Beach and demersal spawning in capelin (*Mallotus villosus*) on the northeast Newfoundland coast: egg developmental rates and mortality

P.M. Penton, G.K. Davoren, W.A. Montevecchi, and D.W. Andrews

Abstract: Timing of spawning and site selection in fish are important fitness-related traits that ultimately influence reproductive success. Capelin (*Mallotus villosus* (Müller, 1776)), a key forage fish in the north Atlantic, spawn eggs that adhere to sediments on beaches and in demersal (deep-water) habitats throughout their geographic range, resulting in divergent thermal regimes for the incubating eggs. We compare the timing and duration of spawning of capelin and its influence on the developmental and survival rates of eggs between a beach and a demersal spawning site on the northeast Newfoundland coast in 2004 and 2005. Spawning events at the beach were at least 10 days earlier and shorter (2–3 days) relative to the demersal site (8–12 days). Hourly and mean daily incubation temperatures at the beach were higher and more variable relative to the demersal site, resulting in two distinct developmental strategies: low to high mortality and rapid development (beach) versus low mortality and slow development (demersal). Higher egg mortality at beach sites was explained by higher and more variable temperatures and potentially limited oxygen replenishment relative to demersal sites. The divergent biology of beach and demersally spawned eggs suggest that each will respond differently to environmental change and, thus, require different approaches for successful management.

Résumé : Le calendrier de la fraie et la sélection du site sont des traits importants reliés à la fitness qui, en fin de compte, influencent le succès de la reproduction. Le capelan (*Mallotus villosus* (Müller, 1776)), un poisson fourrage important dans l'Atlantique Nord, pond des oeufs qui se collent aux sédiments sur les plages et dans les habitats démersaux (d'eau profonde) dans l'ensemble de son aire géographique, ce qui produit des régimes thermiques différents pour les œufs. Nous avons comparé le calendrier et la durée de la fraie chez le capelan et leur influence sur les taux de développement et de survie des œufs dans un site de ponte de plage et dans un site de ponte démersal sur la côte nord-est de Terre-Neuve en 2004 et 2005. Les événements de ponte se produisent sur la plage au moins 10 jours plus tôt et durent moins longtemps (2–3 jours) que dans le site démersal (8–12 jours). Les températures d'incubation horaires et journalières moyennes sur la plage sont plus élevées et plus variables qu'au site démersal, ce qui entraîne deux stratégies de développement distinctes, un développement rapide avec une mortalité basse à élevée (plage), par comparaison à un développement lent avec une faible mortalité (habitat démersal). La mortalité plus élevée des œufs dans les sites de plage s'explique par les températures plus hautes et plus variables et le remplacement potentiellement restreint de l'oxygène par rapport aux sites démersaux. La biologie distincte des œufs pondus sur la plage et dans les habitats démersaux laisse penser que ces différents œufs réagiront au changement environnemental de manière distincte; il faudra donc utiliser des approches différentes pour réussir leur gestion.

[Traduit par la Rédaction]

Introduction

Selection of spawning site and timing of spawning are important fitness-related traits (Bernardo 1996; Reed et al. 2006). They determine the biophysical conditions (e.g., temperature, densities of predators and conspecifics) in which the critical early life-history stages of progeny grow and develop, ultimately influencing reproductive success (Clutton-Brock 1988; Wootton 1990). This is especially true for marine fish whose typical life-history strategy is characterized by high fecundity, small offspring size, and low parental care, charac-

teristics that result in high mortality (>99%) of early stages (i.e., eggs and larvae; Chambers and Trippel 1997).

Capelin (*Mallotus villosus* (Müller, 1776)) is the focal forage fish in the Northwest Atlantic and is largely responsible for transferring energy from lower to higher trophic levels within this ecosystem (Carscadden and Vilhjalmsson 2002). Capelin spawn eggs that adhere to sediments and show high variation in the timing and location of spawning both within and among regions (Table 1). The use of beach and demersal (deep-water) sites throughout their distribution results in divergent thermal regimes for the incubating eggs (Table 1).

Table 1. The depth, temperature, and timing of spawning of capelin (*Mallotus villosus*) throughout the North Atlantic.

Locality	Depth (m)	Temperature (°C)	Timing of spawning	References
Barents Sea, Norway	12–280	1.5 to 6.5	March–April	Sætre and Gjøsæter 1975
Balsfjord, Norway	0	–5.3 to 26.8 (on gravel); 0.7 to 15.7 (4 cm in gravel)	April–May	Vilhjalmsson 1994; Præbel et al. 2009
Iceland	40–80	6.0 to 7.0	March–June	Thors 1981; Jangaard 1974
West Greenland	0	1.9 to 8.5	May–June	Vilhjalmsson 1994
Newfoundland	0	4.6 to 12.7	June–July	Templeman 1948; Frank and Leggett 1981
Southeast Shoal, Newfoundland	50	2.0 to 4.0	June–July	Carscadden et al. 1989
Trinity Bay, Newfoundland	<20	1.4 to 12.1	July–August	Nakashima and Wheeler 2002

Note: Depth equal to zero indicates beach spawning.

Temperature is a critical determinant of developmental and survival rates of fish eggs (Frank and Leggett 1981; Blaxter 1988; Pepin 1991; Rombough 1997). Capelin eggs survive large daily temperature fluctuations (~20 °C; Præbel et al. 2009) and show wide tolerance ranges to both cold and warm temperatures (e.g., Davenport and Stene 1986). Within tolerance ranges, high incubation temperatures result in faster egg development but also higher mortality owing to abnormal growth and development in eggs of capelin (Frank and Leggett 1981) and fish in general (Cossins and Bowler 1987).

Capelin are considered to spawn primarily on beaches in Newfoundland in June and July, with the exception of the Southeast Shoal of the Grand Bank, considered to be an ancestral beach (Carscadden et al. 1989; Table 1; Fig. 1a). It has been hypothesized, however, that capelin are facultative spawners (Dodson et al. 1991) and may switch to demersal spawning in areas adjacent to beaches once beach temperatures become unsuitably warm later in the season (Templeman 1948). Demersal spawning has been persistent in two regions of coastal Newfoundland in the vicinity of spawning beaches since at least 1999 (Nakashima and Wheeler 2002; Davoren et al. 2006). The adhesive nature of capelin eggs and the coexistence of beach and demersal spawning in coastal Newfoundland make this an ideal location to examine the influence of timing and location of spawning on the early life-history characteristics of an important marine forage fish. To examine this, we compare the timing and duration of spawning and incubation temperatures, along with the developmental and survival rates of eggs, at beach and demersal sites on the exposed northeast Newfoundland coast.

Materials and methods

Study area and design

The study area encompassed beach and demersal (17–38 m deep) spawning sites along the northeast Newfoundland coast, referred to as the Straight Shore of Notre Dame Bay (Figs. 1a, 1b). Accessible areas of the coastline along the Straight Shore (~110 km) were surveyed in 2004, resulting in the discovery of five spawning beaches (Andrews 2005; Fig. 1b). Eleven demersal spawning sites have been located since 2002, ranging from 3 to 18 km from shore (Davoren et al. 2006, 2008; Penton 2006; Fig. 1b).

The abundance, development, and mortality of capelin eggs were studied during July–August in 2004 and 2005 at beach and demersal sites within the study area (Fig. 1b). Demersal sites were sampled from the *Lady Easton II*, a 13.4 m commercial fishing vessel, whereas beach sites were sampled during low tide. In both years, gravel at beach and demersal spawning sites was examined for the presence of eggs starting in early July and were monitored through the end of August. Collections of egg-bearing gravel began once spawning started and continued until most eggs hatched at each site. Studies on the larval early life-history stage were conducted and are presented elsewhere (Andrews 2005; Penton 2006; Penton and Davoren 2008).
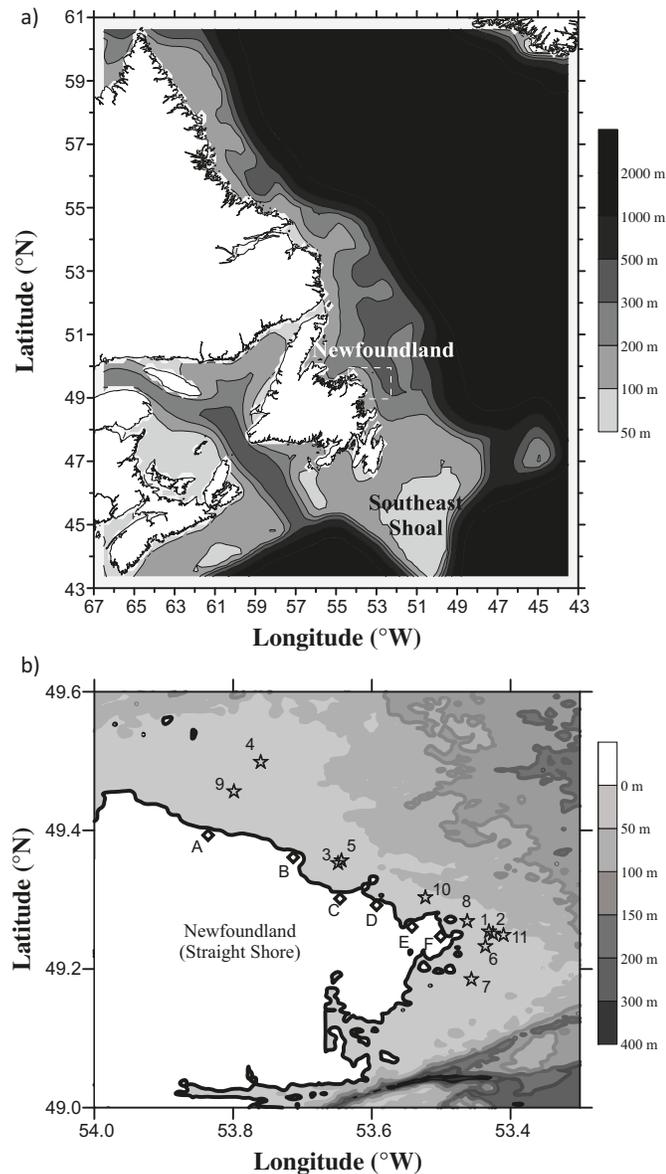
The duration of capelin egg developmental stages are determined by incubation temperature (Nakashima and Wheeler 2002). The same is true for the stages of cleavage that are characteristic of recently fertilized eggs (stages I–II; Fridgeirsson 1976). Using mean incubation temperatures at the spawning sites, we were able to determine sampling intervals to ensure that new spawning events were recorded without resampling previously spawned eggs. In 2004–2005, beaches were sampled every second day. Demersal sites were sampled every third day in 2004 and every second day in 2005, owing to warmer incubation temperatures. Fertilization dates were also calculated based on this relationship, examining cleavage cycles in stage I–II eggs (e.g., on day three at the beach (every second day sampling period), eggs with two cells were fertilized that day. Eggs in the 64-cell stage of cleavage, however, were fertilized on day two).

Egg samples

Egg samples at the beach were collected from the high tide (HT), mid-tide (MT), and low tide (LT) regions of the intertidal zone to get a composite measure of the entire beach because egg densities are not homogeneous across tidal zones (Frank and Leggett 1981). A 6.5 cm internal diameter steel corer was used to collect a standard sample of eggs, following procedures in Frank and Leggett (1981). In 2004, three replicate egg samples were taken from each tidal zone, whereas only two replicate samples were taken from each tidal zone in 2005 because of limited beach spawning in the study area (Reinfort 2006).

Egg samples at demersal sites were collected from the ship using a 0.3 m² Van Veen Benthic Grab System. Three replicate bottom grabs were retrieved from each spawning site on each sampling day, and each sample was placed in a separate 40 L bucket. In 2004, egg samples were collected by mixing the bottom grab sample in the bucket, after which a core sample was collected using a 7.5 cm internal diameter corer. In 2005, water was drained from the grab sample before

Fig. 1. Map of Newfoundland, indicating (*a*) the location of the study area (Straight Shore, Notre Dame Bay; broken-outlined square off the northeast coast of the island) within eastern Canada and (*b*) the location of all demersal sites (stars) discovered from 2002 to 2005 (1, Gull Island I; 2, Gull Island II; 3, Deadman's Bay III; 4, Penguin Island; 5, Deadman's Bay V; 6, Turr Island; 7, Hincke's Rock; 8, Cracker's Rock; 9, Northern Penguin Island; 10, Windmill Bight; 11, Gull Island III) and beach sites (diamonds) discovered in 2004 (A, Shalloway; B, Anchor Brook; C, Long Beach; D, Lumsden Beach; E, Mussel Shells; F, Capelin Cove).

served in a formalin solution buffered with sodium borate (i.e., 50 mL formaldehyde, 37% solution; 2100 mmol/L of boric acid (sodium) buffer solution; 830 mL salt water) for estimation of egg density.

In the laboratory, the adhesive capelin eggs in each core sample were separated from the sediment. Samples were poured over a 0.270 mm sieve and rinsed with water for ~20 min. The sample was then soaked in 2% (*m/v*) KOH solution for 24 h to separate adherent eggs from the sediment. Eggs and other biological material were then decanted off and hardened in 95% (*v/v*) ethanol for 1 week. Eggs were subsampled using a 1 L capacity Motoda splitter (Motoda 1959) and the final split (~200 to 300 eggs) was placed onto a Petri dish and eggs were counted using a dissecting microscope.

At beach and demersal sites, a 20 mL egg/sediment sample was also collected near each of the core samples and preserved in Stockard's solution (50 mL formaldehyde, 37% solution; 40 mL glacial acetic acid; 60 mL glycerin; 850 mL sea water). In the laboratory, a random sample of 50–100 eggs from each sample was examined to determine the proportion of eggs in each developmental stage, based on a modification of Fridgeirsson's (1976) description of capelin egg development. Eggs progress through seven stages of development: recently fertilized eggs when the blastodisk is formed (stages I–II); gastrulation when the endo-, meso-, and ecto-derm are formed (stage III); organogenesis I when the head and part of the embryonic body are formed (stage IV); organogenesis II when the full development of the main organs occurs (stage V); prehatching (stage VI) when the mouth is formed in preparation for independent feeding; and hatching (stage VII). Dead eggs were distinguished from live ones based on a cloudy or opaque appearance and the number of dead eggs per sample was recorded. Unfertilized capelin eggs remain adhesive (Gjøsæter and Gjøsæter 1986), so estimates of dead eggs included a combination of unfertilized eggs and those that died during development.

Estimates of egg density, mortality, and development

A standard estimate of areal egg density (mean number of eggs/cm^2) was calculated to allow comparisons of egg density between sites and years. Egg density measures were averaged within tidal zones and then across all tidal zones to give a composite measure of daily egg density for the entire beach. The mean daily egg density at the demersal site was based on three replicate samples.

Egg mortality on each day was expressed as a percentage of the replicate Stockard's samples using the following equation (Frank and Leggett 1981):

$$[1] \quad \text{Egg mortality} = \left[\frac{\sum_{i=1}^{k} d_i}{\sum_{i=1}^{k} x_i} \right] \times 100$$

where x_i is the total number of eggs in the *i*th sample, d_i is the total number of dead eggs in the *i*th sample, and k is the number of samples. The number of dead eggs on each day was averaged within each tidal zone and then across all tidal zones to give a daily composite measure of egg mortality for

opening it and the sediment was released into the 40 L bucket, allowing the layering of eggs to remain intact to obtain a measure of egg depth for comparison with samples from the beaches. A sample was collected using a core with a 6 cm internal diameter. Although collection methods at demersal sites differed between years, the sample volume was the same. At both beach and demersal sites, egg depth did not exceed the depth of the core and egg concentration and development were assumed to be homogenous throughout the core (Frank and Leggett 1981). Core samples were pre-

the entire beach. The daily mean number of dead eggs at the demersal site was based on three replicate samples.

The start and end of spawning at each site were determined by the presence of recently fertilized eggs (i.e., stage I–II) in the replicate Stockard's samples on each day, which indicated newly deposited eggs. A central measure of egg development was calculated for each day using the following equation from Frank and Leggett (1981):

$$[2] \quad \text{WMDSI} = \frac{\sum_{i=1}^{6} s_i e_i}{\sum_{i=1}^{6} e_i}$$

where WMDSI is the weighted mean developmental stage index, s_i is the developmental stage index, and e_i is the mean number of eggs in each developmental stage over all replicate samples. The mean number of eggs on each day at the beach was calculated for each tidal zone.

Incubation temperature

At the beach, water temperature at waist height during low tide was measured on each sampling day using a handheld thermometer (2004–2005). Temperature loggers (Vemco 8-bit Minilog-TR) that recorded temperature every 60 min throughout the incubation period were buried 6 cm in the sediment at the beach in the low-tide zone in 2005 and were anchored near the seabed at demersal spawning sites in both 2004 and 2005. Hourly measurements were averaged at each site on a daily basis to characterize the mean daily incubation temperature experienced at each beach and demersal spawning site.

Statistical analysis

A two-factor analysis of variance (ANOVA) was used to examine the difference between sites and years for incubation temperature, egg density, and mortality. Tukey post hoc pairwise comparisons were used to examine differences in dependent variables between years within site and between sites within year. To compare developmental rates between beach and demersal sites, indicator variables in an analysis of covariance (ANCOVA) were used to compare the regression of WMDSI on egg age (days since initial fertilization) between the beach and demersal sites and years (Quinn and Keough 2002). The explanatory factors included in the model were egg age, site (or year), and an interaction between the two factors. To test for coincidence (regressions are equal), the p value was obtained by testing the significance of site and age × site simultaneously ($F = [(SS_{site} + SS_{site \times year}) / 2] / MS_{error}$, where SS is the sum of squares and MS is the mean sum of squares). If this hypothesis was rejected, the relationships were tested for parallelism (same slope but different intercept) and equality of intercepts (but different slopes).

All data were tested for normality and homogeneity of variance to meet the assumptions of linear models. Mean proportions were arcsine and square-root transformed prior to analysis. All analyses were conducted using SAS version 8 (SAS Institute Inc., Cary, North Carolina, USA).

Results

All known beach and demersal sites were monitored and sampled in 2004 and 2005 (Table 2). The statistical analysis of the influence of timing and location of spawning on egg development and mortality, however, was limited to sites where spawning occurred in both years and had complete biological and environmental data sets. This resulted in a two-site comparison (beach site D; demersal site 1). These two sites were consistently used for spawning from 2002 to 2006 (Davoren et al. 2008). For a general comparison of incubation temperatures, timing and duration of spawning, and egg density and mortality between beach and demersal sites, data from all sites are presented (Table 2).

Timing and duration of spawning

Spawning at all beach sites was at least 10 days earlier and shorter in duration relative to all demersal sites in both years (Table 2). For the two site comparison, spawning at the beach site (site D) in 2004 began on 10 July and lasted for 3 days. Spawning at the demersal site (site 1) began 18 days later on 28 July and lasted for 10 days (Table 2). In 2005, spawning at the beach site began on 3 July and lasted for 4 days. Initial spawning at the demersal site was missed in 2005, but based on incubation temperatures, we estimated that spawning began on 13 July and lasted for 9 days.

Incubation temperature

Mean daily temperatures were derived from thermister data for both years at the demersal site and from the beach site in 2005. Thermisters were not deployed at the beach site in 2004, but in both years, daily point measurements of temperature at waist height during low tide were recorded. In 2005, daily point measurements of temperature at the beach (14.1 ± 1.3 °C) were not significantly different ($F_{[1,6]} = 0.1455$, $p = 0.888$) from daily means collected using the thermister (14.0 ± 3.4 °C). Therefore, daily point measurements of temperature from the beach in 2004 were used in the analyses with daily means from the thermisters at demersal sites in both years and the beach site in 2005.

Daily incubation temperatures at the beach and demersal site were warmer in 2005 than 2004 ($F_{[1,114]} = 46.4$, $p < 0.0001$). Incubation temperatures were higher at the beach than the demersal site in both 2004 ($p < 0.0001$; Figs. 2a, 2c) and 2005 ($p < 0.0001$; Figs. 2b, 2d). Variation in daily temperature was higher at the beach (Figs. 2a, 2b) compared with the demersal site (Figs. 2c, 2d) in both years, indicated by the fluctuations in hourly temperature recordings throughout incubation.

Egg density

Mean daily egg densities (number of eggs/cm^2) throughout the incubation period (i.e., fertilization to hatch) were higher in 2004 than in 2005 ($F_{[1,90]} = 5.66$, $p = 0.020$), and were higher at the demersal site relative to the beach site ($F_{[1,90]} = 4.79$, $p = 0.031$; Table 2). A significant interaction between site and year ($p = 0.030$) was due to very low egg densities at the beach in 2005 (Table 2). Egg densities were similar at beach and demersal sites in 2004 and between years at the demersal site ($p = 0.999$; Table 2).

Table 2. Summary of depth, timing of spawning, along with hourly incubation temperature, egg density, and proportion of dead eggs at beach and demersal spawning sites of capelin (*Mallotus villosus*) along the Straight Shore in Notre Dame Bay on the northeast Newfoundland coast.

Year and location	Site name (ID)*	Depth	Timing of spawning	Incubation temperature[†] (range)	Density (eggs·cm^{-2})	Proportion dead eggs (range)
2004						
Beach	Capelin Cove (F)	HT	11–13 July	na	868±211	34.9±5.8 (4.0–64.7)
		MT	11–13 July	na	833±216	29.6±3.6 (4.7–50.7)
		LT	11–13 July	na	762±213	27.0±3.8 (4.7–46.0)
	Lumsden Beach (D)	HT	10–12 July	na	202±48	44.7±7.6 (6.8–85.0)
		MT	10–12 July	na	575±99	35.3±6.0 (4.1–90.0)
		LT	10–12 July	na	601±108	31.4±4.5 (6.7–60.0)
Demersal	Turr Island (6)	17.3 m	24–31 July	8.6±3.6 (2.8–16.6)	798±209	5.2±2.7 (0.17–36.8)
	Hincke's Rock (7)	21.9 m	21–29 July	5.6±1.1 (3.2–7.6)	777±279	1.7±0.33 (0.54–4.0)
	Gull Island I (1)	32.7 m	28 July – 6 August	3.1±1.1 (0.7–8.6)	453±58	1.7±0.77 (0–8.8)
	Gull Island II (2)	26.7 m	30 July – 8 August	5.9±3.7 (1.6–16.2)	671±106	3.7±2.0 (0–23.3)
2005						
Beach	Lumsden Beach (D)	HT	3–6 July	14.7±2.9 (5.9–36.3)	13±2	25.5±6.4 (8.0–59.0)
		MT	3–6 July	14.3±2.4 (9.9–32.5)	15±5	16.0±3.0 (8.0–28.8)
		LT	3–6 July	14.5±2.9 (9.5–35.5)	11±3	15.6±5.7 (4.0–36.0)
Demersal	Turr Island (6)	17.3 m	na	10.4±2.6 (4.8–15.2)	1542±173	17.8±5.5 (0–58.2)
	Gull Island I (1)	32.7 m	13–21 July	5.2±1.4 (2.6–12.9)	441±107	10.0±0.3 (0–5.3)
	Gull Island II (2)	26.7 m	13–19 July	na	417±93	4.8±1.9 (0–25.9)
	Gull Island III (10)	37.5 m	31 July – 6 August	4.3±1.1 (2.5–9.2)	179±27	2.8±1.9 (0–21.1)

Note: Values reported for hourly incubation temperature, egg density, and proprtion of dead eggs are mean ± SE. Depths are high tide (HT), mid-tide (MT), or low tide (LT).

*Numbers and letters in parentheses correspond to site locations in Fig. 1.

[†]Hourly incubation temperature recorded with thermisters was not available (na) at beach sites in 2004.

Egg mortality

The mean daily proportion of dead eggs, or egg mortality, was higher at the beach site relative to the demersal site in both years ($F_{[1,90]} = 78.82$, $p < 0.0001$; Table 2). Mortality differed between years ($F_{[1,90]} = 5.03$, $p = 0.027$) owing to higher mortality at the beach in 2004 relative to 2005 ($p = 0.080$; Table 2). At the demersal site, mortality did not differ between years ($p = 0.713$).

A two-way ANOVA was used to examine the influence of egg density (biotic) and temperature (abiotic) on egg mortality. For the beach site, a separate analysis was conducted for each year because of the differences in mortality between years. A single analysis, years combined, was conducted for the demersal site. At the beach site in 2004, egg density ($F_{[1,11]} = 14.89$, $p = 0.003$) and daily incubation temperatures ($F_{[1,11]} = 51.20$, $p < 0.0001$) were significant in explaining the variation in egg mortality. An interaction between egg density and mean incubation temperature was significant ($F_{[1,11]} = 11.31$, $p = 0.006$). Egg density and mean incubation temperature did not significantly influence egg mortality at the beach site in 2005 ($F_{[3,16]} = 0.23$, $p = 0.873$) or at the demersal site, both years combined ($F_{[3,21]} = 0.29$, $p = 0.284$).

Egg developmental rates

Egg developmental rates at each site were determined from the regression slopes of WMDSI against time since fertilization (Fig. 3). Developmental regression slopes were not significantly different between years at the beach site (ANCOVA: $F_{[1,8]} = 0.33$, $p = 0.728$) or at the demersal site

(ANCOVA: $F_{[1,14]} = 0.558$, $p = 0.585$; Fig. 3). Developmental rates were significantly different between beach and demersal spawning sites in 2004 (ANCOVA: $F_{[1,15]} = 9.23$, $p = 0.004$) and 2005 (ANCOVA: $F_{[1,11]} = 9.08$, $p = 0.005$) with equality of intercepts but different slopes (Fig. 3).

Discussion

Capelin spawn at both beach and demersal sites on the northeast coast of Newfoundland. Spawning at beach and demersal sites was separated by at least 10 days and egg densities at demersal sites were similar to or higher than beach sites in this region. Incubation temperatures at beach sites were higher and more variable relative to demersal sites. Overall, two distinct strategies were observed: rapid development and a high proportion of dead eggs at the beach versus slow development and a low proportion of dead eggs at the demersal site. These findings suggest that recently discovered demersal sites in coastal Newfoundland have the potential to contribute to recruitment in capelin populations (Penton and Davoren 2008).

Egg developmental rates

Temperature is a major regulator of fish egg developmental rates (Blaxter 1988; Pepin 1991; Rombough 1997) and constitutes a major environmental difference between beach and demersal sites in this study. Developmental rates of beach and demersally spawned capelin in the study area were significantly different, with slower development occurring at the demersal sites where eggs experience cooler temperatures. This supports the established negative relationship

Fig. 2. Hourly temperature during the egg incubation period of capelin (*Mallotus villosus*) at beach site D (LT, low tide) in 2004 (*a*) and 2005 (*b*) and demersal site 1 in 2004 (*c*) and 2005 (*d*). Temperatures indicated are hourly recordings from data loggers, with the exception of 2004 at the beach site (*a*), when water temperature at waist height was recorded once daily at low tide.
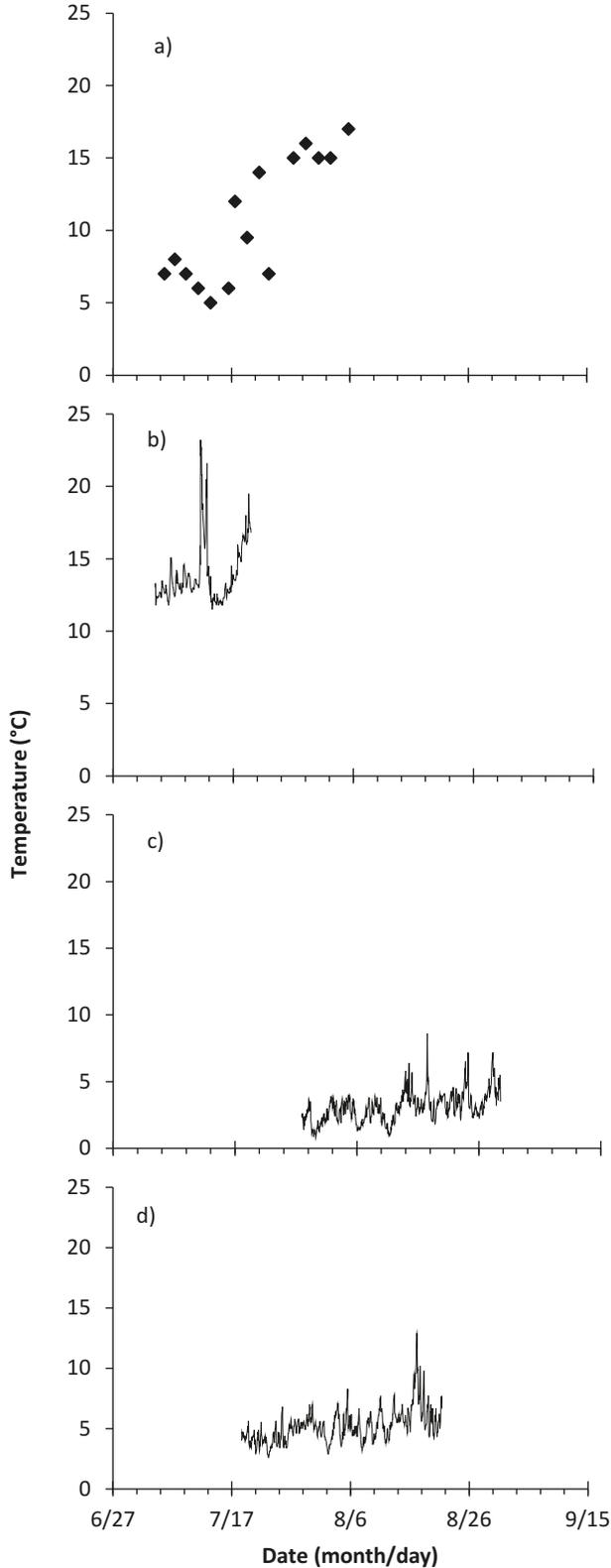

Fig. 3. Developmental rates of capelin (*Mallotus villosus*) eggs determined from core samples at beach site D (squares) and demersal site 1 (circles) in 2004 (open symbols, broken line) and 2005 (closed symbols, solid line). Mean incubation temperature over the entire incubation period at beach site D was 10.6 °C (2004) and 14.5 °C (2005) and at demersal site 1 was 3.1 °C (2004) and 5.2 °C (2005). Beach 2004: $y = 0.3305x + 0.9144$, $r^2 = 0.87$; Beach 2005: $y = 0.3518x + 0.5542$, $r^2 = 0.93$; Demersal 2004: $y = 0.1148x + 0.608$, $r^2 = 0.93$; Demersal 2005: $y = 0.1171x + 0.0353$, $r^2 = 0.78$.
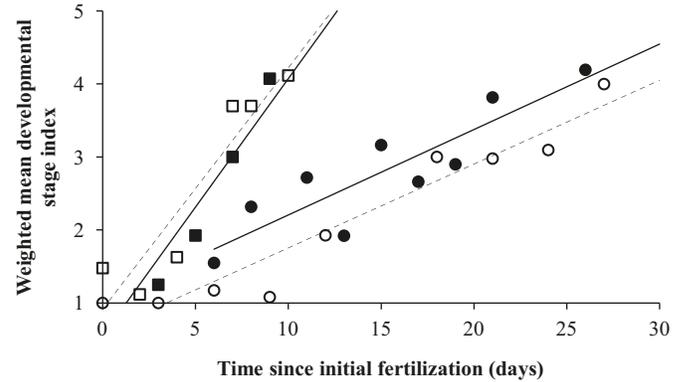
between time to hatch and incubation temperature for capelin (Frank and Leggett 1981). Other factors that could potentially contribute to differences in developmental rates include maternal and multiple cohort effects. For instance, optimal egg size may vary when environmental quality varies throughout the season or between spawning locations (Einum and Fleming 2004). Smaller eggs develop faster than larger ones (Pauly and Pullin 1988), so the possibility exists that eggs deposited at demersal sites are larger than at the beach. Although egg size was not measured in this study, demersal spawning capelin of the northeast Atlantic have larger eggs (1.12–1.17 mm) relative to beach spawning capelin of the northwest Atlantic (0.97 mm; Stergiou 1989). In addition, protracted spawning at demersal sites relative to the beach may result in a multiple cohort effect, thereby skewing WMDSI plots so that developmental rates appear much slower (Penton 2006).

Egg mortality

Temperature influences the normal development of fish eggs, and similarly affects survival (Davenport and Stene 1986; Blaxter 1988; Pepin 1991; Rombough 1997). The beach is a highly dynamic environment and is subject to large fluctuations in temperature owing to the changes in inundation with water as the tide comes in and out, as well as the direct effects of daily solar radiation (Frank and Leggett 1981; Præbel et al. 2009). Although higher temperatures observed at the beach offer the advantage of faster development through the vulnerable egg stage, this comes at the cost of a higher frequency of developmental abnormalities and higher energy requirements for basic metabolic and physiological activities (Pepin 1991). The normal development of marine teleost eggs is sensitive to variations in temperature that can cause thermal stress (Pepin 1991) and at times exceed physiological tolerances (Davenport and Stene 1986; Cossins and Bowler 1987). Therefore, the higher proportion of dead eggs at beach relative to demersal sites is likely due not only to

higher but also to more variable incubation temperatures at the beach.

Water circulation is an important factor contributing to egg mortality, especially among fish with adhesive eggs, such as Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847) (Alderdice and Hourston 1985) and Pacific salmon (genus *Oncorhynchus* Suckley, 1861) (Alderdice et al. 1958; Malcolm et al. 2003). As the egg layer at capelin spawning sites can be up to 15 cm deep (Sætre and Gjøsæter 1975; Frank and Leggett 1981), circulation is essential to replenish oxygen and remove metabolic wastes. Faster developmental rates associated with higher temperatures at beach sites may limit oxygen availability in the egg layer owing to higher metabolic rates, especially when egg densities are high. In support, previous studies on the spawning biology of capelin at beach sites reported that a combination of temperature (determined by inundation with water and solar radiation) and egg density were significant in explaining egg mortality (Frank and Leggett 1981). Similarly, we found a higher proportion of dead eggs at the beach in 2004 when egg densities were higher, despite lower temperatures relative to 2005. Dissolved oxygen was not recorded in either of these studies, but the relatively infrequent inundation of water to egg depth at mid-tidal and high tidal zones on the beach may limit oxygen replenishment and waste removal relative to the more frequently inundated low tidal zone (Frank and Leggett 1981; this study). Results from the demersal sites in this study support this finding. Egg densities at demersal sites in both years were similar to those at the beach in 2004, but egg mortality was lower. In addition, sand ripples found at demersal spawning sites in this study area (Penton 2006) and elsewhere (Sætre and Gjøsæter 1975) indicate that currents are strong enough to move sand along the seabed but are not strong enough to hold the sand in continuous suspension (Middleton 1980). In the context of the physiology of the incubating eggs, this current speed is critical for removing wastes from and supplying oxygen to the egg-bearing sediment layer. Overall, a combination of lower metabolic rates owing to lower temperatures and sufficient water circulation presumably result in lower observed egg mortality at demersal sites.

Although not the focus of this study, predation is an important biotic source of mortality for eggs. At the beach, capelin eggs are preyed upon by beach maggots and can cause 32%–50% mortality among tidal zones in other regions (DeBlois and Leggett 1991). An investigation of winter flounder (*Pseudopleuronectes americanus* (Walbaum, 1792)) predation on capelin eggs in the immediate subtidal zone adjacent to the beach reported mortality of 1.6%–5.0% and suggested that predation is likely higher at demersal sites because of increased accessibility to fish predators and longer incubation times (Frank and Leggett 1984). Although the longer incubation times at the demersal sites lead to longer exposure to predators, egg densities at the demersal site did not show drastic declines during the postspawning period (P.M. Penton, unpublished data) and visual observations of the demersal spawning beds using a remotely operated vehicle did not reveal high densities of flounder or other fish predators (e.g., species of sculpin (family Psychrolutidae); G.K. Davoren, unpublished data).

Conclusions

The general interannual consistency in timing and location of spawning of fish species is a result of adaptations to conditions that are optimal for spawning, egg development, survival, and emergence (Burgner 1991). We hypothesize that capelin achieve at least similar reproductive success within beach and demersal spawning habitats in coastal Newfoundland. This is supported by the persistent spawning of capelin at demersal sites in coastal Newfoundland since at least the late 1990s (Nakashima and Wheeler 2002; Penton 2006; Davoren et al. 2008), as well as the widespread use of demersal spawning habitat throughout the species' range (Table 1). The use of both habitats despite divergent developmental strategies (rapid development, high egg mortality at the beach versus slow development, low egg mortality at demersal sites) suggests that there is some selective advantage to each strategy.

An interesting question is whether the two developmental tactics observed represent phenotypic responses to divergent thermal regimes or genetic divergence of locally adapted subpopulations (Hebert et al. 1998). The latter is supported by the temporal and spatial segregation of beach and demersal spawning capelin in the study area, as well as evidence of divergent larval emergence strategies (Penton and Davoren 2008). This, however, depends on reduced gene flow between spawning habitats, or obligate beach and demersal spawning capelin, a hypothesis that is not currently supported (Dodson et al. 1991).

Further investigation of the spatial extent of demersal spawning combined with comparative studies of egg and larval size, predation, and survival rates at beach and demersal spawning habitats would help resolve the relative contribution of beach versus demersal spawning to recruitment. This, in addition to an examination of possible genetic differences is important because the divergent biology of beach and demersally spawned eggs suggest that each will respond differently to environmental change and, thus, require different approaches for successful management.

Acknowledgements

References

Alderdice, D.F., and Hourston, A.S. 1985. Factors influencing development and survival of Pacific herring (*Clupea harengus*

pallasi) eggs and larvae to beginning of exogenous feeding. Can. J. Fish. Aquat. Sci. **42**(S1): 56–68. doi:10.1139/f85-262.

Alderdice, D.F., Wickett, W.P., and Brett, J.R. 1958. Some effects of temporary exposure to low dissolved oxygen levels on pacific salmon eggs. J. Fish. Res. Board Can. **15**(2): 229–250. doi:10.1139/f58-013.

Andrews, D.W. 2005. Beach spawning of capelin (*Mallotus villosus*) on the northeast coast of Newfoundland. B.Sc. (Hons.) thesis, Department of Biology, Memorial University of Newfoundland, St. John's.

Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. Am. Zool. **36**(2): 216–236. doi:10.1093/icb/36.2.216.

Blaxter, J.H.S. 1988. Pattern and variety in development. *In* Fish physiology. Vol. XIA. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–58.

Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). *In* Pacific salmon life histories. *Edited* by C. Groot and L. Margolis. UBC Press, Vancouver. pp. 1–117.

Carscadden, J.E., and Vilhjalmsson, H. 2002. Capelin—What are they good for? ICES J. Mar. Sci. **59**(5): 863–869. doi:10.1006/jmsc.2002.1283.

Carscadden, J.E., Frank, K.T., and Miller, D.S. 1989. Capelin (*Mallotus villosus*) spawning on the southeast shoal: Influence of physical factors past and present. Can. J. Fish. Aquat. Sci. **46**(10): 1743–1754. doi:10.1139/f89-221.

Chambers, C., and Trippel, E.A. (*Editors*). 1997. Early life history and recruitment: legacy and challenges. *In* Early life history and recruitment in fish populations. Chapman and Hall, London. pp. 515–543.

Clutton-Brock, T.H. (*Editor*). 1988. Reproductive success. *In* Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Illinois, Chicago. pp. 472–486.

Cossins, A.R., and Bowler, K. 1987. Temperature biology of animals. Chapman and Hall, New York.

Davenport, J., and Stene, A. 1986. Freezing resistance, temperature and salinity tolerance in eggs, larvae and adults of capelin, *Mallotus villosus*, from Balsfjord. J. Mar. Biol. Assoc. U.K. **66**(1): 145–157. doi:10.1017/S0025315400039710.

Davoren, G.K., Anderson, J.T., and Montevecchi, W.A. 2006. Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns. Can. J. Fish. Aquat. Sci. **63**(2): 268–284. doi:10.1139/f05-204.

Davoren, G.K., May, C., Penton, P., Reinfort, B., Buren, A., Burke, C., Andrews, D., Montevecchi, W.A., Record, N., deYoung, B., Rose-Taylor, C., Bell, T., Anderson, J.T., Koen-Alonso, M., and Garthe, S. 2008. An ecosystem-based research program for capelin (*Mallotus villosus*) in the northwest Atlantic: overview and results. J. Northwest Atl. Fish. Sci. **39**: 35–48. doi:10.2960/J.v39.m595.

DeBlois, E.M., and Leggett, W.C. 1991. Functional response and potential impact of invertebrate predators on benthic fish eggs: analysis of the *Calliopius laeviusculus*–capelin (*Mallotus villosus*) predator–prey system. Mar. Ecol. Prog. Ser. **69**: 205–216. doi:10.3354/meps069205.

Dodson, J.J., Carscadden, J., Bernatchez, L., and Colombani, F. 1991. Relationship between spawning mode and phylogeographic structure in mitochondrial DNA of North Atlantic capelin *Mallotus villosus*. Mar. Ecol. Prog. Ser. **76**: 103–113. doi:10.3354/meps076103.

Einum, S., and Fleming, I.A. 2004. Does within-population variation in egg size reduce intraspecific competition in Atlantic salmon,

Salmo salar? Funct. Ecol. **18**(1): 110–115. doi:10.1111/j.1365-2435.2004.00824.x.

Frank, K.T., and Leggett, W.C. 1981. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. Can. J. Fish. Aquat. Sci. **38**(11): 1327–1338. doi:10.1139/f81-179.

Frank, K.T., and Leggett, W.C. 1984. Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortality rates, and contribution of egg energy to the annual growth of flounder. Can. J. Fish. Aquat. Sci. **41**(9): 1294–1302. doi:10.1139/f84-158.

Fridgeirsson, E. 1976. Observations on spawning behaviour and embryonic development of the Icelandic capelin. Rit Fiskideildar, **5**: 1–35.

Gjøsæter, H., and Gjøsæter, J. 1986. Observations on the embryonic development of capelin (*Mallotus villosus* Muller) from the Barents Sea. Fiskeridir. Skr. Ser. Havunders. **18**: 59–68.

Hebert, K.P., Goddard, P.L., Smoker, W.W., and Gharrett, A.J. 1998. Quantitative genetic variation and genotype by environment interaction of embryo development rate in pink salmon (*Oncorhynchus gorbuscha*). Can. J. Fish. Aquat. Sci. **55**(9): 2048–2057. doi:10.1139/f98-084.

Jangaard, P.M. 1974. The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition. Bull. Fish. Res. Board. Can. No. 186.

Malcolm, I.A., Youngson, A.F., and Soulsby, C. 2003. Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater–surface water interactions. River Res. Appl. **19**(4): 303–316. doi:10.1002/rra.706.

Middleton, G.V. 1980. Physical processes. *In* Sedimentary processes and animal–sediment relationships in tidal environments. *Edited by* S.B. McCann. Geological Association of Canada, Halifax, N.S. pp. 25–58.

Motoda, S. 1959. Devices of simple plankton apparatus. Mem. Fac. Fish Hokkaido Univ. **7**: 73–94.

Nakashima, B.S., and Wheeler, J.P. 2002. Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters—the interaction between beach and demersal spawning. ICES J. Mar. Sci. **59**(5): 909–916. doi:10.1006/jmsc.2002.1261.

Pauly, D., and Pullin, R.S.V. 1988. Hatching time in spherical, pelagic marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes, **22**(4): 261–271. doi:10.1007/BF00004892.

Penton, P.M. 2006. Demersal spawning in capelin on the northeast coast of Newfoundland. M.Sc. thesis, Department of Zoology, University of Manitoba, Winnipeg.

Penton, P.M., and Davoren, G.K. 2008. Patterns of larval emergence of capelin (*Mallotus villosus*) and environmental cues at demersal spawning sites on the northeastern coast of Newfoundland. Can. J. Fish. Aquat. Sci. **65**(6): 1135–1143. doi:10.1139/F08-037.

Pepin, P. 1991. Effect of temperature and size on development, mortality and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. **48**(3): 503–518. doi:10.1139/f91-065.

Præbel, K., Christiansen, J.S., and Fevolden, S.-E. 2009. Temperature and salinity conditions in a sub-Arctic intertidal spawning habitat for capelin. Mar. Biol. Res. **5**(5): 511–514. doi:10.1080/17451000902729670.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, U.K.

Reed, T.E., Kruuk, L.E.B., Cunningham, E.J.A., Wanless, S., Harris, M.P., and Frederiksen, M. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder.

Proc. R. Soc. Lond. B Biol. Sci. **273**(1602): 2713–2719. doi:10.1098/rspb.2006.3631. PMID:17015329.

Reinfort, B. 2006. Biotic and abiotic factors affecting egg and pre-emergent larval mortality of capelin (*Mallotus villosus*) on a northeast Newfoundland beach. B.Sc. (Hons.) thesis, Department of Zoology, University of Manitoba, Winnipeg.

Rombough, P.J. 1997. The effects of temperature on embryonic and larval development. *In* Global warming: implications for freshwater and marine fish. *Edited* by C.M. Wood and D.G. McDonald. Cambridge University Press, Cambridge, U.K. pp. 177–223.

Sætre, R., and Gjøsæter, J. 1975. Ecological investigations on the spawning grounds of the Barents sea capelin. Fiskeridir. Skr. Ser. Havunders. **16**: 203–227.

Stergiou, K.I. 1989. Capelin *Mallotus villosus* (Pisces, Osmeridae), glaciations, and speciation—a nomothetic approach to fisheries ecology and reproductive biology. Mar. Ecol. Prog. Ser. **56**: 211–224. doi:10.3354/meps056211.

Templeman, W. 1948. The life history of capelin (*Mallotus villosus* O.F. Muller) in Newfoundland waters. Bull. Nfld. Gov. Lab. **17**: 1–151.

Thors, K. 1981. Environmental features of the capelin spawning grounds south of Iceland. Rit Fiskideildar, **6**: 7–13.

Vilhjalmsson, H. 1994. The Icelandic capelin stock. Rit Fiskideildar, **13**: 1–281.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London.