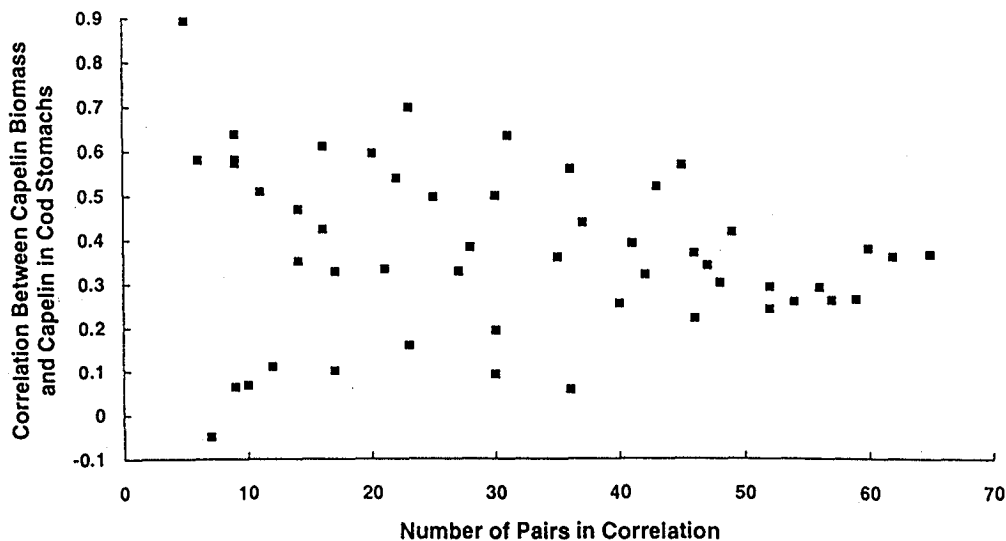
difference that we considered was 4 d, since, for cod feeding on capelin, the time to complete digestion at near-bottom temperatures in the study area (−1 to 3°C) is approximately 4–5 d (dos Santos and Jobling 1991; G. Lilly, unpublished data). The maximum distance we considered was 40 km. Tracking studies of cod migrating toward the coast in the northern part of the study area indicate that the median rate of movement is approximately 10 km/d (G. Rose, Northwest Atlantic Fisheries Centre, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada, personal communication). It is thought that cod over most of the study area were not migrating, and the distance moved within the 4-d time period would usually be much less than 40 km.

Correlations between the stomach content values (log-transformed; see Fig. 1) and the mean capelin biomass (log-transformed; see Fig. 2) were conducted for all 64 possible combinations of eight maximum distances (5, 10, 15, 20, 25, 30, 35, and 40 km) between the vessels and eight maximum time differences (12, 24, 36, 48, 60, 72, 84, and 96 h). The number of points in the correlations ranged from 0 to 65. Figure 3 illustrates the effect of the number of pairs on the variability in the estimate of the correlation; the fewer points, the more variable the estimate. All correlations that included at least eight points (48 of 64) were positive.

Figure 4 illustrates the relationship between the correlation and the maximum time difference between the stomach sample and the acoustic sample. Correlations are low for very low maximum time differences. This is probably a chance occurrence due to the small number of points in these correlations. The correlations are high at 36 and 48 h but then drop steadily. The decline is presumably because as the maximum time difference increases, capelin eaten 3–4 d before have been largely digested, and capelin from other locations may have been consumed. By including points in the mean biomass value with time differences greater than 48 h, we add noise to the relationship, thus reducing the correlation. The relationship between the correlation and maximum distance
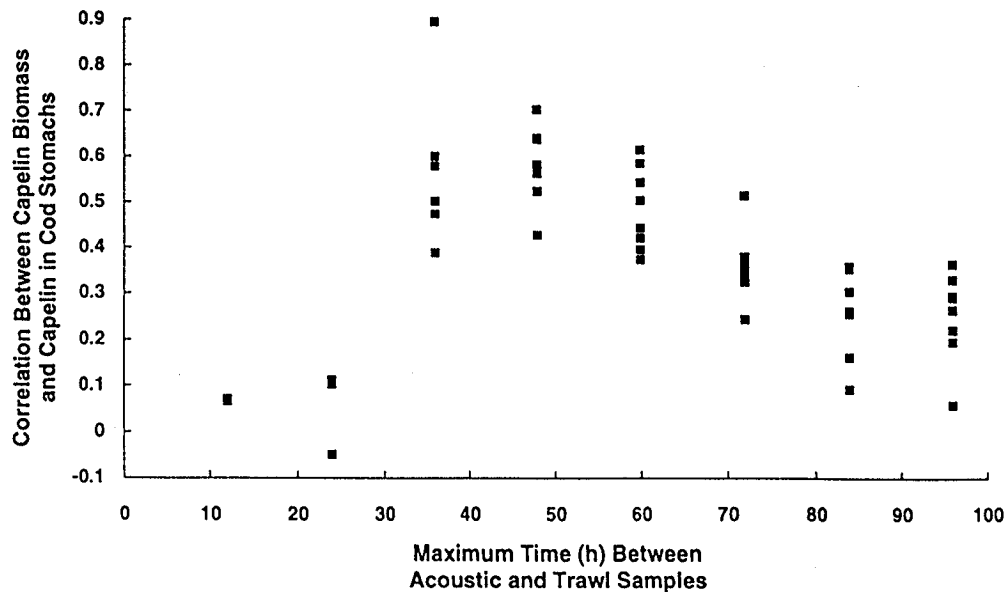

FIG. 3. Correlations between amount of capelin in cod stomachs, ln(F + 1), and capelin biomass as estimated in the acoustic survey, ln(biomass + 1), versus the number of pairs in the sample. The number of pairs is large when maximum time difference and maximum distance permitted between the stomach and acoustic points are large. Only correlations with five or more pairs are plotted.

FIG. 4. Correlations between amount of capelin in cod stomachs, ln(F + 1), and capelin biomass as estimated in the acoustic survey, ln(biomass + 1) versus maximum time difference permited between the stomach and acoustic points.
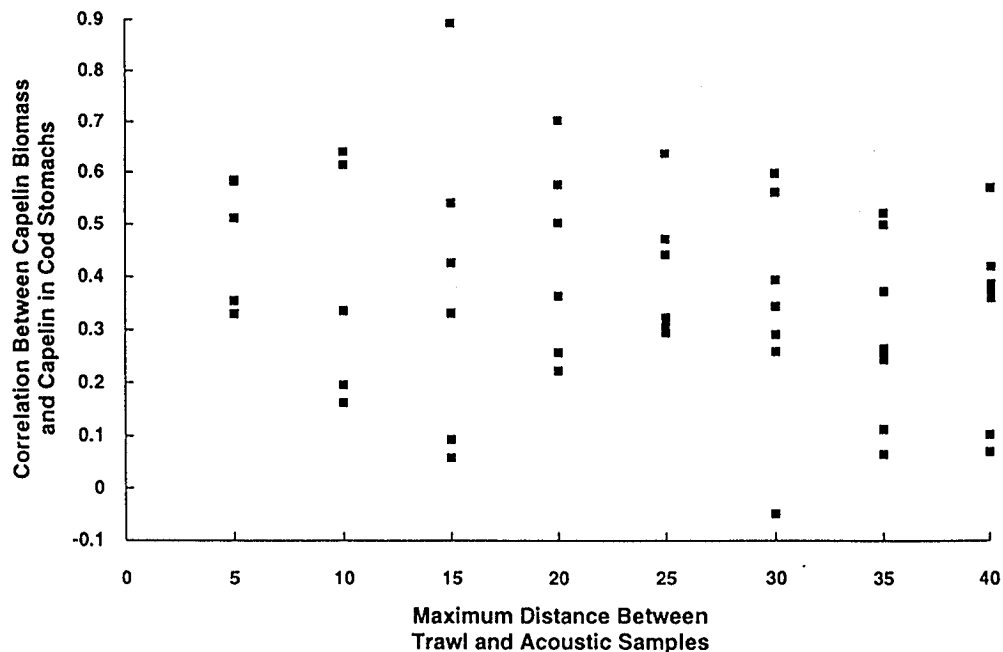

FIG. 5. Correlations between amount of capelin in cod stomachs, ln(F + 1), and capelin biomass as estimated in the acoustic survey, ln(biomass + 1), versus maximum distance permitted between the stomach and acoustic points.

between the stomach sample and acoustic sample is shown in Fig. 5. A relationship with distance is not apparent. For the remainder of the analyses, we restricted the data to those with a time difference maximum of 48 h and a distance maximum of 40 km (to maximize the size of the dataset); this leaves 46 pairs of stomach content and biomass points. None of the points from 1986 met the time difference criterion.

Analyses

From the correlations, there is strong evidence that the amount of capelin found in cod stomachs is an indicator of the

biomass of capelin in the area around the cod sampling point. The purpose of further analyses was to determine whether the amount of capelin in cod stomachs can be used to predict capelin biomass in the environment. An obvious approach to this would be to build a statistical model with ln(capelin biomass) as the dependent variable and ln(stomach content) as the independent variable. However, from a biological point of view, it is more reasonable to reverse the independent and dependent variables; the amount of capelin in cod stomachs is a function of capelin biomass in the environment, not the reverse. Furthermore, there are several factors that might affect the degree to which stomach contents reflect the local biomass. First, the

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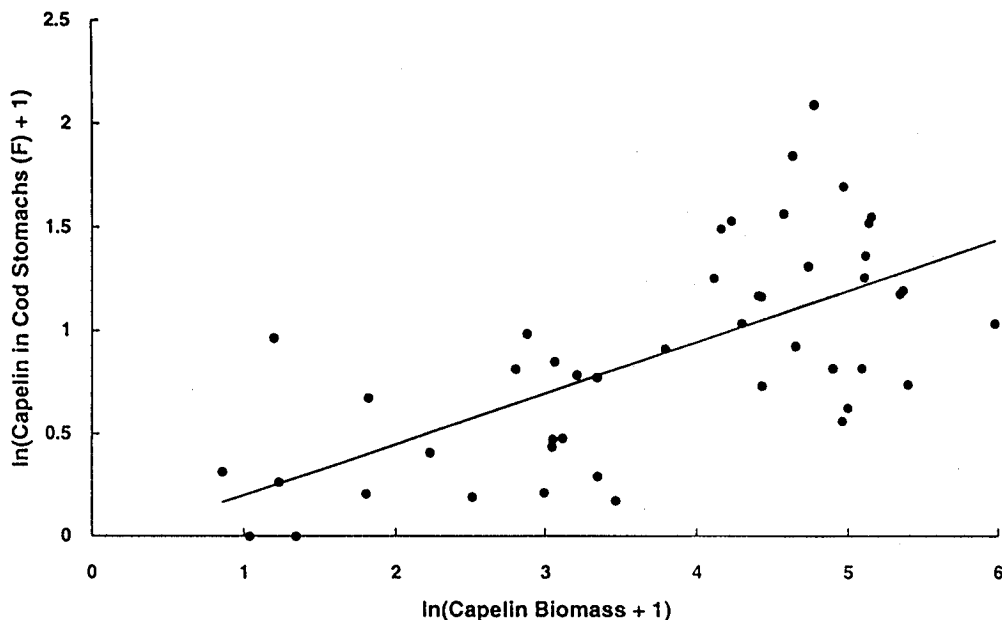*Can. J. Fish. Aquat. Sci., Vol. 50, 1993*

FIG. 6. Capelin content in cod stomachs, $\ln(F + 1)$, versus capelin biomass, $\ln(\text{biomass} + 1)$. Maximum time difference and maximum distance permitted between the stomach and acoustic points were 48 h and 40 km, respectively.

density of cod in the local area may affect the availability of prey to individual cod. Second, if cod switch to other prey when capelin are less abundant, we would expect to find a negative relationship between the amount of other food in cod stomachs and the amount of capelin in cod stomachs. Third, since capelin are pelagic and cod are primarily bottom-dwelling, we might expect a negative relationship between bottom depth and the amount of capelin in cod stomachs; the deeper the bottom, the smaller the vertical overlap between the two species. Our approach was to build a model to pedict stomach contents from these variables; the resulting equation can be rearranged to predict local capelin biomass.

A simple regression analysis of $\ln$(capelin in cod stomachs $+ 1$) on $\ln$(capelin biomass $+ 1$) (Fig. 6) indicated that the relationship is highly significant ($p < 0.0001$; $R^2 = 0.44$). We then used multiple regression analysis to test for the effects of the other factors (above) on the amount of capelin in cod stomachs. The independent variables were: (i) $\ln$(capelin biomass $+ 1$), (ii) local cod density using number of cod in the 36–71 cm length group in the trawl sample (log transformed; Fig. 7), (iii) amount of all other prey in cod stomachs, F_{oth} (log-transformed; Fig. 8), and (iv) bottom depth. F_{oth} is calculated in the same way as F (equation 1), but W_j is replaced with W_{oth}, the weight of all prey items other than capelin. Only bottom depth had a significant additional effect on amount of capelin in cod stomachs ($p = 0.02$); the R^2 value for the regression increased to 0.51. The analysis of variance and parameter estimates are given in Table 1.

Discussion

The results of this study indicate that, at least for this system, the cod stomach can be used as a sampling tool for the distribution (local biomass) of capelin. The results are particularly encouraging because they indicate a strong relationship even though the estimates from both surveys are known to be highly variable (Nakashima 1981; Carscadden et al. 1989; G. Lilly
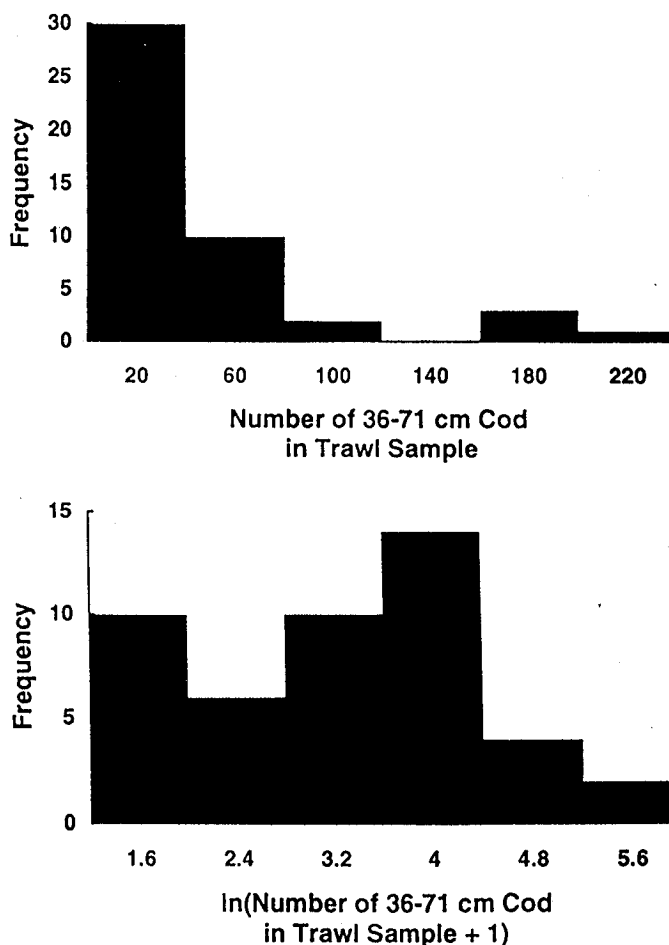

FIG. 7. Frequency histograms of number of cod in the trawl sample in the 36–71 cm length group and $\ln$(number of cod $+ 1$). Data shown are the 46 points used in the analyses, i.e., maximum time difference and maximum distance permitted between the stomach and acoustic points were 48 h and 40 km, respectively.

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FIG. 8. Frequency histograms of amount of food other than capelin in cod stomachs (F_{oth}; see text) and $\ln(F_{oth} + 1)$. Data shown are the 46 points used in the analyses, i.e., maximum time difference and maximum distance permitted between the stomach and acoustic points were 48 h and 40 km, respectively.
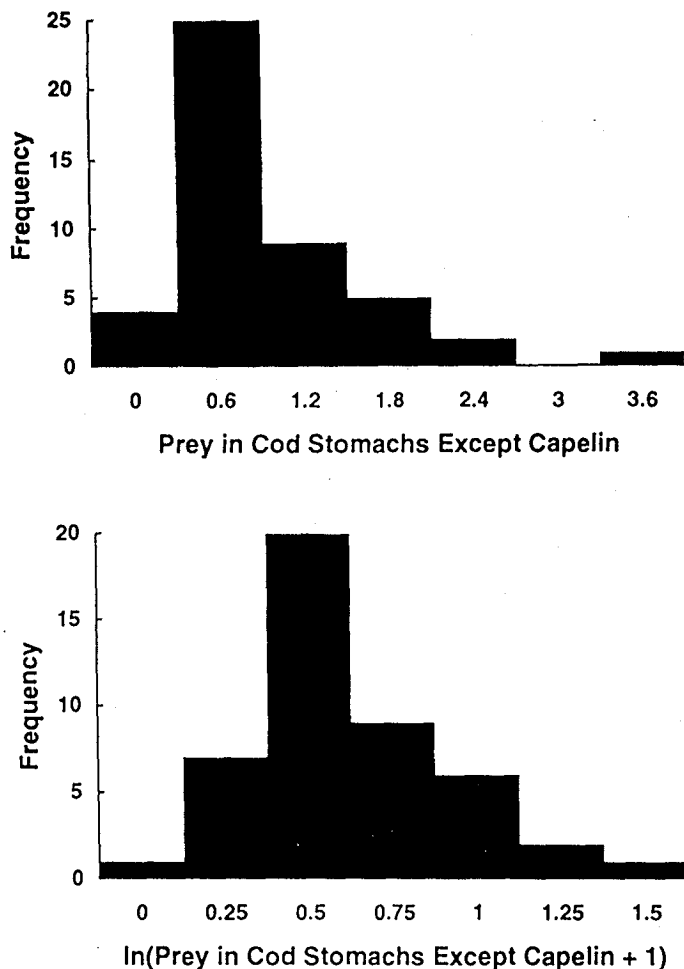
unpublished data), the two surveys were not perfectly coincident in space and time, and the dataset was small ($n = 46$ over 4 years and an area of approximately 70 000 km²). Presumably, the relationship would be stronger if an extensive coincident dataset were available.

The model developed here should be viewed as preliminary. If it were used to predict capelin distributions in places and times for which no other capelin estimates are available, the distributions would be very approximate since there remains a large amount of unexplained variability (approximately half). Furthermore, we did not have sufficient data to test for consistency of the relationship over space and/or time; the data were not randomly selected within years because the subset of the original data that could be used depended on the tracks of the trawling and acoustic ships. To build a more precise model would require an extensive dataset of coincident stomach samples and independent capelin biomass estimates over a broad range of prey density, predator density, depth, and availability of alternative prey.

It is possible that an effect of cod density on stomach content would have been found if weights of the cod were available, thus permitting an analysis in which cod biomass rather than cod number was used. However, given the strong correlation

TABLE 1. Results of multiple regression analysis with ln(amount of capelin in cod stomachs + 1) as dependent variable and ln(capelin biomass + 1) and bottom depth as independent variables.

Source	Type III SS	Estimate	Prob. Type I error
Intercept	—	0.225	0.2559
ln(capelin biomass + 1)	6.01	0.282	0.0001
Bottom depth	0.79	−0.002	0.0201

between cod weight and cod length, we feel that this is not an important drawback in the analysis.

The lack of evidence of prey switching is consistent with results of Lilly (1991) for the northern two thirds of the Northern cod-stock area (NAFO divisions 2J and 3K) in autumn surveys. Lilly (1991) found that over the years 1978–86 the total stomach fullness index (all prey species combined) varied between approximately 1 and 2.5. However, the portion of the stomach contents made up of the various species other than capelin was not related to the overall stomach fullness index. The variability in amount eaten was due entirely to variability in the amount of capelin eaten, indicating that the cod did not switch to other prey when capelin were less available.

We conclude that capelin distribution can be estimated from capelin occurrence in cod stomachs on the northwestern portion of the Grand Bank. It is tempting to think that one could use stomach data for the further purpose of estimating the overall biomass of the prey stock. This would only be true for cases in which the survey area for the predator covers the entire stock area of the prey.

The same approach could be used for other systems. The initial data requirements to build the statistical model are extensive, since simultaneous stomach samples and independent biomass estimates of the prey are required. However, once the model is constructed, it allows estimation of prey distribution in places and times for which there is no direct survey of the prey.

Acknowledgments

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