Abstract—The number of pelagic fish eggs (cod and cunner) found in stomachs of capelin (*Mallotus villosus*) sampled in coastal Newfoundland was used to estimate the encounter rates between capelin and prey, and thus the effective volume swept by capelin. Fish eggs were found in 4–8% of capelin stomachs, represented an average of 1% of prey by numbers, and their abundance increased as relative stomach fullness decreased. The average number of eggs per stomach doubled for each 5-cm increase in length of capelin. The effective volume swept for eggs by capelin ranged from 0.04 to 0.84 m^3/h—a rate that implies either very slow capelin swimming speeds (<1 cm/s) or that fish eggs are not strongly selected as prey. The predation rate estimated from stomach contents was higher than that predicted from laboratory studies of feeding pelagic fish and lower than that predicted by a simple foraging model. It remains uncertain whether capelin play an important regulatory role in the dynamics of early life stages of other fish.

Estimating the encounter rate of Atlantic capelin (*Mallotus villosus*) with fish eggs, based on stomach content analysis

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Capelin (*Mallotus villosus* (Müller, 1776)) is a key species in Arctic ecosystems, serving as a major prey for top predators, from fish to birds and whales (Akenhead et al., 1982; Gjøsæter, 1998; Vilhjálmsson, 2002). Off the coast of Newfoundland and Labrador (eastern Canada), capelin are also the dominant consumers of secondary production (O'Driscoll et al., 2001), as they are in other ecosystems (Skjoldal and Rey, 1989; Hassel et al., 1991). They feed on a wide variety of zooplankton taxa, copepods and euphausiids being the dominant prey (Vésin et al., 1981; Panasenko[1]; Huse and Toresen, 1996; Assthorsson and Gislason, 1997; O'Driscoll et al., 2001). The choice of prey shows some degree of size-dependency; copepod size increases with increasing size of capelin, and euphausiids become more frequent prey items as fish size increases. In most studies of the feeding habits of capelin, fish eggs and larvae have been found to have been eaten by capelin, although these prey types generally represent a minor portion of the diet, occurring in less than 5% of stomachs (Huse and Toresen, 1996; O'Driscoll et al., 2001). Because capelin are dominant consumers of zooplankton in many of the ecosystems in which they are present, their overall impact on the survival of pelagic fish eggs and larvae may be significant depending on their encounter rates with these fish eggs and larvae.

There is evidence that capelin can have a significant impact on the survival of ichthyoplankton through predation on pelagic fish eggs and larvae. In a series of patch studies, Pepin et al. (2002) found that the mortality rate of radiated shanny (*Ulvaria subbifurcata*, Storer 1839) larvae increased in direct relation to hydroacoustic estimates of capelin abundance; this loss could be attributed to predation by capelin on fish larvae. In a study of two coastal areas, differences in the regional patterns of selective loss of radiated shanny larvae, derived from sequential observations of the distribution of growth rates, were strongly associated with differences in the spatial distribution and abundance of capelin (Baumann et al., 2003; Pepin et al., 2003). However, the overall impact of capelin on fish eggs and larvae has been difficult to estimate (Paradis and Pepin, 2001). Much of the basic foraging ecology is unknown (e.g., predator's reactive distance, behavior of both predator and prey, and selection of prey) and laboratory experiments can only provide a rough approximation of encounter rates between capelin and their prey (Paradis et al., 1996).

There have been few studies to provide an estimate of the contribution of predation by planktivorous fish on the overall mortality rates of fish eggs or larvae (Hunter and Kimbrell, 1980; Cowan et al., 1999; Köster and Möllmann, 2000; Munk, 2002; Pepin et al., 2002). Population studies have shown that planktivorous fish can play an important role in regulating the stock-recruitment relationship of other species (Swain and Sinclair,

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[1] Panasenko, L. D. 1984. Feeding of Barents Sea capelin. ICES CM 1984/ H:6, 16 p.

Table 1

Location, average zooplankton density (all organisms), average fish egg density, and number of capelin (*Mallotus villosus*) stomachs collected at each sampling site.

| Site | Latitude | Longitude | Average zooplankton density (/m³) | Average fish egg density (/m³) | No. of stomachs colleccted at each site | | | | | |
					00:01–04:00	04:01–08:00	08:01–12:00	12:01–16:00	16:01–20:00	20:01–24:00
1	47°44′N	53°40′W	1255	0.094	50	45	—	—	—	—
2	48°18′N	53°16′W	319	0.91	35	50	17	30	18	48
3	47°44′N	53°38′W	2766	0.23	—	100	22	—	—	—
4	48°02′N	53°36′W	210	0.29	99	50	99	50	9	49
5	48°19′N	53°15′W	3096	0.58	51	49	44	49	49	47

2000; Köster et al., 2001; Garrison et al., 2002). Individual-based models have often served as a tool to infer the potential effect of predators on early life stages (Cowan et al., 1999; Paradis et al., 1999; Werner et al., 2001) where the likelihood of a prey being eaten by a predator is the product of the probabilities of encounter, attack, and capture. Although the latter two components of the predation process have been estimated in the laboratory for a number of species (see Paradis et al., 1996, for a review), encounter rates are often modeled as the product of predator's swimming speed and reactive distance with limited substantive data to support the overall estimate. Furthermore, encounter rates are assumed to occur randomly and thus follow a Poisson distribution; yet there have been few attempts to validate this assumption (but see Huse and Toresen, 2000). Given that encounter rates represent a key parameter required to estimate the potential impact of predators on early life stages, it is surprising that knowledge of this element in the field is so limited.

The goal of the present study was to estimate effective encounter rates of adult capelin with fish eggs and larvae in coastal Newfoundland. The approach was to obtain a high number of specimens from a series of intensive diurnal collections to provide an accurate estimate of the probability distribution of prey numbers from which encounter rates could be derived. The primary focus of this analysis was on the presence and frequency of occurrence of fish eggs as prey for capelin, because they persist longer in stomachs than do fish larvae (Hunter and Kimbrell, 1980; Folkvord, 1993). I used estimates of prey availability from plankton samples combined with the frequency of occurrence of eggs in stomachs, in relation to the size of capelin and time of day, to estimate effective encounter rates (volume searched) by capelin. Fish eggs are well suited to this objective: they are completely passive and thus the probabilities of their avoidance of both plankton nets and predators can be considered as nil. It is thus possible to measure accurately their abundance in the field, given appropriate choice of mesh size, and their numbers in predator stomachs can provide a measure of the effective volume searched, which is the product of the probabilities of encounter and attack.

Materials and methods

The study was conducted in Trinity Bay, Newfoundland, Canada, between 17 and 31 July 2000, as part of a larger program dealing with the dynamics of ichthyoplankton (Baumann et al., 2003). Five sites were selected at which to conduct diurnal sampling of capelin based on the observation of high juvenile and adult capelin densities from hydroacoustic returns. Sampling was conducted within a 3-km radius of each site and at 4-hour intervals over a single twenty-four hour interval. Each site was treated as an independent observation of the diurnal feeding patterns of capelin. As a result of poor catches, sampling was stopped after two sampling periods at the two sites located at the head of the bay (Table 1).

Capelin were sampled using an international young gadoids pelagic trawl (IYGPT) mid-water-trawl towed in a single oblique haul from the surface to a 100-m depth. Each tow lasted approximately 30 minutes. Up to 50 juvenile and adult capelin were taken at random from the catch. When capelin were highly numerous, sample size was increased to 100. For each specimen, total length (TL) was measured to the nearest mm, the entire intestinal tract was removed by cutting the oesophagus as close to the mouth as possible, and the tract was then preserved in individual numbered vials containing 5% formaldehyde. A total of 1052 specimens were obtained from these collections. After each trawl haul, a plankton sample was taken by using a 60-cm bongo net (fitted with 333-ìm mesh net and flowmeters) towed obliquely from the surface to 100 m along the same path as the mid-water-trawl, and the sample was preserved in 2% formaldehyde solution.

Stomachs were processed by slitting them open and scraping out the contents onto preweighed aluminium weight boat. The contents were blotted dry to remove all excess liquid and weighed to the nearest 0.01 mg by using a Cahn microbalance. Stomach contents from each capelin specimen were placed into individual petri dishes and examined for the presence, number, and taxonomic identification of pelagic fish eggs only. An egg was counted only when the specimen was complete and

the chorion was relatively intact. The presence of empty chorions was noted but these were not included in the analysis because of their potentially longer residence time in the stomach of predators (Hunter and Kimbrell, 1980). As it turned out, empty chorions occurred in less than 2% of capelin with fish eggs present in their gut. For every fifth capelin specimen, all prey items were identified according to broad taxonomic groups: Copepoda, Amphipoda, Euphausia, Pteropoda, molluscan veligers, brachyuran zoeae, Larvaecea, Cladocera, Chaetognatha, Isopoda, and fish eggs and larvae. The number of individuals was determined for each taxonomic group from the entire stomach content and the total weight for each group was determined to the nearest μg by using a Cahn microbalance. This protocol was followed to provide a complete assessment of the presence of fish eggs in the gut and to provide a representative assessment of the patterns of prey composition from each site to confirm that general feeding patterns were consistent with results from previous studies. O'Driscoll et al. (2001) had performed a detailed analysis of feeding patterns of capelin in Newfoundland waters and I perceived no need or advantage in repeating the work. The complete analysis of stomach contents was performed on 218 capelin specimens.

All fish eggs and larvae were sorted from plankton samples and identified to the lowest taxonomic level possible. Because of difficulties in differentiating early developmental stages of two species groups, eggs were lumped into either of two groups: 1) CHW (namely, cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and witch flounder (*Glyptocephalus cynoglossus* L.) or 2) CYT (cunner (*Tautogolabrus adspersus* L.), yellowtail flounder (*Limanda ferruginea*, Storer 1839)). Eggs were most likely those of cod, for the CHW category, and cunner, for the CYT category because only larvae of those species were found in other elements of the research program. A subsample of other zooplankton, yielding 200–300 specimens, was identified to the lowest taxonimic level possible.

For each capelin, the total gut fullness index (GFI) was estimated as $GFI=W_s/W$, where W_s=the weight of stomach contents (g); and W=is the weight of the fish (g), based on the local bias-corrected length-weight relationship ($\log_{10} W=-6.44+3.38 \log_{10} TL$, where W=weight in g and T=total length in mm; r^2=0.98; and the standard error of the intercept and slope are 0.049 and 0.023; Mowbray[2]).

Analysis

Stomach content composition

For each capelin on which the full stomach contents were analyzed, the number of each major prey taxon

was determined. These data, arcsine-square-root transformed, were contrasted using principal component analysis in which the proportion of prey type, log-transformed capelin length and GFI were included to determine if the observations from this study were consistent with those from previous ones.

Frequency of fish eggs

The probability distribution of egg numbers per gut was contrasted with the expectations based on a Poisson process. Encounters between predator and prey can be described by using a modification of Gerritsen and Strickler's (1977) equations where

$$\lambda = \pi \cdot R^2 \cdot A_{prey} \cdot \sqrt{u^2 + v^2}, \qquad (1)$$

where R = the reactive distance (m);
A_{prey} = the density of prey (/m³); and
u and v = the swimming speeds of predator and prey (m/h), which yields an encounter rate λ (per h).

Huse and Toresen (2000) used laboratory estimates of the various parameters to estimate encounter rates between juvenile herring (*Clupea harengus* L.) and capelin larvae. Instead of using their approach, I chose to reduce Equation 1 to its simplest form, such that

$$\lambda = K \cdot A_{prey}, \qquad (2)$$

where K = the effective volume swept (m³/h) during the period during which eggs will remain discernible in the gut of capelin; and
A_{prey} = the observed density of eggs (/m³) in the water column from plankton samples.

The resulting probability of finding N prey in the gut of capelin then becomes

$$P(N) = \frac{\lambda^N}{N!} \cdot e^{-\lambda}, \qquad (3)$$

where λ = the mean encounter rate.

Mean number of eggs per stomach (N), taken as a measure of encounter rates for each four-hour sampling interval, was estimated by fitting a generalized linear model with Poisson error structure using a log link function by maximum likelihood (GENMOD procedure, vers. 8, SAS Inc., Cary, NC) to the data from all 4-hour sampling intervals (T) from all locations, with TL of individual capelin as a linear covariate.

$$f(N) = b_0 + b_1 T + b_2 TL. \qquad (4)$$

The value of N reported in the "Results" section is the least squares adjusted mean, which represents the value of the average length of capelin from field collections. We attempted to include site into the analysis but the

algorithm failed to converge because of missing observations. Effective volume swept (K) was calculated from the estimated mean number of eggs per stomach (as a measure of encounter rates) and the estimated density of eggs based on plankton samples by re-arranging Equation 2 and assuming that encounters between prey and predators were random over the top 100 m of the water column. I define K as the effective volume swept because it implicitly includes some measure of the probabilities of attack and capture. Values of the estimated volume swept were corrected for evacuation rates. Hunter and Kimbrell (1980) found that the evacuation rate of northern anchovy (*Engraulis mordax*, Girard 1854) feeding on fish eggs at 15°C was ~50%/h based on an exponential model (exponential rate of 0.7/h), which is appropriate for microphagic fish (Temming et al., 2002). Based on the duration of our tow and the handling time to process the samples, the observations of stomach content from this study represent 50% of the eggs consumed during the last hour before capture. Hunter and Kimbrell's (1980) estimate of the evacuation rate is approximately twice that obtained in field studies by Arrhenius and Hansson (1994) and Darbyson et al. (2003) for herring (*C. harengus* L.) feeding primarily on copepods. However, the estimates from the latter two studies were based on total gut fullness and not on the disappearance of specific food items, such as fish eggs. As a result, Hunter and Kimbrell (1980) provided the only current measure of the rate of disappearance of eggs in the stomachs of planktivorous fish. Increases or decreases in evacuation rates because of inaccuracies in our knowledge of the rate of disappearance of eggs from stomach contents will result in corresponding changes in the estimate of the effective volume swept. By using the mean number of eggs per stomach as an estimator of the effective volume swept, the probabilities of attack and capture within the reactive distance are assumed to be 100%. The resulting value of the effective volume swept represents an average over the top 100 m of the water column, the depth range over which we sampled both capelin and zooplankton and over which I assume that the encounters are random. Ideally, one would want to obtain a depth-stratified measure of stomach contents, and prey availability and overlap between prey and predator, such as has been inferred in the Baltic Sea (Köster and Möllmann 2000; Köster et al. 2001), but this was not possible in the present study because there were insufficient data on the vertical distribution of capelin.

Results

Capelin used in this analysis ranged from 53 to 195 mm TL (mean=122 mm; median=130 mm). Average zooplankton concentrations ranged from 210 to 3096 organisms/m^3. In most samples, the copepods *Calanus finmarchicus* and *Pseudocalanus* sp. and the larvacean *Fritillaria borealis* (Lohmann 1896) represented 60–80% of the zooplankton by number, based on samples
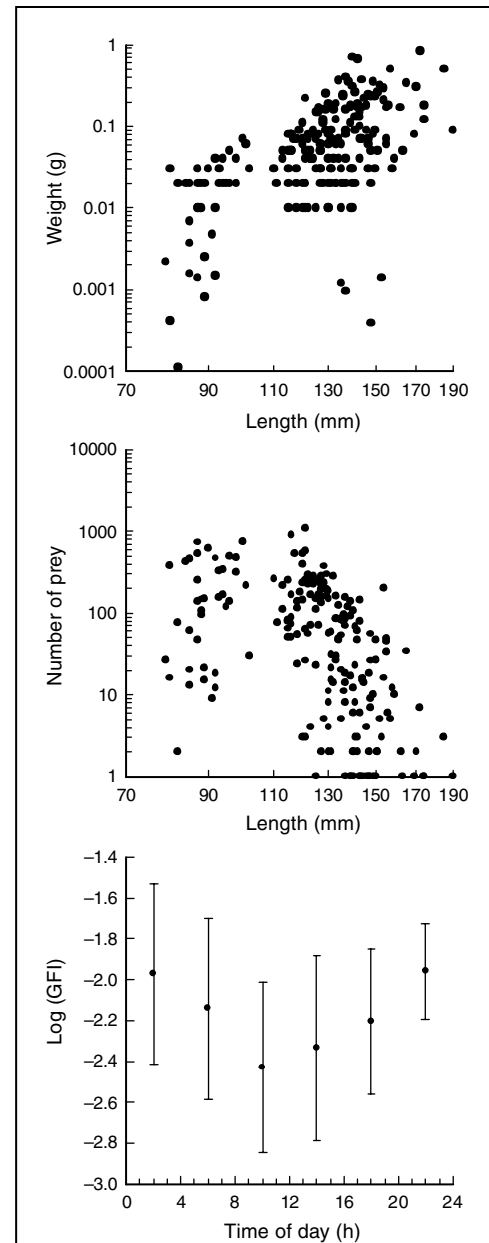

Figure 1

Weight of stomach contents (upper graph) and number of prey per stomach (center graph) in relation to capelin (*Mallotus villosus*) length, for specimens with complete analysis of contents, and average and standard deviation of the log-transformed gut fullness index (GFI) in relation to time of day (lower graph), based on all fish sampled. Statistics were calculated for all samples collected within each 4-hour time interval.

from bongo nets. In both species of copepods, copepodite stages II and III were most abundant. A finer mesh net would have revealed that *Oithoina similis* was also

Table 2

Frequency of occurrence (number of capelin [*Mallotus villosus*] for which complete stomach analysis was performed) and average relative proportion of prey (by number) for the dominant prey categories found in July 2000. The total number of capelin examined for complete stomach analysis was 218. There were 12 fish with empty stomachs.

Prey type	Frequency of occurrence	Relative proportion
Copepoda	176	0.77
Euphausia	50	0.066
Amphipoda	43	0.088
Pteropoda	22	0.010
Larvacea	21	0.032
Cladocera	17	0.022
Fish eggs	16	0.010
Chaetognatha	4	<0.001
Mollusca veliger	3	0.001
Brachyura zoea	2	0.005
Isopoda	1	<0.001

Table 3

Results of the principle components (PC) analysis of proportion of prey categories from capelin stomachs. Values in parentheses along the topmost row represent the proportion of the variance explained by each principle component. Column values represent the average loading of each variable included in the analysis. *GFI*= gut fullness index.

Variables	PC 1 (17%)	PC 2 (12%)	PC 3 (10%)
Ln (*capelin length*)	0.494	−0.068	−0.144
Ln (*GFI*)	0.166	−0.575	0.325
Copepod	−0.598	−0.276	−0.081
Cladocera	−0.035	0.315	0.593
Pteropoda	0.044	−0.131	−0.050
Amphipoda	0.490	−0.017	−0.026
Euphausia	0.330	−0.153	0.122
Cheatognatha	−0.066	−0.083	−0.110
Mollusca	−0.017	0.260	0.550
Isopoda	−0.023	0.003	−0.173
Larvacea	−0.011	0.440	−0.065
Brachyura	0.038	0.280	−0.310
Fish eggs	0.106	0.340	−0.232

numerically important in the area (Pepin and Maillet[3]), but O'Driscoll et al. (2001) did not find this species in any of their stomach samples despite its importance in the regional plankton community. Fish eggs represented an average of 0.13% of the total zooplankton community among all sites sampled (Table 1).

Only 12 of 218 capelin stomachs, for which complete stomach analysis was performed, were found to be empty. The weight of prey in capelin stomachs increased with increasing length but the number of prey decreased with increasing length, indicating that the average size of prey increased with capelin length (Fig. 1). Stomach fullness increased at sunset, peaked shortly after midnight, and then gradually decreased during the remainder of the night and day (Fig. 1). Copepods were the only prey in 73 of the remaining 206 capelin. Euphausiids and amphipods were the next most abundant prey item, found in approximately 25% of capelin stomachs and representing on average 6.5% and 8.8% of prey by number (Table 2). Pteropods, larvaceans, cladocerans and fish eggs were present in approximately 10% of capelin stomachs and represented ~1–3% of prey by numbers (Table 2). Other prey taxa were found in a few capelin stomachs. Principal components analysis showed that the proportion of euphausiids

and amphipods in stomachs increased with capelin length, whereas copepods were more frequent in smaller fish, as indicated by the first principal component (Table 3). Other prey categories, particularly fish eggs and larvaceans, were generally more likely to occur in capelin stomachs when they were relatively empty, as indicated by the second principle component (Table 3). Finally, the third principal component indicated that fish eggs appeared to be less important in areas where mollusks and Cladocera were more frequent in the diet of capelin—a finding that possibly reflects the influence of water masses in which coastal rather than shelf zooplankton were dominant (Table 3). These observations of prey composition were generally consistent with those of O'Driscoll et al. (2001).

When we consider all stomachs analyzed for fish eggs, the overall frequency of occurrence of fish eggs was 4.3% (46 of 1052 stomachs). This is less than the value (7.9% of stomachs with prey) obtained from those stomachs with complete analysis of prey composition. The frequency distribution of fish eggs was well described by a Poisson distribution (Fig. 2). The majority of fish eggs (89%) were of the CHW complex and the remainder (11%) were of the CYT complex. The generalized linear model revealed that there was a significant effect of time of day (Table 4), and the greatest number of fish eggs in capelin stomachs were found between 20:00 and 24:00, following sunset, and the lowest numbers were found between 00:00–04:00 (Fig. 3). There was approximately a 20-fold difference in the least squares

[3] Pepin, P., and G. L. Maillet. 2002. Biological and chemical oceanographic conditions on the Newfoundland Shelf during 2001 with comparisons with earlier observations. Canadian Science Advisory Secretariat, Research Document 2001/073, 60 p. [Available from http://www.dfo-mpo.gc.ca/ csas/ or Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, stn. 12032, Ottawa, Ontario, Canada K1A 0E6.]

Table 4

Analysis of deviance for the effects of time of day and capelin TL with Poisson error based on a generalized linear model. The effect of time of day was based on grouping data into 4-hour classification periods. Probability values were calculated by using a χ^2 function.

Variable	Residual degrees of freedom (df)	Residual deviance	df	Deviance	P
		Difference			
	1052	365.9			
Time of day	1046	321.7	6	44.2	<0.001
Length	1045	317.2	1	4.5	<0.05

Figure 2

Bar chart of the frequency of fish eggs in capelin (*Mallotus villosus*) stomachs for each 4-hour time interval.

Figure 3

Least squares estimates of the mean number of fish eggs per stomach in relation to time of day. Error bars represent 1 standard error.

mean estimate of the number of eggs per stomach over a diurnal cycle. There was a significant and positive effect due to capelin length (χ^2=4.5, P<0.05; Table 4) which would yield a twofold increase in the mean number of eggs per stomachs for each 5-cm increase in capelin length. This finding may indicate that smaller capelin are more effective predators of fish eggs, in terms of body mass, than larger individuals. There were insufficient data to obtain reliable estimates of the diurnal feeding periodicity at each site.

The overall unweighted average density of fish eggs among all sites was $0.52/m^3$ (median=$0.48/m^3$; mean=$0.53/m^3$; SD=$0.43/m^3$; range=0.09–$2.2/m^3$). There were significant differences in the densities of fish eggs among sites (ANOVA $F_{4,21}$=4.56, P<0.01); a Bonferoni *post hoc* comparison revealed that site 2 had significantly higher densities than other sites, with the exception of site 5 (Table 1). However, there was no clear evidence of a diurnal pattern to the density estimates derived from plankton collections. Because there were insufficient data to obtain reliable estimates of the diurnal feeding periodicity at each site and because there was no clear evidence of a diurnal pattern in egg densities estimated from the plankton samples, I chose to use the overall unweighted average density from all collections as the estimate of A_{prey} for Equation 2.

Because it was not possible to obtain a site-specific estimate of diurnal patterns in egg consumption by capelin, the combined data on egg densities were used to estimate the effective volume swept (K). Each estimate of the mean number of eggs per stomach was taken to represent 50% of the eggs ingested in the last hour during each sampling interval (4 h) (see "Methods"). The overall daily average effective volume swept based on mean encounter rates was 0.27 m^3/h, which ranged from 0.04 m^3/h at night (00:00–04:00) to 0.84 m^3/h following sunset (20:00–24:00) (Fig. 4). Based on a reactive distance of 0.15 m (~1 body length) used by Huse and Toresen (2000) (for herring larvae from Utne-Palm, 2000), the effective volume swept estimated from the observations reported in the present study would imply that the
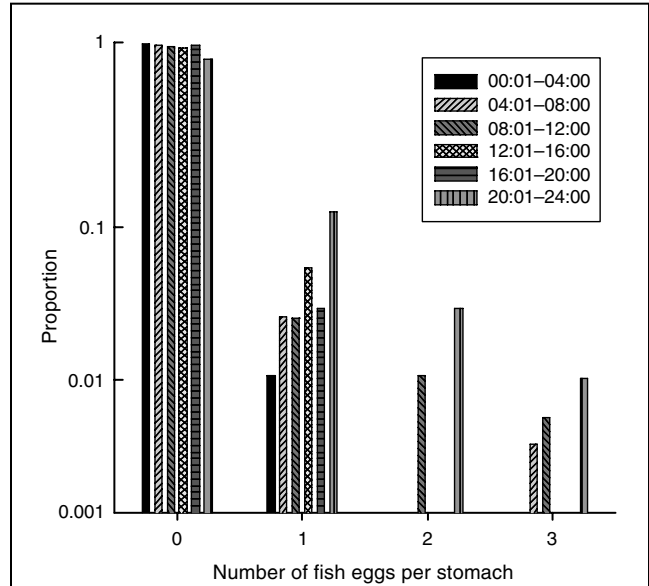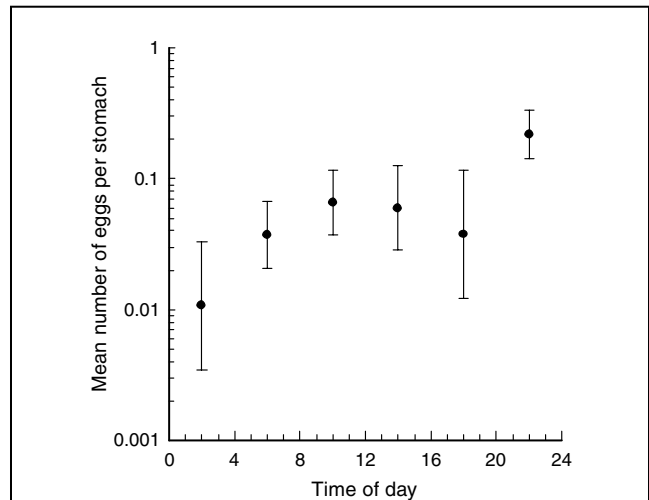
swimming speed of capelin would be very low (≤1 cm/s) or that fish eggs are not strongly selected as prey during feeding. If on the other hand we consider modal capelin (0.13 m) swimming at 0.5–1 body length/s, the reactive distance would range from 0.024–0.034 m at the time of peak foraging activity, assuming 100% probability of attack within the reactive area. To determine the effect of variations in the density of eggs encountered by capelin, I also calculated the variability
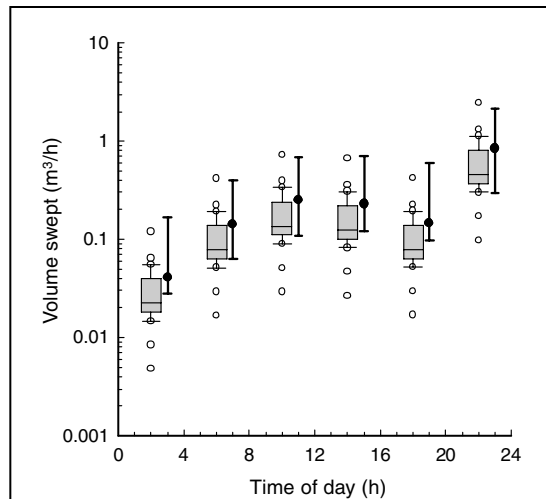
Figure 4

Estimated effective volume swept (K), with ±1 standard error (solid symbols and thick error bars) based on mean number of eggs per stomach and mean density of eggs from plankton collections, in relation to time of day (offset by +1 hour from midpoint of interval). Confidence intervals are based on the maximum likelihood estimates of mean numbers of eggs per capelin stomach. Box plots show the 25th, 50th, and 75th percentiles of the estimated effective volume swept (K) based on the mean number of eggs per stomach and each estimate of egg density based on plankton collections; whiskers show the 10th and 90th percentiles of the distribution and open symbols show the outlying points.

in estimated K using each observation of egg density from the plankton samples. This calculation generally resulted in less variability in the estimate of effective volume swept than the uncertainty in eggs per stomach (Fig. 4, box plots) because of the skewed distribution of egg densities based on plankton tows. The latter reflects the skewed distribution of egg densities based on plankton tows.

Discussion

Capelin prey composition observed in this study is consistent with that observed in previous studies, which show that copepods, euphausiids, and amphipods represent the principal prey items; the overall results of this study may therefore have general applicability. Fish eggs represent a relatively minor part of the diet of capelin. Neither Huse and Toresen (1996) nor Assthorsson and Gislason (1997) reported any occurrence of pelagic fish eggs in the stomachs of capelin from the Barents Sea and waters north of Iceland. O'Driscoll et al. (2001) reported an occurrence of less than 1% in capelin sam-

pled during May–June in inshore waters and during August–September in offshore areas off Newfoundland. In the present study, an occurrence of 4% to 8%, which contributed an average of 1% of prey by numbers, was found for collections in coastal Newfoundland waters during July. There is little basis for explaining the differences between studies because only this analysis provides an estimate of the density of eggs in the water column where capelin were sampled. Fish eggs were approximately 1% of the prey found in the stomachs of capelin but they represented slightly more than 0.1% of the organisms sampled by the plankton nets used in this study. Huse and Toresen (1996) collected plankton data with different gear than that used in the present study, but they did not report the occurrence of pelagic fish eggs in their samples, possibly because pelagic fish eggs were in very low abundance or were absent during the collection periods of their study.

In general, fish eggs were more likely to be found in capelin stomachs as the length of individual fish increased. These fish tend to feed more heavily on larger prey types (e.g., euphausiids and amphipods) but the occurrence of fish eggs in individual fish tended to increase as the relative stomach fullness decreased. When considered with the general pattern in feeding periodicity, fish eggs were more likely to be eaten at the onset of feeding activity shortly after dusk, but as individual fish filled their guts with larger or more numerous prey, feeding on fish eggs tended to decrease. Fish eggs may represent an attractive prey for capelin capable of feeding on larger prey types (e.g., stage V of *C. finmarchicus*, euphausiids, and amphipods) because their weight is comparable to that of large copepods (Darbyson et al., 2003). However, as larger prey types are encountered or as hunger decreases, capelin may become more selective feeders and focus their foraging on energetically more profitable prey. The diurnal pattern of occurrence of fish eggs in capelin stomachs may also reflect differences in the visibility of eggs as a result of changing light levels, as well as predator hunger. Alternatively, the greater number of eggs in stomachs at dusk may reflect increased spatial overlap between predator and prey as capelin move toward the surface in the evening to feed (O'Driscoll et al.[4]).

The effective volume swept by capelin estimated in the present study indicates that the probability that a capelin will attempt to eat a pelagic fish egg is low, because it is highly unlikely that fish will swim at a very slow speed based on an assumed reactive distance. The predation rates based on average densities and encounter rates range from 0.04 to 0.86 egg/h

[4] O'Driscoll R. L., J. T. Anderson, and F. K. Mowbray. 2001b. Abundance and distribution of capelin from an acoustic survey in conjunction with the 1999 pelagic juvenile survey. Capelin in SA2 + Div. 3KL during 1999, Canadian Science Advisory Secretariat Research Document 2001/161. [Available from http://www.dfo-mpo.gc.ca/csas/ or Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, stn. 12032, Ottawa, Ontario, Canada K1A 0E6.]

based on an evacuation rate of 50% of eggs per hour. A low predation rate on fish eggs is not entirely unexpected. The eggs of cunner and cod from our samples had an average diameter of 0.86 and 1.3 mm, whereas the modal length of capelin from our collections was approximately 130 mm, making the eggs ~1% of the predator's body length. Based on Paradis et al.'s (1996) analysis, maximum predation rates by fish feeding on ichthyoplankton occur when the prey are 10% of the predator's length, and the minimum predation rates were observed when prey were ~0.5–1% of the predator's length. Paradis et al.'s (1996) summary equations indicate that an average predation rate of 0.007–0.03 eggs/h would not be inconsistent with laboratory estimates of predation rates for a range of evacuation times from 1 to 4 hours and would be considerably lower than the predation rates estimated in the present study. However, estimates based on a simple foraging model (e.g., Paradis et al., 1999) for a modal capelin swimming at 1 body length/s and with a reactive distance of 1 body length yield a mean of 12 eggs/h, and halving these parameter values yields a predation rate of 1.6 eggs/h. These alternative methods of estimating predation rates indicate that capelin are somewhat more likely to feed on fish eggs in the field than laboratory studies would indicate but less likely than would be anticipated from a simple foraging model. The results from this study do not provide an exhaustive estimate of encounter rates between capelin and pelagic fish eggs, but the range of effective encounter rates derived from the different approaches highlights the lack of understanding of this key parameter essential for any model of multispecies interactions. Such a broad range of expected predation (and encounter) rates indicates that in order to develop predictive skills in estimating the potential impact of planktivores on fish eggs, a better understanding of the factors that prompt a predator to feed on a fish egg is needed. Most laboratory studies dealing with predation by fish on fish eggs and larvae have used single prey and few have provided a measure of the probability of attack (Bailey and Houde, 1989; Paradis et al., 1996). Feeding patterns can be affected by the complexity of the available prey community (Kean-Howie et al., 1988; Gotceitas and Brown, 1993; Pepin and Shears, 1995), but methods to relate prey consumption with prey availability in the field are still limited.

Uncertainty in encounter and predation rates are due partly to errors in the estimation of prey availability and stomach content and partly due to our general lack of knowledge concerning the evacuation rate of fish eggs from predator stomachs. For this study I relied on Hunter and Kimbrell's (1980) observations of evacuation rates for northern anchovy from experiments conducted at 15°C. Water temperatures in Trinity Bay in July 2000 showed considerable variation with depth, ranging from ~13°C at the surface to –1°C at 100 m, with the overall average temperature over the water column being ~3–4°C. Given that most metabolic processes increase by 1.3–2 times over ten degrees Celsius (e.g., Brett and Groves, 1979), evacuation rates in the pres-

ent study could have been half of those measured by Hunter and Kimbrell (1980) and thus would imply that our observations of stomach contents could represent 70% of the eggs consumed in the last hour rather than the 50% assumed in the analysis. The result would be that estimates of volumes swept by capelin would have to be reduced by ~30%, further reducing their potential impact on ichthyoplankton populations. The general uncertainty in our knowledge of evacuation rates for fish eggs from the stomachs of capelin, and from most other planktivorous fish, therefore limits the inferences that can be derived about their impact on ichthyoplankton survival.

A second source of uncertainty is due to the inherent sampling variability associated with the study of elements that form a small fraction of the prey of a predator. This study was based on more than 1000 specimens from a small region in order to provide the greatest accuracy possible within the confines of the study area. Stomach sampling is often restricted to fewer specimens sampled over a much broader geographic range. Without a large number of observations from a local environmental setting (i.e., site), estimates of mean numbers of rare prey types would likely be unable to reflect the effect of site-specific differences in environmental conditions on predator feeding and would thereby increase the uncertainty around the estimated effective encounter rates. The situation is well illustrated by the doubling in the frequency of occurrence of fish eggs in the specimens that were randomly selected for complete gut analysis versus all the specimens collected for analysis. Further uncertainty comes from the variability in estimates of egg density encountered by capelin—a variability that tended to result in slightly tighter confidence intervals in estimates of effective volume swept than the uncertainty due to variability in the number of prey per predator stomach. Variations in egg densities from plankton samples did result in lower estimates of effective volume swept, partly as a result of the rare high densities (typical of highly skewed distribution) that characterize the variability in plankton catches (Power and Moser, 1999). Although this study is not intended to provide a general estimate of the effective encounter rate of capelin feeding on fish eggs, the approach provides a useful example of the sampling requirements for the study of feeding on prey that are a minor part of the diet of a predator but which may be greatly affected by the predator's impact on the prey population.

Greater efforts must be directed at understanding patterns of predation in the field, in relation to prey availability, if the role of planktivorous fish in ichthyoplankton dynamics is to be understood. The assumptions in the estimation approach could affect the effective volume swept: estimates of the effective volume swept are based on average prey densities integrated over the water column, and the simplification of the encounter model (Eq. 1) incorporates possible variations in the probability of attack (e.g., due to diurnal variations in visibility of eggs) into the value of K. Pepin et

al. (2005) noted that in the study region, pelagic fish eggs are generally more abundant near the surface and decrease exponentially in abundance with increasing depth. As a result, if feeding by capelin occurs predominantly in surface waters, the effective density of prey encountered would be greater than the average density over the water column, which would in turn decrease the estimate of the effective volume swept based on our estimates of encounter rates. However, the patterns of vertical distribution of both eggs (Pepin et al., 2005) and capelin (O'Driscoll et al., 2001) are highly variable among sites and without accurate estimates of these elements from the current study, inferences about the impact on estimates of the effective volume swept would be speculative. In contrast, I implicitly incorporated the probability of attack into the estimate of the effective volume search, essentially giving it a value of 100%. However, Wieland and Köster (1996) found that the visibility of eggs increased with developmental stage and hence may alter the probability of attack by a predator. Lower visibility of early stage eggs could lead to an increase in the estimate of the effective volume swept, but because we could not stage most eggs sampled from the stomachs, the net effect on the estimated volume swept is unclear.

Planktivorous fish represent important forage for piscivores in several marine ecosystems but they can also play a significant role as predators of early life stages. In the Baltic Sea, spratt (*Sprattus sprattus* L.) feed extensively on cod eggs (Köster and Möllmann, 2000) and they may play an important role in regulating the underlying form of the stock-recruitment relationship (Köster et al., 2001). In upwelling systems, anchovies and sardines may also have a significant impact on egg and larval mortality rates (Smith et al., 1989). It has also been suggested that herring (*C. harengus* L.) and mackerel (*Scomber scombrus* L.) predation on ichtyplankton may play an important role in fish population dynamics in the Gulf of St. Lawrence (Swain and Sinclair, 2000) and on Georges Bank (Garrison et al., 2002). However it is unclear whether capelin play a significant role in the fish community dynamics in the ecosystems they inhabit, despite evidence that they are likely to have a significant impact on zooplankton abundance (Vésin et al., 1981; Akenhead et al., 1982; Skjoldal and Rey, 1989; Hassel et al., 1991). Clupeids, scombrids and engraulids can alternate between filter- and particulate-feeding modes, which may allow them to more effectively consume relatively small prey (~1 mm), such as fish eggs. There is no information on the feeding modes of capelin, but another osmerid, rainbow smelt (*Osmerus mordax*, Mitchill 1814), is known to be a primarily particulate feeder (Mills et al., 1995). Particulate feeding is generally directed toward larger prey, whereas filter feeding is used when prey are smaller or more abundant. Gill raker structure does not provide significant insight into the possible feeding modes of these various planktivorous fish. The estimate of reactive distance from the present study (0.024–0.034 m) is of the same order as the gape width of capelin (3.6% for TL; Pepin, unpubl. data), making filter feeding a distinctly possible mode of feeding. For known filter feeders, Uotani (1985) reported a maximum gill raker length of 6 mm in *Engraulis japonicus* (100 mm TL), Gibson (1988) reported an average gill raker length of 4 mm in *Clupea harengus* (150 mm TL), and Molina et al. (1996) reported gill raker lengths ranging from 5 to 9 mm in *Scomber japonicus* (150–250 mm SL). On the other hand, Lecomte and Dodson (2004) reported gill raker lengths of 3.3–3.9 mm in *Osmerus mordax* (150 mm TL). In the case of capelin, I found that gill rakers ranged from 3.0–4.5 mm in length (130–170 mm TL) (Pepin, unpubl. data). Inter-raker gaps among all these species ranges from 0.19 mm (*E. japonicus*) to 0.4 mm (*S. japonicus*) and from 0.36 to 0.45 mm in capelin (Pepin, unpubl. data). Thus all these species, which feed extensively on zooplankton but which use different ingestion modes, are equipped with gill rakers designed to retain small particles. To better understand the role of capelin in Arctic ecosystems, a greater knowledge of feeding will be required. If filter feeding is a dominant feeding mode, a simple filtration or volume-swept model may provide an accurate measure of the potential impact of capelin on fish eggs, whereas greater knowledge of behavior and selectivity will be required if particulate feeding is the dominant feeding mode because selection for or against fish eggs could be influenced by availability of alternate prey (e.g., Kean-Howie et al., 1988).

In most of the areas where planktivores can have a significant impact on the mortality of fish eggs, the ecosystems can be characterized as being "wasp-waisted" (Cury et al., 2000), i.e, as having a relatively high diversity of plankton species and top predators that are all influenced by the abundance and productivity of relatively few and dominant forage fish species that act to transfer energy from secondary producers to upper trophic levels in a manner similar to that found in many Arctic regions. It is clear that capelin are important prey for a number of top predators in the waters of the Barents Sea (Gjøsæter, 1998), Iceland (Vilhjálmsson, 2002), and on the Newfoundland and Labrador coast (Akenhead et al., 1982), and they may also have an important impact on the plankton community (Skjoldal and Rey, 1989; Hassel et al., 1991). What remains uncertain is whether they play an important regulatory role in the dynamics of the early life stages of fish. Observations from this study revealed that the highest occurrence of fish eggs in the stomachs of capelin came from capelin near one of the few remaining major spawning aggregations of the northern cod stock (Rose, 2003). The dynamics of such circular prey-predator interactions need to be studied further in order to understand their potential importance to population regulation (Walters and Kitchell, 2001) but to do so will require consideration of the spatial and temporal patterns of predator-prey interactions if predictive relationships are to be derived (Pepin et al., 2002, 2003; Baumann et al., 2003).

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