

# Do bigger fish arrive and spawn at the spawning grounds before smaller fish: Cod (*Gadus morhua*) predation on beach spawning capelin (*Mallotus villosus*) from coastal Newfoundland

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## Abstract

A relationship between body size and time of spawning has often been described for both pelagic and non-pelagic fish species that migrate for the purpose of spawning. The present study investigates this relationship for capelin (*Mallotus villosus*), a pelagic smelt-like species that spawns on the beaches of Newfoundland. Simple linear regressions were carried out separately for three groups of capelin: ovid females, spent females and males in three successive years (1982–1984). Bigger fish arrived near the spawning grounds first, for all three groups in all three years and was most obvious for female capelin. Analyses of stomach contents of Atlantic cod (*Gadus morhua*), an important predator of capelin in the Newfoundland area, showed a similar decrease in mean size of capelin throughout the capelin spawning season in June, July and August. Furthermore, analyses strongly suggest that early in the spawning seasons, when capelin abundance was high, cod selected for bigger capelin, whereas towards the end of the spawning seasons, when capelin abundance was low, cod did not show any size preference.

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## 1. Introduction

Migration is a common feature of many pelagic and demersal fish species that move between nursery areas, spawning and feeding sites (Harden-Jones, 1968; Secor, 1999). Migration routes, timing of migration and other features of migration are highly variable and often species specific. Some species segregate by size (Templeman, 1948; Libby, 1982; Nakashima, 1983; Rose, 1993) or sex (Morgan and Trippel, 1996) when migrating, other species have large individuals leading the migration that act as scouts (Rose, 1993). Immature fish can follow mature

fish in a dummy-run (Harden-Jones, 1968) or can remain at the feeding grounds (Nakashima, 1992; Shackell et al., 1994a).

Associated with these migrations for some non-pelagic species is a relationship between time of spawning and body size. The spawning season starts later and ends earlier for small sand smelt (*Atherina boyeri*) (Tomasini et al., 1996) and mummichog (*Fundulus heteroclitus*) (Kneib, 1986) relative to larger individuals. Similarly, large Norwegian and Icelandic Atlantic cod (*Gadus morhua*) arrived on the spawning grounds first (Harden-Jones, 1968; Thorsteinsson and Marteinsdottir, 1998), while the size of the females was positively associated with the duration of spawning (Harden-Jones, 1968; Hutchings and Myers, 1993; Thorsteinsson and Marteinsdottir, 1998).

A relationship between body size and time of spawning has also been observed in many pelagic species that migrate for the purposes of spawning. Spawning by Pacific (*Clupea*

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*palasii*) and Atlantic (Norwegian and Gulf of St Lawrence) herring (*Clupea harengus*) occurs as a series of waves (5–6 days with 8–26 day intervals) with larger repeat spawners arriving first at the spawning grounds, followed by smaller younger individuals and finally recruit or first time spawners (Lambert, 1987; Lambert and Messieh, 1989; Ware and Tanasichuk, 1989). The number and intensity of waves thus reflects the size and age structure of the mature population (Lambert, 1987). A similar pattern was observed for Baltic herring (*Clupea harengus membras*) and Norwegian spring spawning herring (Slotte et al., 2000; Rajasilta et al., 2001). In all these populations males are reported to mature before females. Comparable patterns have been reported for other pelagic fishes. Large Atlantic mackerel (*Scomber scombrus*) (Dawson, 1986) and alewife (*Alosa pseudoharengus*) spawn before smaller individuals (Kissil, 1974; Libby, 1982; cited in Collette and Klein-MacPhee, 2002). Large Arctic char (*Salvelinus alpinus*) (Dempson and Kristofferson, 1987; Svenning and Gullestad, 2002) and Atlantic salmon (*Salmo salar*) (O'Connell et al., 1992) are the first to arrive near the spawning grounds. For brown trout (*Salmo trutta*) Elliot (1984) found that large females matured earlier in a migratory population, but not in an adjacent resident population, that did not migrate.

Some studies have reported a relationship between body size and time of spawning in capelin (*Mallotus villosus*), but data are often lacking (Atkinson and Carscadden, 1979) or have not been formally evaluated and reported for each sex (Templeman, 1948; Nakashima, 1983; Carscadden et al., 1997). Nonetheless, it is generally accepted that large females spawn first, whereas for males no clear trend was observed (Templeman, 1948; Nakashima, 1983). Capelin is a small pelagic smelt-like schooling species inhabiting Arctic and sub-Arctic zones of the Atlantic and Pacific oceans (Templeman, 1948; Scott and Scott, 1988; Collette and Klein-MacPhee, 2002). During spring, in Newfoundland and Labrador generally in March or April, maturing capelin migrate from offshore feeding grounds (Nakashima, 1992). Newfoundland capelin are, with some exceptions (Carscadden et al., 1989; Nakashima and Wheeler, 2002), primarily beach spawners, with spawning generally taking place in June and July (Templeman, 1948; Therriault et al., 1996; Nakashima and Wheeler, 2002). It is an important forage species for fish, marine mammals and seabirds, especially during the spawning period (Templeman, 1948; Piatt, 1990; Friis-Rødel and Kanneworff, 2002).

Cod (*Gadus morhua*) is an important predator of capelin in the western Atlantic and one of the most important predators in the Newfoundland area (Lilly, 1987; Scott and Scott, 1988; Methven, 1999), both offshore (Minet and Perodou, 1978) and inshore (Methven and Piatt, 1989). During the capelin spawning season, cod are reported to move inshore (Templeman, 1965; Akenhead et al., 1982) and feed almost exclusively on capelin (Lilly and Botta, 1984; Lilly and Osborne, 1984; Methven and Piatt, 1989). Studies have focussed on diet composition and importance of capelin (Daan, 1973; Lilly and Botta, 1984; Lilly and Osborne, 1984; Lilly, 1994; Methven, 1999; Link and Garrison, 2002a,b), on selectivity of cod in relation to predator size (Daan, 1973; Lilly, 1987;

Methven, 1999) and prey abundance (Methven and Piatt, 1989; Methven, 1999), but few have analysed selectivity with respect to prey size (Floeter and Temming, 2003) and sex of prey.

In this study we examine the body size–spawning time relationship in capelin and compare this with capelin removed from stomachs of Atlantic cod, one of the dominant predators of capelin in the Newfoundland area. The objectives of the present study are to (i) characterise the relationship between fish size and spawning time in beach spawning capelin, (ii) investigate how this affects the size of capelin ingested by cod and (iii) compare size composition between capelin collected in traps of the commercial fishery and cod stomachs to determine if cod are selecting for bigger capelin when cod and capelin co-occur inshore during the capelin spawning season in June and July. Analyses were carried out separately for three groups, ovid females, spent females and males, and for three successive years (1982–1984).

## 2. Materials and methods

### 2.1. Trap collections

Capelin were collected during the capelin spawning season by a commercial fisherman, A. Dalton, using a capelin pound trap located at Lance Cove, Cape Broyle Bay Newfoundland (47°05'N, 52°57'W) in June and July 1982–1984. The trap was set perpendicular to and about 10 m from the shoreline in approximately 7 m of water. The trap sampled from the surface to the bottom and was designed and operated as described by Jangaard (1974). Stretch mesh size of the trap was 19.5 mm. Although the sampling was not spatially replicated, the patterns we report likely occur over a larger geographical area, because capelin are known to spawn synchronously over a much wider area (Frank and Leggett, 1981; Nakashima and Winters, 1995; cited in Carscadden et al., 1997).

Samples of approximately 200 capelin were collected usually on alternating days, between 0400 and 1000 h. Capelin were selected from top, middle and bottom layers of fish in the trap boat to ensure selection was not biased by heavier fish sinking to the bottom. Due to the large number of capelin, most samples were frozen and later thawed for examination, however a small number of samples were examined immediately in fresh (unfrozen) condition. Each sample of capelin was sorted to determine the sex composition and proportion of females that were ovid (with eggs) and spent (most eggs gone having already spawned). A sub sample of at least 15 males, 15 ovid and 15 spent females were then selected for measurement of total length (mm, TL) and weight (g). Sex determination was very easy and did not require examination of the gonads. Mature males were distinguished from females by 2–4 rows of modified scales along the lateral line that form a prominent ridge consisting of many tiny fingerlike projections during spawning (Templeman, 1948; Scott and Scott, 1988; Collette and Klein-MacPhee, 2002). Ovid female capelin were distinguished from spent females by the presence of thousands of approximately 1 mm diameter eggs, golden

yellow in colour that noticeably distended the gut cavity prior to spawning. Spent females contained very few if any eggs. The gut cavity of spent females was not distended and often appeared concave.

## 2.2. Stomach collections

Stomachs (1982:  $n = 180$ , 1983:  $n = 182$ , 1984:  $n = 228$ ) were removed and examined from randomly selected Atlantic cod caught at depths between 20 and 100 m at Witless Bay Newfoundland (47°14'N, 52°50'W) approximately weekly from late May to August 1982–1984. Most cod were taken less than 2 km offshore by bottom set gillnets deployed by commercial fishermen, approximately 15 km from where the commercial capelin trap was located. Cod examined in 1984 and occasionally in 1983 were measured (cm fork length, FL) before stomachs were removed. Cod fork lengths ranged from approximately 50 to 70 cm. This allows us to encompass the change in feeding preference with predator size, because this size range is well within the size range of cod that feed on mature capelin (Lilly and Fleming, 1981; Methven, 1999). Floeter and Temming (2003) analysed the size-preference of North Sea cod for fish prey and calculated that cod in the 50–70 cm size range had an optimum preference function for prey in the size range of 22 and 26 cm. Several studies have pointed out that this size of cod feed almost exclusively on capelin, when capelin aggregate near shore off Newfoundland to spawn (Akenhead et al., 1982; Lilly and Botta, 1984; Lilly and Osborne, 1984; Methven and Piatt, 1989). Stomachs were usually examined within 2 h after removal with each food type being identified (Methven and Piatt, 1989). Capelin in relatively undigested condition were measured (mm TL) and when possible sexed. The number of capelin removed from cod stomachs each year (1982:  $n = 173$ , 1983:  $n = 220$ , 1984:  $n = 290$ ) and available for analyses depended on capelin prey meeting three criteria: (i) prey had to be positively identified as capelin (*Mallotus villosus*), (ii) had to be in relatively undigested condition to be sexed and measured accurately and (iii) had to be removed from cod stomachs during the capelin spawning season to allow for comparison with capelin from commercial traps.

## 2.3. Analyses

Linear regression was used to investigate: (i) the relationship between size (dependent variable) and time of capelin spawning to determine if larger capelin arrived at the spawning grounds and spawned prior to smaller capelin, and (ii) if the size of capelin taken from cod stomachs was comparable to capelin from traps of the commercial fishery. Regressions were carried out for each sex and year separately using Minitab Version 13.1 statistical software. As recommended by Freund (1971 cited in Zar, 1999), all size measurements of capelin from each collection were included in the regression analysis rather than using mean size thus limiting loss of information. All tests of significance were done at  $\alpha = 0.05$ .

Length and weight measurements of frozen capelin samples from the commercial trap were corrected for the effects of freezing prior to analyses. Limited information is available on the effects of freezing on body dimensions. Shrinkage of total length was 2.35% in *Mullus barbatus*, 4.01% in *Mullus surmuletus* (Al-Hassan et al., 2000), 6.07% in *Nematalosa nasus* (Al-Hassan et al., 1993), 5.5% in *Barbus luteus* (Al-Hassan and Abdullah, 1992), 2.1% in *Coregonus artedii* and 2.0% in *Perca flavescens* (Engel, 1974). Shrinkage for weight was 2.0% in *Coregonus artedii* and 1.7% in *Perca flavescens* (Engel, 1974). Length and weight data collected from trap capelin that were frozen were adjusted upwards to account for a mean shrinkage of 3.5% and 1.85% observed in length and weight respectively as determined from the literature above. Regression residuals were plotted against predicted values and were examined visually to determine homogeneity of variance and if pattern was evident (Zar, 1999). Frequency histograms of residuals were plotted and examined to determine if residuals were normally distributed.

Capelin from cod stomachs were examined to determine if they were larger or smaller than capelin taken in traps of the commercial fishery using two tailed *t*-tests. Regression equations for capelin caught in pound traps of the commercial fishery were used as a model to generate a hypothesised mean length for capelin at that particular time of the spawning season. This was carried out for each day for which length data on capelin from cod stomachs were available and which fell within the capelin spawning season. For each of these selected days, a *t*-test was used to test for differences between the hypothesised mean and the population mean of the lengths from the stomachs. Analyses were performed for each date and each sex separately following Zar (1999):

$$t = \frac{\bar{X} - \mu}{s_{\bar{X}}}$$

where  $\bar{X}$  is the population mean (of capelin from cod stomachs),  $\mu$  is the hypothesised mean (from regressions of capelin from traps of the commercial fishery),  $s_{\bar{X}}$  is the standard deviation of the population mean.

A comparison of capelin lengths from the trap fishery and from capelin removed from cod stomachs was done using *t*-tests rather than by analysis of covariance for the following reasons: (i) there may or may not always be a time effect on length of capelin taken from traps of the commercial fishery, and (ii) not all the length data on capelin from cod stomachs were collected within the same period as the length data from the trap and, in general, the sampling days of cod stomachs and the trap did not always correspond.

## 3. Results

### 3.1. Trap collections

For all years male capelin were on average larger than females, reflecting well established sexual dimorphism for this species (Table 1). Spent female capelin weighed

approximately 5 g less than ovid females (Table 1). Small capelin were generally present throughout the entire sampling period except for the first 2–4 days in June each year. This was the time when the largest capelin were usually collected (Figs. 1 and 2).

All regressions of capelin length and weight plotted against date of capture had negative slopes for all three years (1982, 1983, 1984) and all groups of capelin (male, ovid, spent) indicating larger capelin arrived and spawned before smaller capelin (Table 1; Figs. 1 and 2). Although some regressions are highly significant, the explained variance in the regressions is generally low (Table 1).  $r$ -Squared values and slopes of length and weight regressions were usually lower for males than females, indicating relationships were stronger for females (Table 1; Figs. 1 and 2). The only exception was the weight regression for 1982, where both the  $r$ -squared value and slope were lower for ovid females than for males (Table 1; Fig. 2). Of the length regressions for male capelin only the one from 1983 is significantly different from a slope of zero.

Significance levels and  $r$ -squared values for weight regressions were generally higher than for length regressions, with exception of 1982 ovid females (Table 1). For this group, no weight data were available for the first sampling day of 1982. For males, the slopes of the weight regressions are steeper than the length regressions, whereas the opposite was observed for the females (Table 1).

Most residuals of regressions from commercial traps were judged to be without pattern, randomly distributed when plotted against predicted values and normally distributed when examined visually as frequency histograms. Exceptions included residuals from regressions of ovid and spent females from the commercial trap fishery in 1984 which showed a  $\sim$  shape pattern for both weight and length when plotted against fitted values. No such patterns were evident for other regressions.

In addition some frequency histograms of residuals tended to be bimodal (length regressions of 1982 ovid females, 1983 males and ovid females) suggesting the presence of two age groups.

### 3.2. Stomach collections

Capelin removed from cod stomachs showed patterns very similar to capelin sampled in traps of the commercial fishery: (i) male capelin were larger than female capelin (Table 2), (ii) slopes of all regressions were negative (with the exception of male capelin from cod stomachs in 1984) and significantly different from zero when lengths of male and female capelin were plotted against date (Table 2; Fig. 3). Only capelin from 1984 had slopes that were not significantly different from zero for either males or females (Table 2). Although some regressions are highly significant, the explained variance in the regressions is generally low (Table 2). Spent females were not collected in sufficient numbers from cod stomachs to warrant analyses.

Plots of regression residuals against fitted values revealed no pattern, showed a homogenous distribution and were judged to be normal with the exception of ovid females from 1982 when only a small number of capelin were available for analysis.

### 3.3. Comparisons between capelin from pound trap data and cod stomachs

Regression slopes for 1982 and 1983 male and female capelin collected from cod stomachs were generally steeper (i.e. more negative) than comparative slopes for capelin caught in the commercial trap (Tables 1 and 2; Figs. 1 and 3). The only exception was the slope for 1982 ovid females. For 1982 and 1983 male and female capelin,  $r$ -squared values

Table 1  
Summary of total length and weight versus time regressions for capelin collected from a pound trap located at Lance Cove, Cape Broyle Bay, during the capelin spawning season in June and July.  $n$  is the number of male and ovid and spent female capelin collected each year; \* indicates significant regression slopes at  $\alpha = 0.05$

Dependent variable	Group	Year	$n$	Mean ( $\bar{X}$ )	Max	Min	Slope	$p$ -Value	$r^2$	
Length (mm TL)	Male	1982	168	185	209	152	-0.185	0.198	0.01	
		1983	561	173	201	143	-0.132	0.027	*	
		1984	255	183	207	151	-0.057	0.393	0.00	
	Ovid	1982	216	155	211	120	-0.921	<0.001	*	
		1983	543	152	191	124	-0.258	<0.001	*	
		1984	245	158	191	124	-0.483	<0.001	*	
	Spent	1982	171	160	197	125	-0.163	0.495	0.00	
		1983	500	154	190	122	-0.527	<0.001	*	
		1984	156	155	190	123	-0.691	<0.001	*	
	Weight (g)	Male	1982	132	39.1	58.2	20.9	-0.560	<0.001	*
			1983	561	30.5	53.1	15.0	-0.175	<0.001	*
			1984	239	35.0	51.0	17.6	-0.246	<0.001	*
Ovid		1982	180	21.1	53.7	10.9	-0.279	0.009	*	
		1983	543	19.2	43.0	9.1	-0.198	<0.001	*	
		1984	228	20.9	43.2	9.0	-0.346	<0.001	*	
Spent		1982	171	17.8	32.4	7.7	-0.137	0.071	0.02	
		1983	500	14.8	27.0	6.6	-0.218	<0.001	*	
		1984	144	14.5	28.9	5.7	-0.321	<0.001	*	



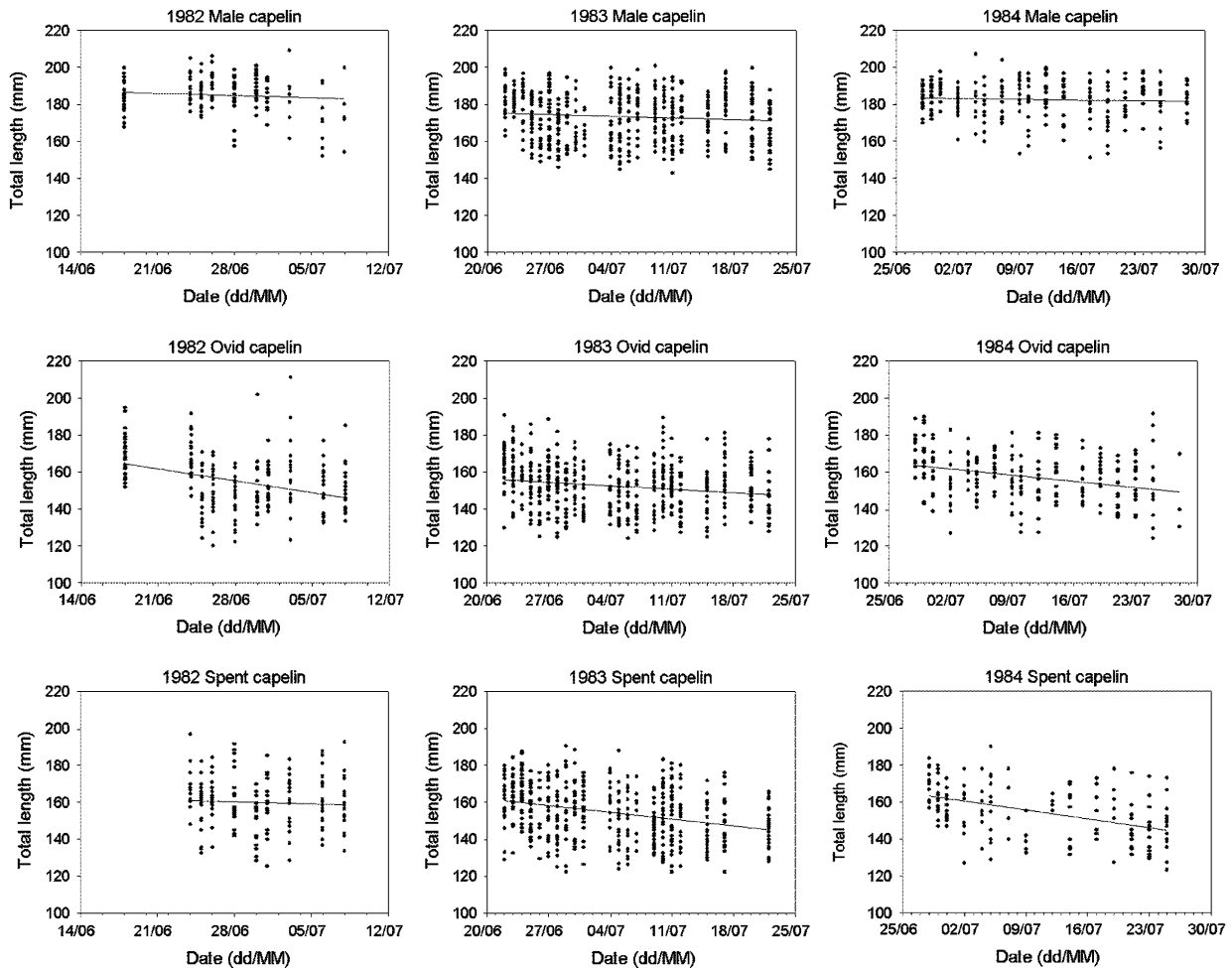


Fig. 1. Plots of total length versus spawning time regressions for capelin collected from a pound trap located at Lance Cove, Cape Broyle Bay, during the capelin spawning season in June and July (1982–1983).

were higher for capelin collected from cod stomachs than from the commercial fishery.

Differences in mean lengths of capelin from cod stomachs and from the commercial trap fishery were positive or zero for both sexes early in the spawning seasons of 1982 and 1983 (Table 3). Differences in mean lengths declined and became negative later in the season (Table 3) indicating cod selected bigger capelin early in the season and did not show any size preference at the end of the season. This difference was significant for three of nine tests in 1982 and 1983, i.e. only in the beginning of the spawning season (Table 3).

For 1984 male capelin, the regression slopes were not significant for both capelin collected from cod stomachs and capelin from the commercial fishery, whereas for the female capelin the regression was significant for the capelin from the commercial trap, but not for the capelin collected from cod stomachs (Table 3). In 1984, for both males and females, the observed mean length of capelin collected from cod stomachs was significantly smaller than the predicted mean length, based on the commercial trap data (Table 3). Four of six differences were significant in 1984. Maximum differences were observed at the end of the

season (Table 3). For each sex, the difference on the first sampling day was negative, was not significant on the second sampling day and was very negative at the end of the season (Table 3). Similar to 1983 and 1984, the difference early in the season was more positive for females than for males.

#### 4. Discussion

Length and weight regressions of capelin taken in traps of the commercial fishery clearly indicate that larger capelin arrived at coastal spawning sites before smaller capelin. This relationship was significant for 14 of 18 regressions and was less pronounced for males than for females. The largest male and female capelin were taken in the first 2–4 days of the trap fishery. Both small and large capelin were present throughout the rest of the spawning season. To observe the pattern of larger fish spawning before smaller (i.e. negative slope) it is critical to sample on these first few days, given that the large capelin taken on these days strongly influence the slope of the regression.

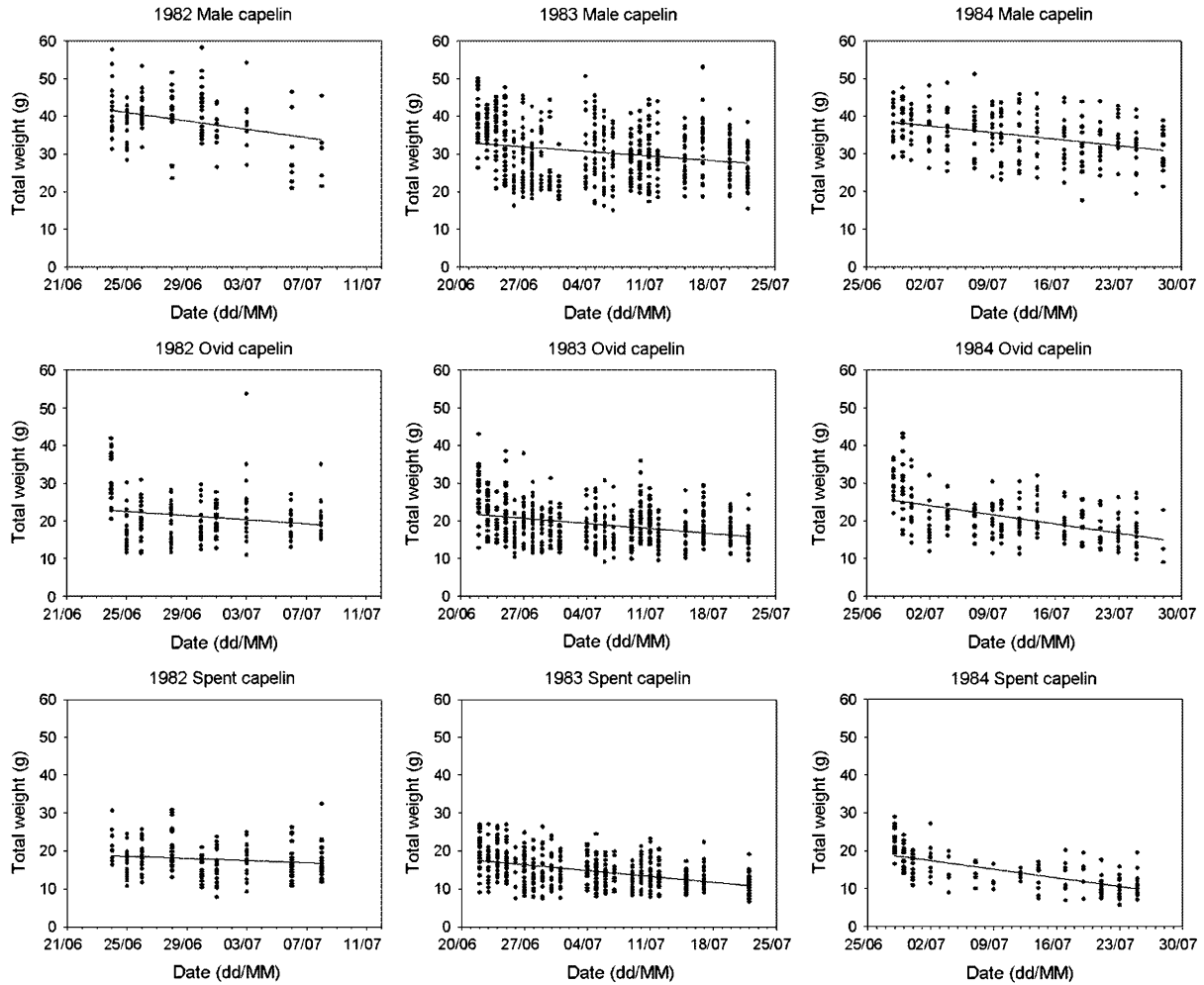


Fig. 2. Plots of weight versus spawning time regressions for capelin collected from a pound trap located at Lance Cove, Cape Broyle Bay, during the capelin spawning season in June and July (1982–1983).

The body size and time of spawning relation for capelin has been reported previously (Templeman, 1948; Atkinson and Carscadden, 1979; Nakashima, 1983), although data and statistical tests of the data are often lacking. Templeman (1948) suggested that males are mature and spawn over a longer period of time relative to females. Females mature in deeper water, relatively close to the beaches, and undertake a spawning run when they reach maturity with the largest females reaching maturity earlier. This conclusion was based on a high proportion of males (83.5%) on the beach at Holyrood

(Newfoundland), while 27 m offshore they constituted only 23.4% of the catches (Templeman, 1948). Nonetheless, our observations indicate that the relationship also exists for males, and this is well illustrated by the absence of small males during the first days of the spawning season.

A similar pattern has been observed for herring (*Clupea* species) (Lambert, 1987; Lambert and Messieh, 1989; Ware and Tanasichuk, 1989; Ware and Tanasichuk, 1990; Slotte et al., 2000; Rajasilta et al., 2001). Males reach maturity before females and wait until females reach maturity before

Table 2  
Summary of total length versus time regressions for capelin collected from stomachs of Atlantic cod, caught in the commercial gillnet fishery in Witless Bay. *n* is the number of male and female capelin collected each year; \* indicates significant regression slopes at  $\alpha = 0.05$

Group	Year	<i>n</i>	Mean ( $\bar{X}$ ) (mm TL)	Max (mm TL)	Min (mm TL)	Slope	<i>p</i> -value		<i>r</i> <sup>2</sup>
Male	1982	157	174	198	139	-0.282	<0.001	*	0.12
	1983	158	168	191	141	-0.767	<0.001	*	0.25
	1984	117	170	193	140	0.0022	0.953		0.00
Ovid	1982	16	158	186	115	-0.543	0.043	*	0.25
	1983	62	152	183	119	-0.507	0.023	*	0.08
	1984	173	154	188	110	-0.084	0.448		0.00

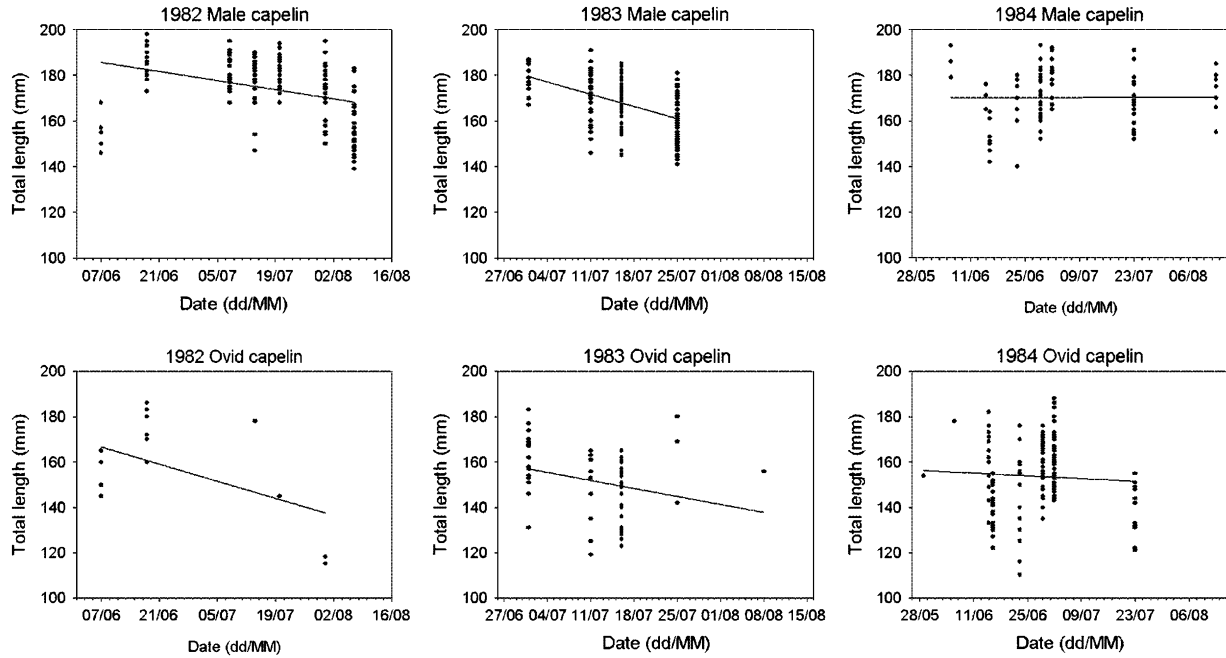


Fig. 3. Plots of total length versus time regressions for capelin collected from stomachs of Atlantic cod, caught in the commercial gillnet fishery in Witless Bay (1982–1983).

initiating their spawning run (Lambert, 1987). Males arriving at the spawning grounds before females has also been observed for other pelagic species, e.g. alewife (*Alosa pseudoharengus*) (Libby, 1982), mackerel (*Scombrus scombrus*) (Dawson, 1986) and for non-pelagic species, e.g. Atlantic cod (Morgan and Trippel, 1996). Lambert (1987) and Ware and Tanasichuk (1989) noted that bigger herring of both sexes spawned before smaller herring, and that this was evident among as well as within the different spawning waves. Slotte et al. (2000) observed a similar pattern but only distinguished two waves, a first wave composed of repeat spawners and a second wave composed of recruit or first time spawners.

A similar mechanism may occur for capelin, but is apparently more difficult to observe because the spawning season is shorter, creating more overlap between the spawning runs. Some of our data, especially weight and length regressions for 1984 spent and ovid females suggest that there might be two spawning waves of mature females. The pattern might be more apparent for 1984, because of the lower abundance of capelin during that year at Witless Bay Newfoundland (Methven and Piatt, 1989). No such pattern was apparent for males, supporting the hypothesis that males do not arrive in distinct waves. Males apparently stay near the beach, waiting for successive waves of females to arrive. For 1983, Methven

Table 3

Results of two-tailed *t*-tests, testing for significant differences between the hypothesised mean, calculated with the regression equations for the trap data, and observed population mean for capelin collected from cod stomachs. *n* is the number of male and female capelin collected from cod stomachs; \* indicates significant differences at  $\alpha = 0.05$

Group	Year	Date	Hyp. mean ( $\mu$ ) (mm TL)	Obs. mean ( $\bar{X}$ ) (mm TL)	St. Dev. ( $s_{\bar{x}}$ )	<i>n</i>	<i>t</i> -value		df	Critical value ( $\alpha = 0.05$ )	( $\bar{X} - \mu$ ) (mm)
Male	1982	18 June	187	187	7.047	16	0.213		15	2.131	0
		8 July	183	181	7.082	20	-1.803		19	2.093	-2
	1983	1 July	174	177	5.586	18	2.729	*	17	2.110	3
		11 July	173	171	10.077	40	-0.820		39	2.023	-2
		16 July	172	170	9.980	56	-1.364		55	2.005	-2
		29 June	183	173	9.972	31	-5.941	*	30	2.042	-10
Ovid	1982	2 July	183	179	8.733	12	-1.454		11	2.201	-4
		23 July	182	166	10.556	27	-7.746	*	26	2.056	-16
		18 June	164	174	9.052	7	2.914	*	6	2.447	10
Ovid	1983	1 July	153	161	12.022	21	2.797	*	20	2.086	8
		11 July	151	147	16.978	9	-0.662		8	2.306	-4
		16 July	149	146	12.124	29	-1.656		28	2.048	-3
	1984	29 June	163	160	9.795	44	-2.100	*	43	2.017	-3
		2 July	162	160	11.244	51	-1.064		50	2.009	-2
		23 July	152	137	10.704	14	-4.960	*	13	2.160	-15

and Piatt (1991), observed two peaks of capelin abundance near Witless Bay, but only one peak in 1984. A noteworthy exception to this was reported by Templeman (1948) when a distinct second spawning event, composed of smaller individuals, occurred 1 month after the first wave.

Weight regressions were more significant and explained a greater part of the variability than the length regressions for male and female capelin because weight is generally a cubic function of length. Comparison of length and weight slopes shows length slopes are greater than weight slopes for females while the reverse is true for males (Table 1). This observation implies that body weight of males for a given length is smaller at the end of the season than earlier in the spawning season. This may be closely linked to the distinct behaviour of males, who stay longer at the spawning sites, are often in very bad condition at the end of the season (Templeman, 1948) and are believed to die in mass after spawning, concentrating all their reproductive effort into one season (Shackell et al., 1994b; Huse, 1998).

Different mechanisms have been proposed to account for larger fish arriving at the spawning grounds before smaller fish: (i) size-dependent swimming speeds (Carscadden et al., 1997, 2001), (ii) size-dependent maturation rates (Lambert, 1987; Ware and Tanasichuk, 1989; Hutchings and Myers, 1993; Carscadden et al., 1997) and (iii) size-dependent onset of maturation (Slotte et al., 2000). Size-dependent swimming speed is an intuitively appealing process to explain why larger individuals arrive near the spawning grounds first. However some species aggregate close to the spawning area, before spawning actually starts. This behaviour may abolish differences in swimming speed during migration (Lambert, 1987; Hutchings and Myers, 1993) or might obscure whether larger fish actually spawn before smaller fish. During the spawning migration, capelin are reported to approach Newfoundland beaches from the south, generally swimming against the prevailing current (Nakashima, 1992). Under the hypothesis of size-dependent swimming speed being a mechanism, this would enhance the observed pattern. Thus the question remains: Do capelin spawn upon arrival or do they aggregate in schools close to the spawning grounds prior to spawning. Our data for capelin collected from cod stomachs, show cod, caught just a few kilometres offshore at Witless Bay, had capelin in their stomachs at least one month before spawning started on the beaches. This observation and other studies suggest that capelin are present in coastal waters before spawning actually starts (Atkinson and Carscadden, 1979; Methven and Piatt, 1989, 1991; Nakashima, 1992). Friis-Rødel and Kanneworff (2002) describe that for Greenland capelin, males migrate directly to the spawning grounds, while females pause somewhat outside the spawning grounds and stay in pelagic schools, while maturation proceeds.

Hutchings and Myers (1993) observed that small Atlantic cod matured before larger cod and proposed a largely size-independent production of gonadal tissue to be the cause. This implies a negative size-dependent rate of maturation, while others suggested a positive size-dependent rate of

maturation to cause bigger fish to spawn first for herring (Lambert, 1987; Ware and Tanasichuk, 1989) and for capelin (Carscadden et al., 1997). Both hypotheses still support the conclusions by Slotte et al. (2000), who linked the onset of maturation with condition and fat content. Low energy reserves force first time spawners to feed after overwintering before maturation can be completed, resulting in a delayed onset of maturation (Slotte et al., 2000; Rajasilta et al., 2001). Moreover, condition will likely also affect the swimming speed (Slotte et al., 2000). After a review of the literature and the methods used, especially with respect to the quantification of the maturation process (see Slotte et al., 2000 for a discussion), the hypothesis by Slotte et al. (2000) for Norwegian spring spawning herring that size-dependent onset of maturation is the determining factor, certainly seems worth considering, although the different mechanisms may be working together in some combination.

Lengths of capelin collected from cod stomachs showed a similar trend as the lengths from capelin caught in commercial pound traps, i.e. the mean length of capelin ingested by cod became smaller as the capelin spawning season proceeded thus agreeing with Gerasimova et al. (1991) that prey in stomachs of Atlantic cod generally reflect the size structure of the capelin available to cod. However, for 1982 and 1983 and for both male and female capelin respectively, the results of the *t*-tests suggest that early in the season cod were feeding on capelin that were larger or from the same size as the mean length of capelin available in the environment, while towards the end of the season mean prey size was equal to or became smaller than what was available to them. In 1984 mean prey size was equal to or smaller than what was available in the environment over the entire spawning season, possibly due to 1984 being a year of relatively low abundance of capelin in the Witless Bay area (Methven and Piatt, 1991).

Cod has often been characterised as a generalist feeder, prey availability being the determining factor affecting its diet (Lilly, 1987; Link and Garrison, 2002b). Floeter and Temming (2003) analysed feeding preference of North Sea cod preying on fish in relation to prey size and concluded that more than 75% of the diet consisted of fish originating from the least preferred quartile of the size range, based on a preference function. This is in accordance with our findings, mean size of capelin ingested by cod paralleled the decrease in size of capelin available to them, but throughout the entire season cod fed on a wide size range of capelin. Additionally our analyses suggest that during 1982 and 1983, cod not only fed on smaller capelin as the season advanced, but also that cod were selecting larger capelin early in the season, when capelin abundance was high (Methven and Piatt, 1989, 1991). At the end of the season, when capelin abundance was lower (Methven and Piatt, 1989, 1991), cod preyed on capelin that were equal to or smaller than predicted by the length distribution of capelin available to them. Floeter and Temming (2003) came to the conclusion that for North Sea cod preying on fish, abundance was the first determinant of cod feeding behaviour and that when abundance was low, cod did not show any preference with respect to the size of the prey. In our study this is



emphasised by the patterns in 1984, when cod were feeding on capelin that were smaller than was on average available throughout the entire season. Methven and Piatt (1989) observed a low abundance of capelin during this year and related this to the anomalous low water temperatures. Additionally, this influenced the appearance of the seasonal thermocline, concentrating the capelin in the upper water layers (Schneider and Methven, 1988; Methven and Piatt, 1989) and thus reducing the spatial overlap with cod, which are primarily demersal feeders. This resulted in a relatively higher proportion of invertebrates in the diet of cod in 1984.

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