

DEMERSAL SPAWNING IN CAPELIN (*MALLOTUS VILLOSUS*) ON THE
NORTHEAST COAST OF NEWFOUNDLAND

A thesis submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the degree of Master of Science

UNIVERSITY OF MANITOBA
Department of Zoology

Winnipeg, Manitoba, Canada

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Demersal Spawning in Capelin (*Mallotus villosus*) on the Northeast Coast of Newfoundland

BY

Paulette Penton

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
Of
MASTER OF SCIENCE**

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Abstract

Demersal spawning in capelin (*Mallotus villosus*) on the Northeast coast of Newfoundland

Paulette Penton

I investigated the physical characteristics of spawning sites and early life history stages of demersally spawning capelin (*Mallotus villosus*) on the Northeast coast of Newfoundland. I found that the eleven demersal spawning sites discovered during this study (2003-2005) were located primarily in depressions. Site use was associated with the suitability of both the thermal habitat and sediment distribution, demonstrating the importance of these features to the characterization of favourable spawning habitat in demersally spawning capelin. Egg abundance at demersal sites was similar to or higher than at a nearby beach site and egg mortality was higher at the beach in both years of this study. Developmental rates observed at demersal sites in this study do not support previous findings on egg development at the beach. Egg development was slower than at the beach, resulting in demersally spawned eggs hatching 8-10 days later than predicted. Environmental cues that stimulate the release of larvae from the sediment at beaches in Newfoundland occur at demersal spawning sites, but do not appear to stimulate larval emergence. Instead, larvae in good condition appeared to emerge continuously from the sediment. Results from this study suggest that demersal spawning is a viable reproductive mode on the Northeast coast of Newfoundland.

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Chapter 1. General Introduction

Habitat selection is performed by animals that are able to move and make behavioural decisions regarding where to live (Shepherd and Litvak 2004). Parental care is defined as “any behaviour that increases fitness, defined in terms of development and survival of an animal’s offspring” (Clutton-Brock 1988). Breeding habitat selection is a form of parental care and is determined not only by the physiological requirements of the breeding adults, but also those of the developing progeny (Krebs 2001). The proximal approach to the study of habitat selection investigates the behavioural decisions made by an animal in the context of the physiological consequences of selecting a particular habitat (Krebs 2001). Investigation of the physical characteristics of spawning habitat can provide insight into the requirements for successful spawning and development of the early life history stages in fishes (Wootton 1998). The evolutionary approach to the study of habitat selection investigates the adaptive significance of habitat choice in an evolutionary context (Krebs 2001). Spawning habitat selection has implications for the survival of offspring because it directly influences the conditions under which progeny grow and develop. As a result of differing fitness among habitats, habitat selection is roughly equivalent to fitness in evolutionary time (Krebs 2001).

Temperature is a key variable that influences the life history of fishes through developmental and growth patterns of adults and their progeny. Cooler temperatures can cause delayed gametogenesis and growth in adults and slower developmental rates of fish eggs (Cossins and Bowler 1987). As such, temperature can significantly influence population parameters in fish populations (Cossins and Bowler 1987). Growth and

development in fish species are often reported to occur over a narrow range of temperatures (Wootton 1998), suggesting that alterations in temperatures normally experienced by fish would have a deleterious effect on the demographic parameters of fish populations. Individuals, however, can exhibit flexibility in response to changes in temperature in many life history stages, expressed as phenotypic variation (Cossins and Bowler 1987). If these changes produce different fitness values and are heritable, phenotypic plasticity can lead to genetic divergence of populations, acting as a selective force in speciation (Cossins and Bowler 1987). Temperature, therefore, directly influences the life history of fish by altering growth, developmental and survival rates.

Prediction of recruitment success is of major concern and importance to fisheries management (Ricker 1954, Cowan and Shaw 2002). A standard assumption in stock-recruitment relationships is that spawning stock biomass provides a direct measure of recruitment potential (Trippel *et al.* 1997). Difficulties in applying this generality arise when the effects of environmental conditions that regulate survival of early life history stages are not taken into consideration (Frank and Leggett 1994, Chambers and Trippel 1997). Cushing's Match-mismatch hypothesis, similar to the Critical period hypothesis (Hjort 1914), predicts that for successful larval survival and recruitment, marine fish should spawn so that hatching of larvae "matches" peaks in the abundance of its planktonic prey (Cowan and Shaw 2002). A "mismatch" would result in starvation and increased predation due to poorly fed larvae (Mertz and Myers 1994). This has largely been described in temperate species spawning annually in either spring or fall at a time when the ocean environment regulates seasonal plankton blooms (Carscadden *et al.* 1997), and has also been demonstrated within a spawning season, when a water mass

with higher abundance of planktonic prey and lower abundance of larval predators is associated with specific wind events (Frank and Leggett 1982a).

Capelin (*Mallotus villosus*)

Capelin are a small, schooling forage fish that inhabit most northern marine ecosystems. As a short-lived species with the majority of individuals not surviving past four years, capelin populations are subject to large fluctuations in abundance, in part due to predation and fishing pressure (Carscadden and Vilhjalmsson 2002). Consisting of five major stocks, capelin are native to the Northern Hemisphere (Vilhjalmsson 1994) and are thought to have originated in the Pacific, colonizing North Atlantic waters following glaciation (Dodson *et al.* 1991). A genetic comparison of the North Atlantic stock complexes revealed that the spawning populations in Newfoundland (including the Southeast Shoal) are genetically divergent from the demersal spawning stocks of Iceland and the Barents Sea (Dodson *et al* 1991). Historically, the largest stocks in the Atlantic are in Iceland, the Barents Sea, and in Newfoundland and Labrador (Huse 1998) where capelin are important as both a commercial and forage species (Carscadden and Nakashima 1997). As a forage species, capelin transfer large amounts of energy from lower to upper trophic levels and are a vital component in the diets of large predatory fish, such as Atlantic cod (*Gadus morhua*), marine mammals and seabirds (Carscadden and Vilhjalmsson 2002).

Throughout their distribution in the North Atlantic, capelin spawn demersally in depths up to 280 m but spawning primarily takes place on sediments in water less than 75 m deep (Saetre and Gjosaeter 1975). The Barents Sea and Icelandic capelin stocks

occupy deep-water (demersal) spawning beds (Thors 1981), whereas beach spawning is the primary reproductive mode for the Newfoundland population (Templeman 1948). Templeman (1948) hypothesized that demersal spawning in coastal areas may occur late in the spawning season if beach temperatures become too warm. A study investigating this hypothesis, however, reported simultaneous beach and demersal spawning in the summer of 2000 (Nakashima and Wheeler 2002). This study also concluded that capelin "prefer" to spawn intertidally because they found larval emergence from demersal spawning to be negligible in 2000.

In Newfoundland, a large area of demersal spawning occurs 350 km from the nearest beach on the Southeast Shoal in Newfoundland (Templeman 1948). Carscadden *et al.* (1989) proposed that the capelin spawning in this region were once a population of beach spawners when the Southeast Shoal was exposed prior to the late Wisconsin glaciation but as the glaciers melted, the Southeast Shoal became submerged. Capelin still spawn in this region, representing the only known historical demersal spawning site in Newfoundland (Carscadden *et al.* 1989).

Although the timing is different among the geographically distinct stocks, the general life cycle of capelin remains the same. Capelin spend most of their life (~3-5 years) feeding in offshore waters and at maturation undergo extensive inshore migrations to spawning grounds (Carscadden and Nakashima 1997), ranging in depth from 0 – 90 m throughout their circumpolar distribution. Males form dense aggregations near the spawning beds and as females ripen, they enter the male spawning schools to engage in the spawning act (Vilhjalmsson 1994). After the brief spawning act, the spent females

leave the spawning areas while males rejoin the spawning school to complete several matings in a spawning season (Fridgeirsson 1976).

Because large numbers of dead capelin that wash up onto the beach after spawning, capelin are typically considered to be semelparous with adults dying after a single breeding season (Jangaard 1974). Recent studies, however, have shown that the life history of capelin is sex-specific; males are semelparous batch spawners while females exhibit varying degrees of iteroparity (Huse 1998). Males allocate the majority of their energy resources to physical activity (Huse 1998), allowing them to complete multiple spawnings under the high physical and physiological demands of the male spawning act (Shackell *et al.* 1994). In contrast, females allocate resources to egg production but because they are total spawners, extruding all eggs at once, they are able to increase their fitness by switching to an iteroparous strategy and maintain just enough energy reserves to commence feeding (Huse 1998). Almost half of spawning females are found to survive to the next spawning season (Shackell *et al.* 1994). This change in life-history strategy, however, depends on predation pressures after spawning, with iteroparity advantageous only when adult mortality is low (Roff 2002).

Capelin eggs are adhesive, sticking to the sediment throughout the incubation period. As a result of several spawning pairs mating at the same location, a thick layer of sediment and eggs is formed (Fridgeirsson 1976), up to 15 cm deep (Saetre and Gjosæter 1975). Different larval emergence mechanisms in capelin have been proposed to suggest different stocks (Fortier *et al.* 1987). Upon hatching, capelin larvae of the Barents Sea and Icelandic stocks are thought to drift to the surface, although this hypothesis has not been tested (Vilhjalmsson 1994). In the beach spawning populations of capelin in

Canada, when the eggs hatch, the resulting pre-emergent larvae remain in the sediment until synchronous active emergence into the water column is stimulated by environmental cues in the form of wind events and low light intensities (Frank and Leggett 1981, Fortier *et al* 1987). In coastal Newfoundland, capelin that spawn at the beaches are stimulated to emerge into conditions that are ideal for their survival by the infrequent occurrence of onshore wind events that cause Coastal Water Mass Replacement (Frank and Leggett 1981, 1983). Onshore winds cause warm surface water associated with high larval capelin prey densities and low predator densities to move into the coastal region (Frank and Leggett 1982). In capelin, the yolk sac is quickly depleted after hatching (3.2-10 days at mid- and high-tide Frank and Leggett 1982b) and as such, pre-emergent larvae represent a critical stage in larval survival. If the time interval between environmental cues is too long, there is an increasing proportion of larvae in poor condition at the onset of drift due to starvation. Upon emergence, the emergent yolk-sac larvae drift into the water column where they commence exogenous feeding (Carscadden and Nakashima 1997). Once in the pelagic environment, larvae are quickly and passively transported to offshore waters to feed and mature (Leggett *et al.* 1984).

Northwest Atlantic Ecosystem

In the 1990s, the Northwest Atlantic experienced an anomalous cold water event, with 1991 identified as the coldest year on record (Colbourne *et al.* 1994, Nakashima 1996). Since 1991, the population mean length of mature capelin has been smaller due to both a higher proportion of age two fish, and smaller 3- and 4- year-old fish in the spawning population (Nakashima 1996, Carscadden *et al.* 1997). In addition, capelin spawning was

delayed and protracted during the early 1990s, presumably because of colder than normal water temperatures during gonadal maturation in late-winter and early-spring (Nakashima 1996). Nakashima and Wheeler (2002) have hypothesized that this may result in increasing occupation of demersal spawning locations in coastal areas due to high temperatures that are unsuitable for spawning at the beach late in the season (Nakashima and Wheeler 2002). Conditions have been warming since the 1990s (Dalley *et al* 2002) but evidence of two spawning tactics have been documented on the Northeast coast of Newfoundland since 2002 (Davoren *et al* 2006). If demersal spawning does not contribute to recruitment but it is predicted to increase with increasing climate warming (Nakashima and Wheeler 2002), this may result in significant population declines of the focal forage fish in the Northwest Atlantic.

Thesis Objectives

The goal of my thesis is to examine demersal spawning in capelin and the relative egg survival of beach versus demersally spawned capelin. My research is partitioned into three major sections. Initially, I investigated the physical characteristics of demersal spawning sites of capelin on the Northeast coast of Newfoundland (Chapter 2). I quantified observed sediment size and temperature, the critical physical characteristics of capelin spawning habitat, and compared this to observed ranges across their circumpolar distribution. Habitat preferences were inferred from variability in spawning site use among years.

The second component of my research involved an investigation of the viability of demersal spawning as a reproductive tactic in capelin (Chapter 3). Egg deposition,

developmental and survival rates at demersal sites were examined relative to beach sites. I tested if there was a difference in 1) the number of eggs deposited, 2) rate of egg development, and 3) egg survival between beach and demersal sites. I predicted that egg deposition would be higher at demersal sites in warmer years and that developmental rates would be slower and that mortality would be lower at demersal relative to beach spawning sites, owing to divergent temperature regimes.

The third component of my research investigated the larval stage of capelin spawned at demersal sites (Chapter 4). This involved an investigation of the importance of environmental factors to the emergence and survival of demersally spawned larvae. I tested if destratification of the water column resulted from Coastal Water Mass Replacement (Frank and Leggett 1982) during the post-hatching period and, if so, whether this resulted in the synchronous emergence of larvae from demersal spawning sites.

These investigations have major implications for stock assessments and the determination of recruitment and year class strength for capelin in Newfoundland and Labrador. The results of these investigations are synthesized in the context of stock structure and recruitment of the keystone forage fish in the Northwest Atlantic (Chapter 5).

Chapter 2. Ecological investigations of demersal spawning grounds of capelin (*Mallotus villosus*) on the Northeast coast of Newfoundland

2.1. Introduction

Spawning site selection and timing of spawning are major components of parental care in fish (Mann *et al.* 1984) and determine the habitat in which the critical early life stages of progeny grow and develop. Most marine fish are non-guarding, egg-scattering pelagic spawners (Balon 1984), a strategy that is utilized by 45% of the most common teleosts in the North Atlantic (Mann *et al.* 1984). Less common is the substrate spawner whose reproductive strategy prevents the dispersal of eggs from nursery areas and is considered a fundamental step in the evolution of parental care in fish (Mann *et al.* 1984).

Capelin are substrate spawners and spawn at both beaches and at demersal sites throughout their circumpolar distribution. The beach-spawning Pacific capelin are thought to have colonized the Atlantic after the Wisconsin glaciation (Dodson *et al.* 1991). Stergiou (1989) hypothesized that a lack of suitable beach habitat in the North Atlantic led to the evolution of demersal spawning. In the Barents Sea and Icelandic stocks, capelin spawn demersally (Table 2.1) but also spawn on beaches in local fjords. Conversely, in Newfoundland, capelin are thought to spawn primarily on beaches with the exception of the Southeast Shoal (Table 2.1), a demersal spawning location that is 350 km from shore.

Table 2.1: Physical characteristics and timing of spawning at spawning sites of capelin (*Mallotus villosus*) throughout the North Atlantic.

	Barents Sea	Balsfjord	Iceland	West-Greenland	Newfoundland (beach)	Newfoundland (Southeast Shoal)	Source
Depth (m)	12-280 (but most <75 m)	0	40-80	0	0	8-90	1,2
Temperature (°C)	1.5-5.0	?	5.0-7.0	1.9-6.6	5.5-10.8	2.8-6.3	1,3,4-7
Grain Size (mm)	5.0-15.0	?	1.0-4.0	?	2.0-25.0	0.5-2.2	1,5,7-8
Timing of Spawning	March-April	May	March	May-June	June-July	?	2

Sources: 1) Thors 1981, 2)Vilhjalmsson 1994, 3) Saetre and Gjosætre 1975, 4) Sleggs 1933, 5) Templeman 1948, 6) Frank and Leggett 1981, 7) Carscadden 1989, 8) Taggart and Nakashima 1987

For beach spawning capelin of Newfoundland, sediment size, water temperature and beach orientation are considered to be abiotic factors critical for spawning habitat (Templeman 1948, Nakashima and Taggart 2002). The criterion for habitat selection of capelin that spawn demersally in the North Atlantic are hypothesized to be water circulation (Thors 1981), temperature and sediment size (Carscadden *et al.* 1989). Although these physical characteristics of spawning sites appear to be critical to both reproductive tactics, they vary widely among the different stocks in the North Atlantic (Table 2.1).

For capelin, preferred spawning sediment size varies, ranging from coarse sand (0.5 mm) to cobble (25.0 mm) (Table 2.1). The preference for sediment in the observed size range offers several advantages for spawning capelin. Male capelin bury the eggs in the sediment, resulting in physical damage to the male that would be increased at larger grain sizes, perhaps preventing several matings of male capelin (Vilhjalmsson 1994). Although the spawning motion buries the eggs somewhat, waves further bury eggs up to 20 cm deep in the sediment at beaches (Leggett and Frank 1990). If the particle sizes of the sediment were too small, both the eggs and sediment could potentially be transported away from the beach (Templeman 1948). At demersal spawning sites, the grain size selected is related to the mixing energy at the sediment/water interface (Frank and Carscadden 1989) and is related to the Hjulstrom (1939) curve that describes the relationship between grain size and the current velocity required to move the sediment (Saetre and Gjosæter 1975, Frank and Carscadden 1989). According to this curve, sediment is selected in an optimal size range. The preferred spawning sediment is large enough to prevent transport but small enough to allow mixing of the eggs with the

sediment (Frank and Carscadden 1989). In addition, selection of sediments in the observed ranges provide adequate surface area for egg attachment and prevents siltation, which reduces circulation of water through the egg layer (Thors 1981). Because capelin eggs can be buried up to 20 cm in the sediment (Leggett and Frank 1990), circulation of seawater through this layer is essential both to remove metabolites and to supply the eggs with oxygen necessary for embryonic development (Templeman 1948, Thors 1981).

Temperature has been cited as an important factor in explaining variability in the timing of spawning in capelin (Carscadden *et al.* 1997). Seasonal timing of spawning in capelin is determined by annual migration patterns that are linked to temperature through maturation (Shackell *et al.* 1994, Carscadden *et al.* 2001). In Newfoundland, zooplankton production is later in cold years, resulting in delayed feeding and maturation of adult capelin and later migration to inshore spawning grounds (Carscadden *et al.* 1997). The timing of spawning at coastal sites is also influenced by temperature. Capelin spawn at a range of temperatures but generally exhibit a preference for spawning at water temperatures between 3-10°C (Table 2.1) (Vilhjalmsson 1994, Nakashima and Wheeler 2002).

Many species of fish exhibit critical upper and lower thresholds of temperature for spawning (Cossins and Bowler 1987). These thresholds may act as environmental cues associated with ideal conditions for survival of early life history stages, or as a physiological constraint that limits when and where to spawn. The temperature threshold for spawning in capelin affects the location of spawning sites throughout their circumpolar distribution. For example, on the Southeast Shoal of Newfoundland, demersal spawning is spatially restricted to areas where temperatures exceed 2°C

(Carscadden *et al.* 1989). In the Northeast Atlantic, relatively warm Atlantic waters dominate and capelin spawn demersally with the exception of beach spawning in fjords. Alternatively, capelin are thought to spawn primarily on beaches during the summer months in Newfoundland where polar waters are dominant and thermal requirements for spawning can be met only in shallow water during summer months as a consequence of solar heating of the surface layer (Vilhjalmsson 1994). Templeman (1948) proposed, however, that if beach temperatures become too warm late in the season, capelin will spawn demersally in the subtidal region.

Demersal spawning in capelin was recently documented in coastal Newfoundland (Bellevue Beach and the Straight Shore) since 2000 (Nakashima and Wheeler 2002, Davoren *et al.* 2006). Fisheries and Oceans Canada has been conducting research at a major capelin spawning area (Bellevue Beach, Trinity Bay; Fig. 2.1) since 1990 (Nakashima and Slaney 1999 cited in Nakashima and Wheeler 2002) and described the biophysical characteristics of shallow (<20 m) spawning sites in a large embayment (Nakashima and Wheeler 2002). The objectives of this study were to describe the spawning behaviour and physical site characteristics of demersally spawning capelin on the exposed Northeast coast of Newfoundland.

2.2. Methods

Study Design

This study was conducted within the 50 m depth contour on the exposed Northeast coast of Newfoundland ($49^{\circ}11'N$, $53^{\circ}27'W$ to $49^{\circ}27'N$, $53^{\circ}47'W$) during July-August 2003-

2005 (Fig. 2.1). Each year aboard the *Lady Easton II*, a 13.4 m commercial fishing vessel which operated 12 h·d⁻¹ during daylight, the first seven days of the survey were dedicated to the discovery of new demersal spawning sites and revisiting all previously identified sites to check for presence of capelin and capelin eggs. Discovery efforts were focused within the 50 m depth contour because historical temperature data within this area in July and August is consistently >0°C (Davoren *et al.* 2006). After the initial discovery period, research focused on monitoring egg development, survival, and hatching, along with physical habitat features, including temperature and sediment characterization.

Spawning site discovery

During the study period, demersal spawning sites were located using a combination of methods. Large aggregations of birds and whales were a good indicator of demersal spawning sites (Davoren *et al.* 2006). Potential spawning sites were visited based on the location of traditional capelin fishing grounds of a local fisher (Larry Easton). The presence of concentrations of capelin schools observed acoustically was also used as a potential sign of demersal spawning sites. These methods have been used for identifying demersal spawning sites in the Barents Sea (Saetre and Gjosæter 1975). Upon identification of a potential site through any combination of these methods, a Remotely Operated Vehicle (ROV) equipped with an underwater video camera (VideoRay PRO; Video Ray LLC, Phoenixville, Pennsylvania) was deployed for visual confirmation of the presence of capelin eggs and to observe capelin spawning behaviour. All observations were recorded on VHS tape with a VCR and video recordings were later viewed to

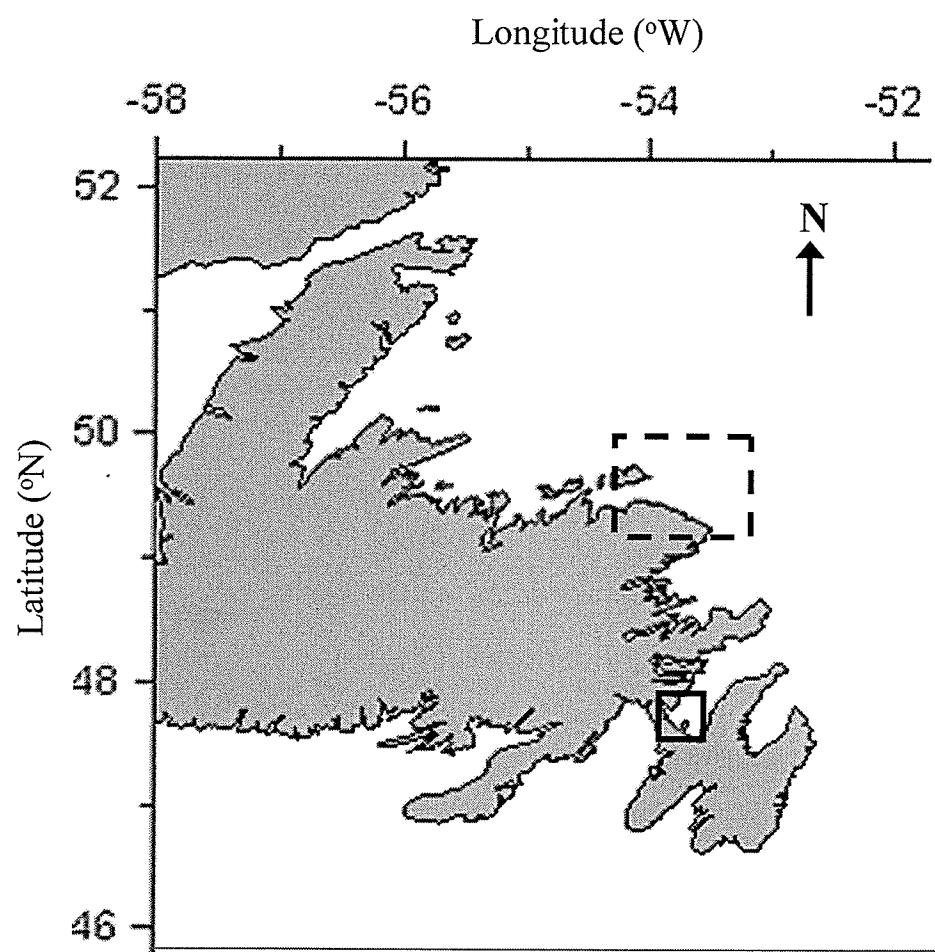


Figure 2.1: Map of Newfoundland with the study area (the Straight Shore-dotted line) and Fisheries and Oceans study area (Bellevue Beach-straight line) indicated.

describe the physical characteristics of spawning sites and the behaviour of capelin, both in response to the ROV moving into the shoal, and behaviour when accustomed to the presence of the ROV.

Biological Samples

After initial discovery, demersal spawning sites were sampled to determine egg densities as well as their developmental and survival rates. In each year (2003-2005), egg bearing gravel was collected at demersal spawning sites using a 0.3 m² Van Veen Benthic Grab System. For each grab sample, the bottom depth and location (latitude and longitude) were recorded. Eggs in Stages I-II (Table 3.1) are associated with recent fertilization and the time interval of each stage is determined by the incubation temperature (Nakashima and Wheeler 2002). Sampling intervals in 2004-2005 were determined in each year based on average daily incubation temperatures at the spawning sites to ensure that new spawning events were recorded without re-sampling previously spawned eggs. Consequently, in 2004, sampling occurred every third day after the start of spawning, and every second day in 2005.

On each sampling day, three replicate bottom grabs were retrieved from each spawning site and each sample was placed in a separate 40 L bucket. Over the three years, two samples of eggs/sediment were collected from each grab sample: one sample of varying volume was preserved in 5% formalin solution buffered with sodium borate for determination of egg density and particle size composition (Formalin sample), and a 20 mL sample (minimum 50 eggs) was preserved in Stockard's solution to determine development rates and egg survival (Stockard's sample). Stockard's solution clears the

yolk-sac and allows determination of developmental stages (Frank and Leggett 1981). A random sample of 50 eggs from each Stockard's sample was examined to determine the proportion of eggs in Stage I-II. I determined the approximate timing and duration of spawning events by the presence of Stage I-II eggs.

The Formalin sample was not sampled consistently among years of this study, as the most appropriate methodology was being determined. In 2003, samples were used specifically to characterize particle size composition and egg densities were not determined. 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 opening the grab and releasing the sediment into the 40 L bucket, allowing the layering of eggs to remain intact. A sample was collected using a core with a 6 cm internal diameter and the egg depth was recorded. For each core, egg depth did not exceed the depth of the core sample.

For each egg/sediment sample, capelin eggs were removed from the sediment in the laboratory. Samples were poured over a 0.270 mm sieve and rinsed with water for ~20 min. The sample was placed back into the jar and topped up with 2% KOH solution and soaked for 24 hours to separate adherent eggs from the sediment. Eggs and other biological material were then decanted off into the sieve. Sediment samples were saved for later particle size composition analysis and eggs were placed into 95% ethanol for one week to harden the eggs, reducing buoyancy. Eggs were sub-sampled using a 1 L capacity Motoda splitter (Motoda, 1959) and the final split (~200-300 eggs) was placed into a Petri dish and eggs were counted using a dissecting microscope.

A standard egg abundance estimate was developed to compare abundances between years and among sites. Egg abundance was expressed as an areal density by dividing the average number of eggs per core by the surface area of the apparatus used to core the sample. The number of newly deposited eggs on each day was determined by multiplying the average number of eggs in the three replicate Formalin samples by the average proportion of eggs in developmental Stage I-II in the three replicate Stockard's samples. This allowed the determination of peak spawning, which is defined as the day(s) when the average Stage I-II egg densities were highest over the entire spawning period.

Total annual deposition of eggs during spawning at each site was estimated using trapezoidal integration to interpolate between point estimates of average Stage I-II egg densities:

$$\sum(t_n - t_{n-1})1/2[X(t_n) + X(t_{n-1})]$$

where t is date, n is number of sampling days, and $X(t)$ is the average number of Stage I-II eggs on day t . To correct for missed spawning events in 2005 (i.e. all eggs were beyond the Stage I-II on the first sampling day), all eggs on the first sampling day ($t=1$) were considered Stage I-II (i.e. $X(t)=$ average number of eggs counted, regardless of what developmental stage they were in) to allow previously spawned eggs to be included in calculation of annual deposition.

Physical Samples

Temperature profiles of the water column were measured in 2003-2004 using a Sea Bird SBE-19, deployed from the ship at $1\text{m}\cdot\text{s}^{-1}$, allowing data capture every 20-50 cm from the ocean floor to the surface. In 2003, temperatures recorded at the seabed were used to

characterize incubation temperatures of eggs at demersal sites, whereas in 2004-2005 *in situ* thermisters were used. In 2004-2005, Vemco Miniloggers (Vemco 8-bit Minilog-TR) were moored at the seabed and temperature was recorded every 20 min to determine daily incubation temperatures. In both years, thermisters were deployed at all known spawning sites on the first day of sampling to characterize pre-spawning thermal habitat if spawning had not begun, and at new sites upon discovery. I calculated mean daily temperature throughout the incubation period to characterize temperatures during development of eggs at each site and to make among-site and interannual comparisons.

Sediment samples were analyzed for particle size composition at demersal sites in 2003 and 2004. The sediment retained after removal of eggs was oven-dried (75 °C) for 48 h. Dried sediments were then sorted using a series of sieving screens (in mm; 0.15, 0.25, 0.5, 0.7, 1.0, 2.0, 4.0, 8.0, 11.2, 16.0, 22.4, and 31.5). The size fraction remaining on each screen was weighed to determine the proportion that each size fraction contributed to the total sample according to the Udden-Wentworth scale of sediment/rock size classification (Wentworth 1922). We summarized the categories as: <0.50 mm (silt and fine sand), 0.5-1.0 mm (coarse sand), 1.0-2.0 mm (very coarse sand), 2.0-4.0 mm (gravel), 4.0-8.0 mm (pebble), and >8 mm (cobble).

The position (latitude, longitude) and depth of all bottom grab deployments at each demersal site from all three years were combined to construct a fine-scale depth contour map of each demersal spawning site using the Krigging Method in Surfer 8.0 (Golden Software). Mean depth of each spawning site was calculated from those samples where eggs were collected at each site in each year.

2.3. Results

Spawning behaviour

In 2004, capelin were observed acoustically in the study area on the first day aboard the ship (July 21) and were absent after August 14. In 2005, the majority of spawning had occurred prior to the start of sampling. Acoustic signals of capelin at spawning sites were dominated by two shoal types: capelin that were distributed loosely, occupying ~10 m (range: 5-20 m) of the water column (Fig. 2.2A) or as a densely packed thin layer tight against the spawning bed (Fig. 2.2B). When capelin were distributed throughout water column, the echo-sounder registered the top of the school as the bottom depth (Fig. 2.2). Video observations of these shoal types revealed that the first shoal type (Fig. 2.2A) was composed of pre-spawning male capelin. These fish immediately responded to the presence of the ROV by dispersing; however, once the ROV remained stationary on the seabed for 30-60 s, males resumed their activity, all swimming in the same direction in a circular pattern around the spawning site. This shoal type will be hereafter referred to as the dispersed shoal. The second shoal type (Fig. 2.2B) was observed only when spawning had been confirmed by the presence of eggs adhered to sediment. This shoal was characterized by a very dense, thin layer that was close to the seabed, approximately 1-2 m in vertical height. Scattered, unresponsive males were observed in the water column, above the second shoal type during descent of the ROV to the seabed. Fish in the shoal did not respond to the presence of the ROV and remained tight against the seabed as the ROV descended from the ocean surface and dispersed laterally only when the ROV was

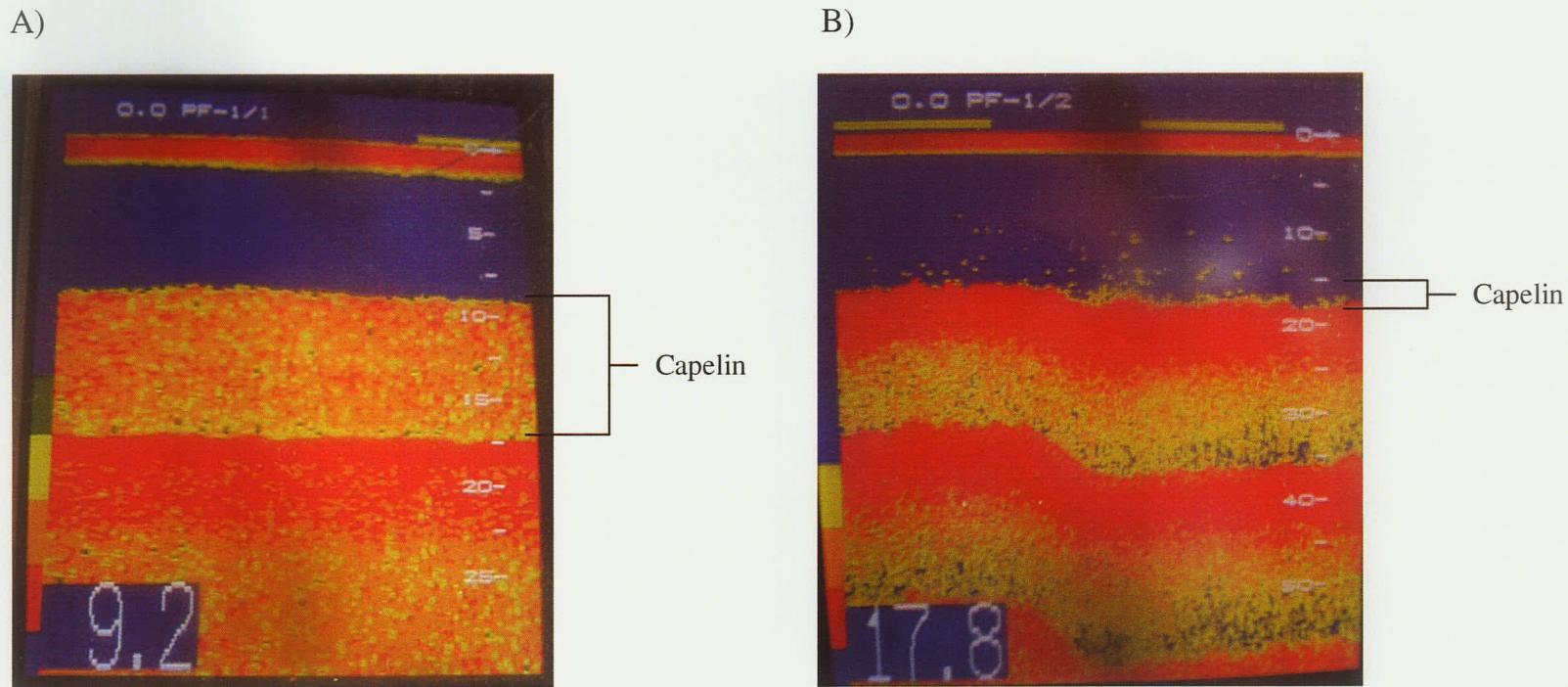


Figure 2.2: Image taken from the sounder on the ship of the acoustic signals of capelin at demersal spawning sites showing: (A) pre-spawning capelin school with males distributed 12.3 m in the water column, and (B) spawning capelin with males and females forming a dense thin layer, indistinguishable from the bottom. Depth shown (blue background) in each figure is in meters.

about to touch down on the seabed. In the shoal, individual fish could not be distinguished from one another so visual confirmation of the sex composition of this shoal type was not possible. Bottom grab samples ($n=4$), however, incidentally collected both male ($n=17$) and female ($n=1$) adult capelin in spawning condition. This shoal will be referred to hereafter as the dense shoal.

Physical Characteristics

Eleven demersal spawning sites were discovered during 2003-2005 (Fig. 2.3). Demersal sites were located 2.5-17.7 km from shore and ranged in depth from 17.2 to 37.5 m (Table 2.2).

With the exception of Cracker's Rock, Northern Penguin Island, Deadman's Bay III and IV, capelin spawning sites were located in depressions or hollows ranging from 2-10 m deeper than the surrounding area (Table 2.2). Capelin were found spawning primarily in two types of depressions in the study area: gently sloping, shallow bathymetric trenches that run parallel to the shore (Fig. 2.4), and those that were located in discrete bathymetric hollows, confined by steep walls of bedrock on more than one side (Fig. 2.5).

Sediment size distribution at demersal spawning sites was variable and ranged from coarse sand to pebble (Fig. 2.6). The sediment at sites within hollows was composed primarily of sand (Fig. 2.6). Those sites that were not within depressions or

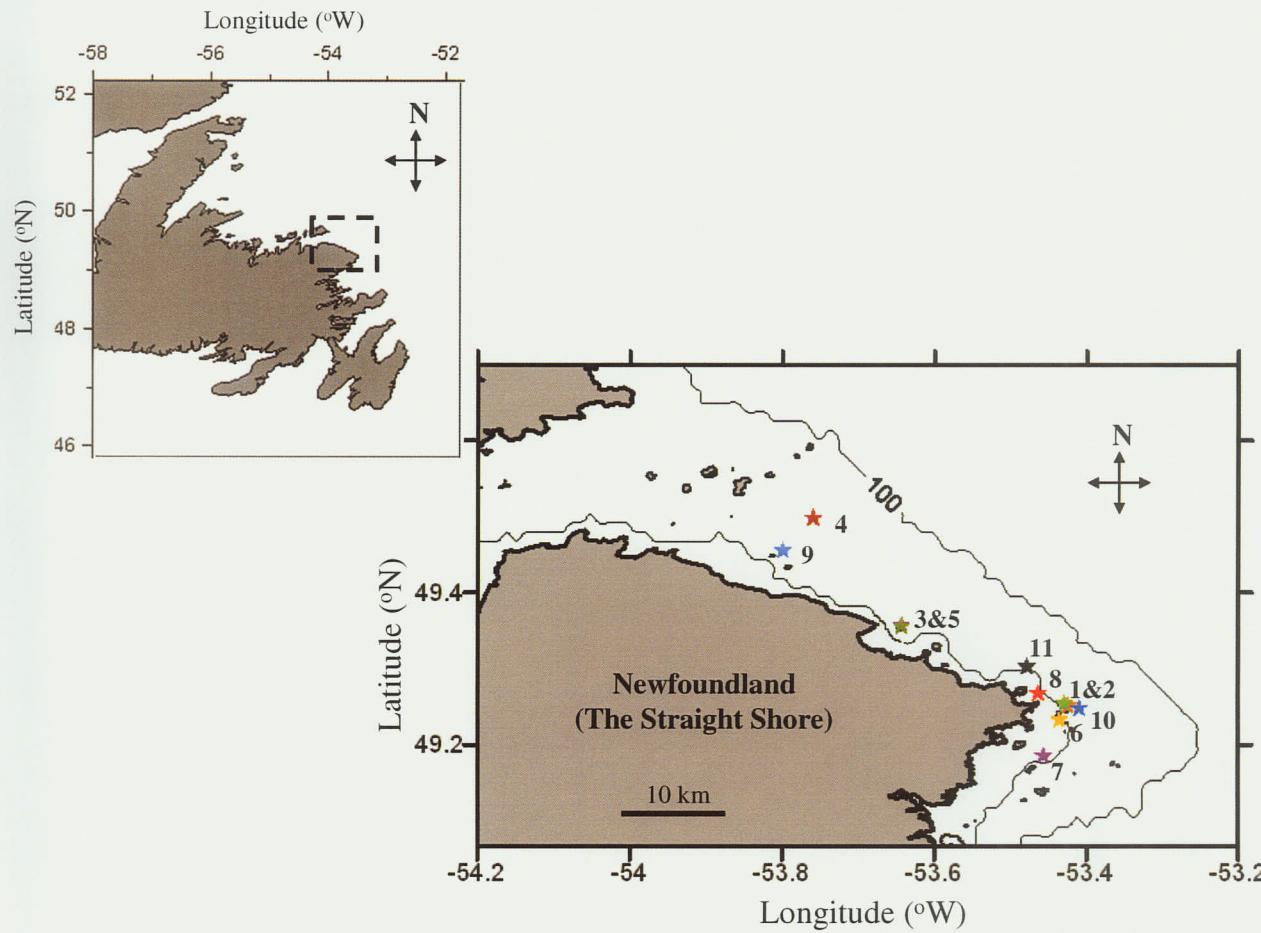


Figure 2.3: Study site on the Northeast Coast of Newfoundland (the Straight Shore) with the location of demersal spawning sites discovered from 2003-2005 (star). Inset: Map of Newfoundland. (1=Gull Island I, 2=Gull Island II, 3=Deadman's Bay III, 4=Penguin Island, 5=Deadman's Bay V, 6=Turr Island, 7=Hinckes Rock, 8=Cracker's Rock, 9=Northern Penguin Island, 10=Gull Island III, 11=Windmill Bight).

Table 2.2: Physical characteristics of demersal spawning sites on the Northeast coast of Newfoundland (2003-2005), where S=spawning site used, NS=no spawning, and ND=not discovered.

Site	Distance from shore (km) ¹	Mean Depth ± SD (m) ²	Mean Daily Incubation Temperature ± SD (°C) ³		
			2003	2004	2005
Gull Island I (hollow)	4.3*	32.7± 0.2	4.3 ± 0.5 (3.6-4.8) S	3.1 ± 1.1 (0.7-8.6) S	5.2 ± 1.4 (2.5-12.9) S
Gull Island II (hollow)	3.8*	26.1± 0.2	7.0 ± 1.9 (4.7-9.2) S	5.9 ± 3.7 (1.6-16.2) S	— S
Deadman's Bay III (no depression)	3.9	29.3± 0.1	4.6 ± 1.2 (2.9-5.7) S	3.7 ± 0.1 (1.7-16.9) NS	6.0 ± 0.0 (3.4-11.7) NS
Penguin Island IV	17.7*	23.5± 3.5	4.3 ± 0.5 (3.7-4.7) S	2.8 ± 0.0 (1.3-5.2) NS	6.1 ± 0.0 (4.6-8.3) S
Deadman's Bay V (no depression)	3.9	30.1± 0.1	3.2 ± 0.2 (3.0-3.3) S	— NS	— NS
Turr Island (depression)	3.2*	17.3± 0.1	— ND	8.6 ± 3.6 (2.8-16.6) S	10.4 ± 2.6 (4.8-15.3) S
Hinckes Rock (depression)	5.4*	21.9± 3.6	— ND	5.6 ± 1.1 (3.2-7.6) S	— NS
Cracker's Rock (no depression)	2.5	19.0± 0.2	— ND	8.6 ± 4.0 (2.2-16.9) S	10.4 ± 2.9 (4.3-16.2) S
Northern Penguin Island (no depression)	10.1	24.4± 1.0	— ND	3.76 (3.2-4.1) S	9.0 ± 0.0 (6.2-15.4) NS
Gull Island III (hollow)	5.9	37.5± 3.3	— ND	— ND	4.3 ± 1.1 (2.5-9.2) S
Windmill Bight (hollow)	5.8	38.3	— ND	— ND	— S

¹ Asterick indicates sites that are located near (<1 km) from an island that shelters the southward moving Labrador Current

² Depth is taken as an average of all bottom grab samples that yielded egg samples

³ In 2003, temperature data at demersal sites were collected with a SeaBird 19, whereas in 2004 and 2005, data were collected with thermisters. Data in parentheses is the overall temperature range at the site.

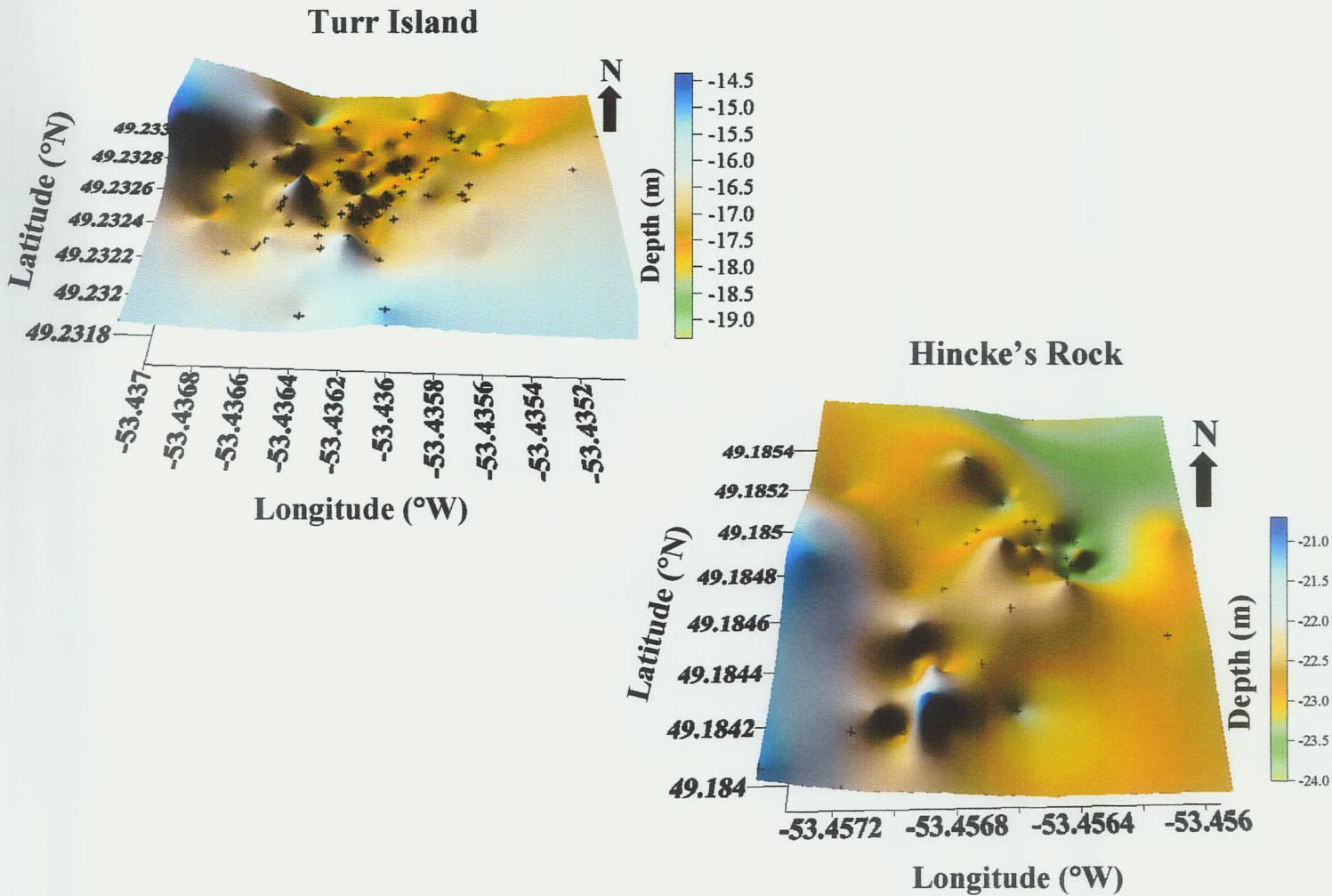


Figure 2.4: Surface maps of shallow depressions (Turr Island and Hinckes Rock). Note: x's indicate bottom grab samples where eggs were collected.

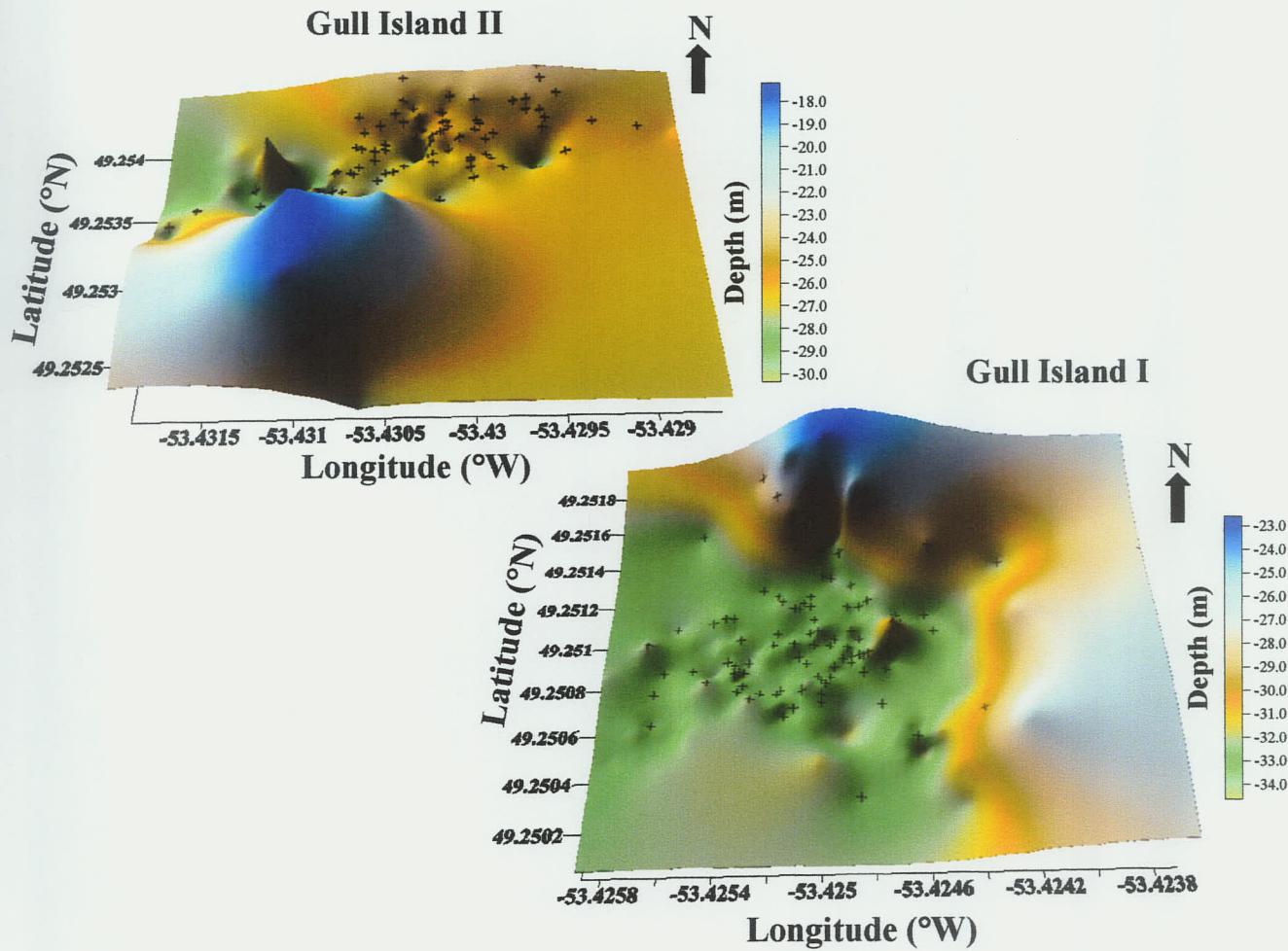


Figure 2.5: Surface maps of deep bedrock hollows (Gull Island I and II). Note: x's indicate bottom grab samples where eggs were collected.

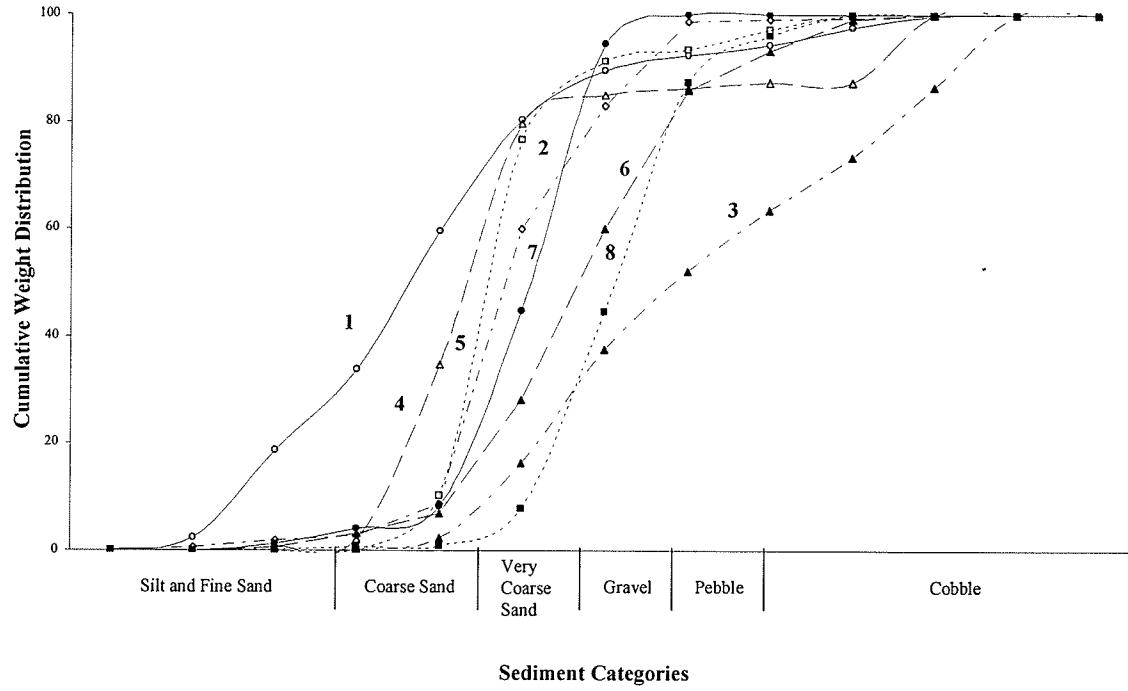


Figure 2.6: Cumulative percentage sediment grain size (geometric mean, mm) at eight demersal spawning sites on the Northeast coast of Newfoundland. (1=Gull Island I, 2=Gull Island II, 3=Deadman's Bay III, 4=Penguin Island, 5=Deadman's Bay V, 6=Turr Island, 7=Hinckes Rock, 8=Cracker's Rock).

hollows (Table 2.2) were dominated by bedrock with patchy areas of suitable sediment with adhered eggs. The availability of suitable sediment size varied interannually at these bedrock sites. For instance, at Deadman's Bay in 2004, 48 grab samples were collected but only seven contained suitable sediment. The same was true for both Deadman's Bay sites in 2005. Spawn was observed both as a thin layer on bedrock, and on large cobble (up to 17 cm at maximum width) with coralline algae covering the surface of these large rocks. Interestingly, visual assessment suggested that the size of the protuberances on the coralline algae covering cobble was within the range of appropriate sediment sizes. Video observations revealed sand ripples at all sites not dominated by bedrock.

Average daily water temperatures during incubation were variable both within (Fig 2.7) and among years (Table 2.2). A single factor ANOVA (year) revealed significant differences in mean incubation temperatures at demersal sites between years ($F_{[2,88]}=6.28$, $p=0.003$), primarily influenced by 2005 (7.58 ± 3.3 °C) being warmer than 2004 (5.93 ± 2.3 °C) (*post hoc Scheffe's test*, $p=0.05$). Although data were limited in 2003 and, thus excluded from the above statistical comparison, a comparison of temperatures among years at a single site demonstrated that water temperatures were warmest in 2005, followed by 2003 and 2004. To illustrate, from 8-21 August, water temperature at Gull Island I ranged from 3.6-4.8°C in 2003 ($n=4$), 1.5-3.3°C in 2004 ($n=5$) and 4.8-8.9°C in 2005 ($n=7$).

In 2004, when temperatures during the spawning period were recorded at all sites, spawning occurred over a narrow range of temperatures (range: 2.7-6.9°C; Fig. 2.7). At Penguin Island and Gull Island I and II, acoustic signals of the dispersed shoal type were

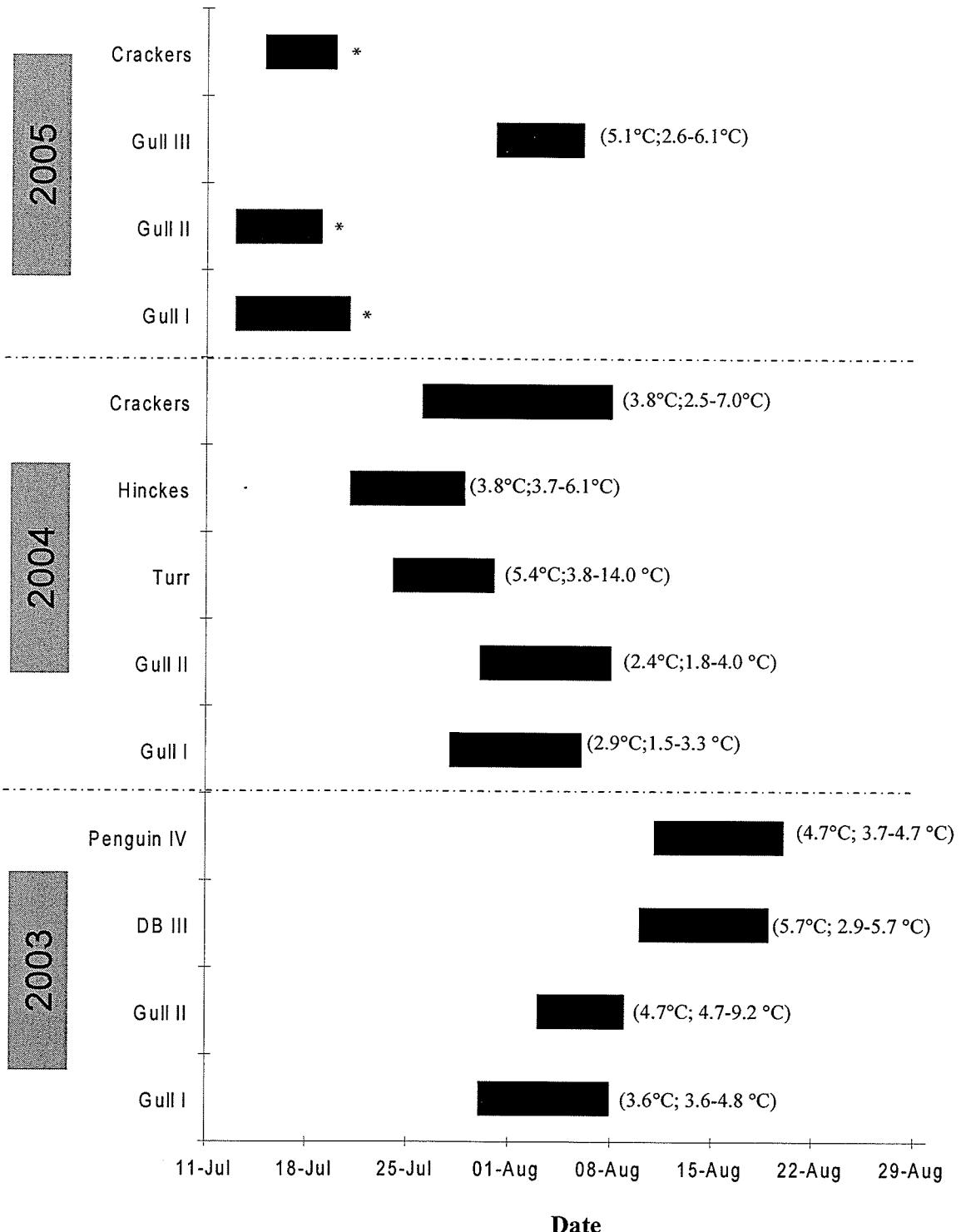


Figure 2.7: Timing and duration of spawning (estimated from developmental rate plots- see Chapter 3) indicating temperature on the first day of spawning and range during spawning at sites from 2003-2005. Note: * Indicates missed temperatures during spawning.

observed for up to seven days at spawning sites during the discovery period but eggs were not deposited immediately. At Gull Island I and II, capelin spawned when temperatures increased above 2°C and continued to spawn when temperatures decreased again after the initiation of spawning. At Penguin Island, water temperature did not increase above 2°C until after capelin were absent from the coastal area and there was no spawning at this site in 2004. This was not observed in 2003 or 2005 as spawning had already occurred at all sites prior to the first day of sampling.

Site Use

Sites showed variability in their use among years. Two sites (Gull Island I and II) were initially discovered in 2002 (Davoren *et al.* 2006) and were persistently used in all years of this study (Table 2.2). Three additional sites were located in 2003, two of which (Deadman's Bay III and V) were not used after this year. Although acoustic signals revealed the presence of large schools of capelin in 2004, suitable sediment was difficult to obtain in bottom grab samples and eggs were not found at these sites. The remaining site discovered in 2003, Penguin Island IV, was used again in 2005, but not in 2004. Four new spawning sites were discovered in 2004, two of which (Turr Island and Cracker's Rock) were used again in 2005. Two new sites were discovered in 2005 (Gull Island III and Windmill Bight).

Timing, Duration and Magnitude of Spawning

Among years, spawning at sites used in all years was progressively earlier from 2003 to 2005 and less protracted in 2005. All sites combined, however, revealed that spawning

began on July 30th, July 21st and July 13th and lasted for a total of 25, 29 and 32 days in 2003, 2004 and 2005, respectively (Fig. 2.7). The mean duration of spawning at all sites in each year was 8 ± 1 , 9 ± 1 and 6 ± 1 days in 2003, 2004 and 2005, respectively. In 2004, spawning started later at deeper sites (Gull Island I and II) but temporally overlapped with spawning at shallower sites (Turr Island, Cracker's Rock and Hinckes Rock).

Peak spawning varied temporally among sites within a year, suggesting variable use of spawning sites throughout the spawning season. Peak spawning at Hinckes Rock in 2004 occurred on 22 July and although spawning ended at this site on 8 August, spawning did not occur on 2 August, which was the day of peak spawning at all other sites. Spawning did not occur at Turr Island from 5-8 August when spawning was recorded at all other sites. Capelin spawned at Turr Island again from 14-20 August when spawning had ceased at all other sites.

The total annual egg deposition in 2005 was 27% of the egg deposition at spawning sites in 2004 (Table 2.3). In 2005, the site with the highest annual egg deposition was lower than the lowest egg deposition in 2004. Annual egg deposition was highest at Turr Island in both 2004 and 2005. In 2004, spawning at Hinckes Rock represented 26% of the total egg deposition over all five sites, but was not used in the following year. With the exception of Cracker's Rock, there appeared to be less spawning at sites of greater depth in both years (Fig. 2.8). In addition, there appeared to be more spawning at shallower sites in 2004 relative to 2005 (Fig. 2.8).

Table 2.3: Total annual deposition of eggs (per standard core estimate) at spawning sites in 2004 and 2005.

Site	Total Annual Egg Deposition·cm ²	
	2004	2005
Turr Island	10327	2262*
Cracker's Rock	3037	1215
Hincke's Rock	7666	0
Gull Island II	5793	1826*
Gull Island I	2901	1484*
Gull Island III	—	1130

Note: * indicates where deposition is corrected when initial spawning was missed

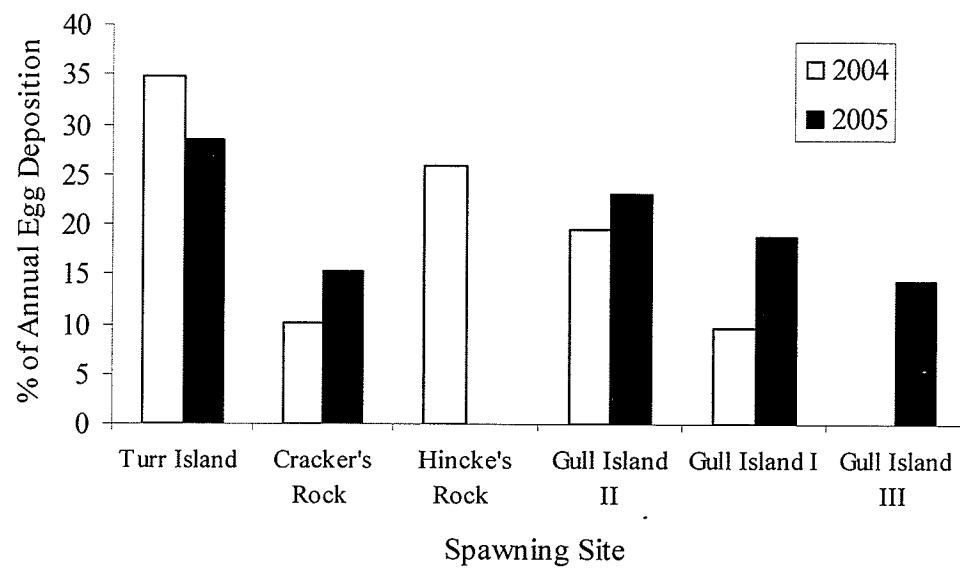


Figure 2.8: Proportional contribution of spawn (# Stage I-II eggs) from demersal spawning sites in 2004 and 2005, arranged in order of increasing depth (left to right).

2.4. Discussion

Overall, a combination of sediment size and temperature appeared to be important in characterizing favourable spawning habitat. The presence of suitable sediment size likely determined whether a site was used among years, whereas water temperatures determined if and when a site was used within years. For instance, if unsuitable temperature ($< 2^{\circ}\text{C}$) occurred at sites with suitable sediment size when capelin moved inshore to spawn, these sites were not used. The accumulation and retention of spawning sediments in bathymetric depressions and hollows created favourable spawning habitat that was persistent in space interannually. Habitat preferences inferred from egg deposition suggests that suitability among spawning depressions was equal, with deeper and shallower sites used differentially among years depending on the temperature near the seabed.

Behaviour at spawning sites

Capelin shoal types and behaviour described in this study appear to be consistent with reports of capelin behaviour throughout their North Atlantic distribution. Dispersed shoals were observed before spawning events at known demersal sites and shoals were widely dispersed both laterally and throughout the water column. In studies of the Barents Sea spawning capelin, this shoal type occupied up to 20 m of the water column off the seabed (Bakke and Bjørke 1973). Investigators reported that this shoal type was also dominated by pre-spawning males that were 15-80 cm apart and made wide circular swimming motions (Bakke and Bjørke 1973, Saetre and Gjosaeter 1975). The dense shoals in my study were observed on days when spawning was confirmed. These shoals

were close to the seabed and individual fish were not distinguishable. A second shoal type that exhibited these same characteristics was also reported in the Barents Sea. Investigators reported a maximum distance of 5 cm between individuals (Saetre and Gjosaeter 1975) and vertical height <2 m off the seabed (Bakke and Bjørke 1973).

The predominance of males in the dispersed shoal type before spawning indicates that males move to the spawning sites before females. Laboratory observations of spawning behaviour in Icelandic capelin documented that three days before the initiation of spawning, males began to leave mixed-sex schools to search the bottom for suitable spawning substrate (Fridgeirsson 1976). This pre-spawning segregation of the sexes has also been reported in the beach (Templeman 1948) and the Southeast Shoal (Carscadden, pers comm. *In* Vilhjalmsson 1994) spawning populations in Newfoundland. This suggests that, in agreement with most mating systems in fish, males are responsible for spawning site selection (Potts 1984). Female capelin move onto spawning grounds to spawn once, then leave the area whereas males remain at the spawning site to perform several matings (Templeman 1948, Fridgeirsson 1976).

My study area was identified as an important area for capelin-seabird interactions based on the location of the Funk Island Ecological Seabird Reserve (Davoren *et al.* 2006). This is particularly relevant to my study of demersal spawning sites because as capelin are the key forage fish in the North Atlantic, high concentrations of pre-spawning capelin that are persistent at spawning sites provide a predictable high energy prey source for top vertebrate predators (Davoren *et al.* 2003). High concentrations of whales and seabirds were observed at demersal spawning sites during the study (personal observation). Anti-predator behaviour of capelin shoals was inferred thorough

behavioural responses to the presence of the ROV (Davoren *et al.* 2006). Dispersed shoals resumed activity ~30 s after contact with the ROV and dense shoals moved laterally away from the ROV, exhibiting a minimal flight response to ROV approaches in both cases. This suggests that during spawning, capelin may be more focused on spawning than anti-predator behaviour.

Habitat Use

Carscadden *et al.* (1989) postulated that for demersally spawning capelin on the Southeast Shoal, the ultimate factor in determining the location of spawning is substrate suitability, whereas the proximate cause is bottom temperature. My results support this for demersally spawning capelin in coastal Newfoundland. The extent to which a known demersal spawning site was used within and among years primarily appeared to be determined by the presence of coarse sand and gravel and secondarily by bottom temperature. The availability of suitable sediment sizes determined whether a site was used among years but bottom temperature appeared to determine when a site was used within a year.

Sediment size range and Depressions

Marine sediments are subject to transport, the rate of which is determined by the size of the sediment and current velocities (Hjulstrom 1939). In regions of strong currents, sediment is quickly transported away, leaving only bedrock (Middleton 1980). In hollow areas of the continental shelf, however, finer material accumulates (King 1962). This is a function of decreased current speed at greater depths, resulting in the deposition of the

suspended sediment, with finest sediment in the top layer (King 1962). The predominance of bedrock outside depressions in the study area suggests that current velocities exceed $30 \text{ cm}\cdot\text{s}^{-1}$, the speed required to transport gravel, the largest spawning sediment (Hjulstrom 1939). This is comparable to current speeds ($\geq 20 \text{ cm}\cdot\text{s}^{-1}$) on the demersal spawning grounds of the Southeast Shoal (Frank and Carscadden 1989). Additionally, sand ripples were found in both depressions in the study area and at the demersal spawning beds of the Barents Sea capelin (Saetre and Gjosæter 1975). The maintenance of this bedform over time indicates that currents within depressions 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 is critical for removing wastes from and supplying oxygen to the egg bearing sediment layer.

Evidence for the importance of depressions in maintaining size ranges of sediment suitable for demersal spawning is provided by the variable use of known demersal sites among years. This was evidenced by the lack of spawning at Deadman's Bay sites after 2003. These two sites lack the shelter provided by depressions and small coastal islands at other sites, which presumably led to considerable turnover and movement of substrata during winter storms and due to ice scour. Even though capelin shoals were present at these sites for up to one week in 2004 when bottom temperatures were adequate for spawning ($>2^\circ\text{C}$), spawning did not occur, likely due to the lack of sediment in the appropriate size range.

The density of animals at a particular site is often used to indicate habitat preferences of animals (Railsback and Harvey 2002) and, thus, the quantity of eggs

deposited at sites may indicate habitat quality. High egg densities were thought to indicate high quality spawning habitat for beach spawning capelin of Newfoundland (Nakashima and Taggart 2002). If this is true, the relatively low magnitude of egg deposition in two years at another non-depression site (Cracker's Rock) may indicate lower habitat quality, likely due to thin layers of suitable sediment distributed in small patches over an area dominated by bedrock.

Temperature

In addition to sediment turnover rates causing variability in the use of known demersal spawning sites among years, temperature also likely played a role. The critical temperature threshold for the initiation of spawning in the study area appeared to be 2°C as found by Frank and Carscadden (1989) for the Southeast Shoal. Penguin Island was not used in 2004, presumably because temperatures remained < 2°C until the majority of capelin in the area had finished spawning. When water temperature was warmer early in July 2005, capelin spawned at this site. Additionally, capelin were observed acoustically at both Gull Island sites in 2004, but did not spawn until temperatures were >2 °C.

In 2004, there was a depth-related trend in egg deposition that led to a hypothesis that capelin prefer to spawn at shallower sites, assuming again that egg densities indicate habitat preferences (Nakashima and Taggart 2002). This, however, was confounded by the influence of decreasing temperature with depth. Water temperatures were coldest in 2004 and, thus, temperature was <2 °C at deep (>25 m) sites early in the season when pre-spawning male capelin began to occupy spawning sites. Therefore, deep sites may have been thermally unsuitable for capelin when spawning occurred at shallower sites.

Spawning ended at approximately the same time at all sites, resulting in a longer period of spawning at shallower sites and, thus, higher egg deposition at shallower sites. In contrast, when water temperatures were the warmest in 2005, capelin utilized deeper sites to a greater extent, suggesting that bottom temperature was more important in determining spawning site selection among years than depth.

Interestingly, water temperature alone did not account for the variability in timing of spawning among years. The timing of spawning in the study area was earliest in 2005 when water temperatures were warmest over the three years of the study. Water temperatures were also warm in 2003; however, spawning was delayed relative to 2004. Previous studies have reported that fish length and the mean monthly temperatures from February – June (TEMPSUM) are critical factors in determining the timing of spawning in capelin (Carscadden *et al.* 1997). TEMPSUM was 1.3 °C, 1.6 °C and 1.3 °C from 2003 to 2005, respectively (Station 27, St. John's, Newfoundland). These yearly TEMPSUM trends neither complement trends in bottom temperature during spawning nor provide further explanation to the timing of spawning in the study area. Fish size is associated with timing of spawning because larger fish mature earlier, resulting in larger capelin spawning earlier in the season (Carscadden *et al.* 1997). Anecdotal observations of the size of spawning capelin between years from local fishers (Larry Easton, pers comm.) suggests that spawning capelin were larger in 2004 than in 2003. Earlier spawning in 2004 despite the bottom temperatures being higher during spawning in 2003, therefore, may have been a result of the size and condition of the spawning population.

Implications and Future Study

In 2002, Nakashima and Wheeler hypothesized that demersal spawning made no contribution to the reproductive success of capelin in Newfoundland. I suggest that current speeds and temperature patterns within the 50 m contour on the exposed Northeast coast of Newfoundland create suitable spawning habitat for demersally spawning capelin. Owing to the persistence of demersal spawning since 2003 at a number of sites in my study area, I suggest that it is important to examine the contribution of demersally spawned capelin to recruitment in Newfoundland. Therefore, determining the spatial extent of demersal spawning sites in coastal Newfoundland, as well as the survivorship of eggs and larvae at demersal sites, are critical to this future work.

Chapter 3. Egg developmental and survival rates in capelin (*Mallotus villosus*): a comparison between beach and demersal spawning

3.1. Introduction

Reproduction is a key component in an organism's life history and ultimately determines the fitness of an individual. Therefore, a successful reproductive strategy is one that maximizes not only the production of offspring, but also the survival of the progeny. R-selected species such as fish exhibit a Type III survivorship curve characterized by high mortality in early life stages. Intrinsic causes of mortality in fish eggs include genetic defects, physiological failures and disease (Wootton 1998). Extrinsic mortality can be partitioned into abiotic factors such as temperature, salinity and turbulence or biotic factors such as depredation and egg density, often with an interaction between these two factors (Houde 2002, Wootton 1998). Because up to 99% of young fish do not survive to adults (Chambers and Trippel 1997), selective processes acting in the early stages largely determine year-class strength and recruitment.

The timing and location of spawning in fishes directly influences the mortality risk of eggs and larvae, ultimately affecting reproductive success (Wootton 1998). Spatially and temporally consistent patterns in spawning, therefore, reflect long-term selection processes that maximize the fitness of individuals (Houde 2002). Environmental variability can have major consequences for fish populations if it results in higher mortality in the early life history stages, thereby lowering recruitment potential. If environmental variability persists over time, lower reproductive output could drastically reduce populations (Hoffmann and Parsons 1997). Individuals, however, can

exhibit a phenotypically plastic response to environmental variability by altering behavioural tactics and, thus, may be flexible to adapt in response to change (Potts 1984). An example of this is excursion into new habitats to avoid unfavourable conditions (Hoffmann and Parsons 1997). Alterations of spawning habitat, however, may also negatively influence reproductive success if mortality is higher and, thus, newly colonized habitats are not conducive to the survival of early life history stages.

Temperature is a critical factor in determining developmental rates in poikilotherms (Cossins and Bowler 1987). Developmental rates within fish species may differ depending on the thermal regime in which the eggs incubate, but a negative relationship between time to hatch and average incubation temperature is often consistent across a species' geographic range (Fuiman 2002). Faster egg developmental rates at high temperatures could result in higher mortality due to abnormal growth and development as a result of a stress response when temperatures fluctuate above the upper limit of physiological tolerance (Cossins and Bowler 1987). Conversely, lower incubation temperatures prolong development, causing the potential for a "mismatch" with planktonic prey (Benoit and Pepin 1999, Houde 2002). Slower development due to lower temperature conditions can be minimized through the effects of countergradient variation whereby genetic and environmental effects oppose one another in the development of early life history stages of fish (Conover and Schultz 1997). A highly cited example of this is in salmonids where slow development at lower temperatures is minimized by compensatory development so that they hatch earlier (Beacham and Murray 1987, Brannon 1987, Chambers and Trippel 1997, Hebert *et al.* 1998, Hendry *et al.* 2002).

Such temperature-specific developmental rates may be an adaptation to specific thermal regimes due to the fitness consequences for early life history stages (Hebert *et al.* 1998).

In the 1990s, the Northwest Atlantic experienced an anomalous cold water event, with 1991 identified as the coldest year on record (Colbourne *et al.* 1994; Nakashima 1996). Since 1991, capelin spawning has been delayed by approximately one month and more protracted, presumably due to colder than normal water temperatures during gonadal maturation in late-winter and early-spring (Nakashima 1996). In coastal Newfoundland, capelin are thought to spawn primarily on beaches, but may switch to subtidal, or demersal, spawning in areas adjacent to beaches once beach temperatures become unsuitably warm later in the spawning season (Templeman 1948). Researchers recently hypothesized that delayed and protracted spawning due to anomalous conditions in the 1990s may result in an increasing occupation of demersal sites (Nakashima and Wheeler 2002). Additionally, these researchers hypothesized that demersal spawning makes little or no contribution to the reproductive success of capelin in Newfoundland, owing to high egg mortality observed at demersal sites (Nakashima and Wheeler 2002). Therefore, increasing occupation of demersal spawning sites may have major negative implications for the capelin stocks of Newfoundland and Labrador.

Demersal spawning sites were recently discovered on the exposed Northeast coast of Newfoundland (Davoren *et al.* 2006), where capelin also are known to spawn on beaches. The goal of my study is to characterize the viability of these two reproductive tactics of capelin (beach and demersal) by comparing developmental and survival rates of the egg stage in relation to temperature and egg density trends between a beach (Lumsden) and demersal (Gull Island I) spawning site during July – August 2004 and

2005. My first objective was to determine if there was a difference in egg densities and total annual deposition between the beach and demersal spawning sites. My second objective was to determine if developmental rates differed between sites due to the differences in temperatures experienced during incubation. My third objective was to compare the environmental mortality of eggs between the beach and demersal sites and to examine mortality in relation to abiotic (temperature) and biotic (egg density) factors. This study is critical to furthering our knowledge of the effects of environmental variability on the spawning biology and, thus, recruitment of this focal forage fish in the North Atlantic.

3.2. Methods

Study Design

This study was conducted along the Northeast coast of Newfoundland (Fig. 2.1 in Chapter 2) during July-August, 2004 and 2005. Accessible areas of the coastline along the Straight Shore (~110 km) were surveyed in 2004 to document the location of major spawning beaches in the study area, resulting in the discovery of five spawning beaches (Andrews 2005, Fig. 3.1). Two beaches (Capelin Cove and Lumsden Beach) had intense spawning activity and both were sampled in 2004 but capelin did not spawn at Capelin Cove in 2005 so only Lumsden Beach was monitored.

Eleven demersal spawning sites have been located since 2002 (Davoren *et al.* 2006) during daylight hours aboard the *Lady Easton II*, a commercial fishing vessel

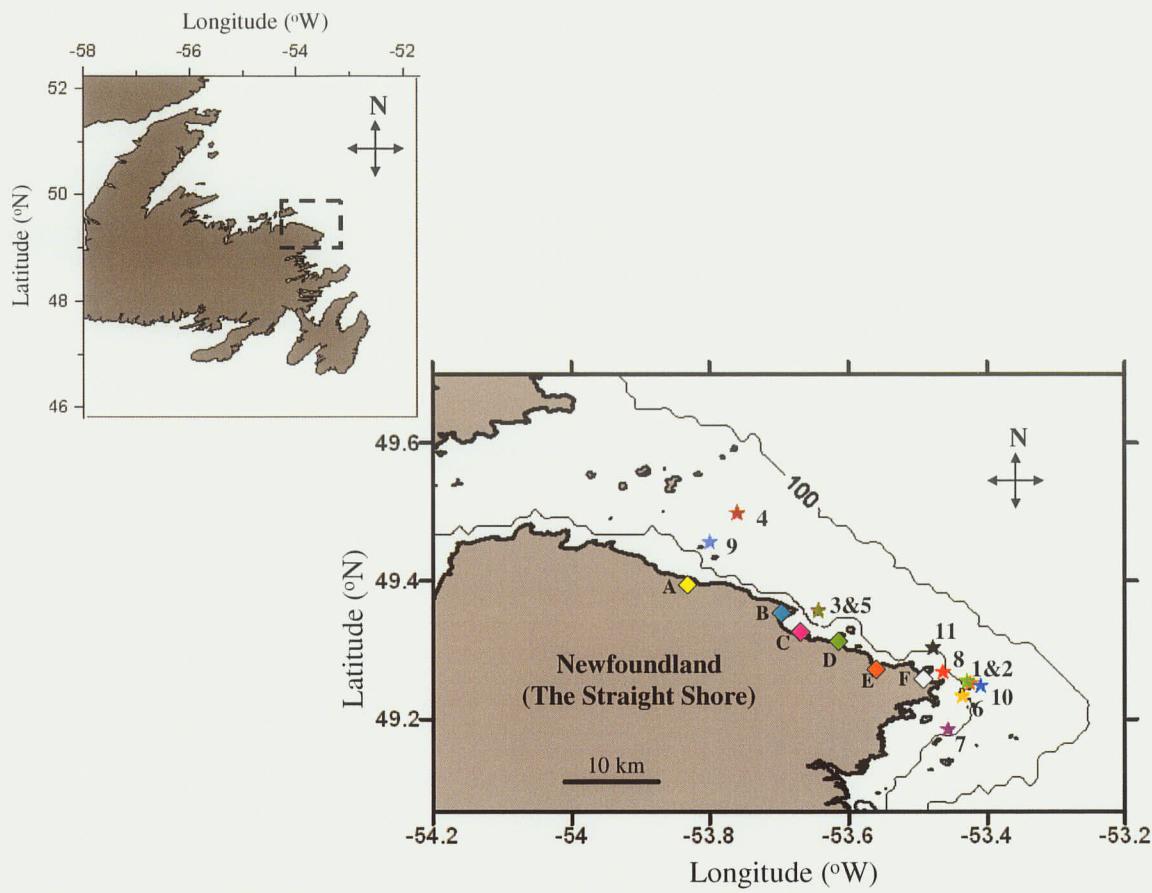


Figure 3.1: Study site on the Northeast Coast of Newfoundland (the Straight Shore) with the location of demersal spawning sites discovered from 2002-2005 (star) and beach sites discovered in 2004 (diamond). Inset: Map of Newfoundland. (Demersal: **1=Gull Island I**, **2=Gull Island II**, **3=Deadman's Bay III**, **4=Penguin Island**, **5=Deadman's Bay V**, **6=Turr Island**, **7=Hinckes Rock**, **8=Cracker's Rock**, **9=Northern Penguin Island**, **10=Gull Island III**, and **11=Windmill Bight**; Beach: **A= Shalloway**, **B=Anchor Brook**, **C=Long Beach**, **D=Lumsden**, **E=Mussel Shells**, and **F=Capelin Cove**).

which operated $12 \text{ h} \cdot \text{d}^{-1}$ within the 50 m depth contour of the study area ($49^{\circ}11' \text{N}$, $53^{\circ}27' \text{W}$ to $49^{\circ}27' \text{N}$, $53^{\circ}47' \text{W}$) (Fig. 3.1). For details about the discovery and description of demersal spawning sites in the study area, see Chapter 2.

The density, development and survival of capelin eggs were studied in both years at beach and demersal sites. Lumsden beach was chosen to represent beaches in the study area for the comparison of beach and demersal spawning sites in this chapter because it was the only beach used by capelin in both years of the study (Andrews 2005, Reinfort 2006). Gull Island I was chosen to represent demersal sites in the study area because it has been consistently used since its discovery in 2002 (see Chapter 2). This site is also the deepest demersal spawning site monitored in both years and, as such, represents an extreme for investigating the effects of divergent environmental characteristics at beach versus demersal sites on the spawning biology of capelin. These sites will be referred to as beach and demersal throughout this chapter.

In 2004-2005, egg-bearing gravel was collected at beach and demersal spawning sites beginning near the start of spawning. Eggs in developmental Stages I-II are associated with recent fertilization, with the time interval of each stage determined by the incubation temperature (Nakashima and Wheeler 2002). Therefore, sampling intervals were determined in each year based on average daily incubation temperatures at the spawning sites to ensure that new spawning events were recorded without re-sampling previously spawned eggs. In 2004-2005, the sampling interval at the beach was every second day. Sampling of demersal spawning sites occurred every third day in 2004 and every second day in 2005 owing to warmer incubation temperatures in 2005 (Chapter 2).

Biological Samples (Egg Density, Development and Mortality)

Egg samples were collected from the high tide (HT), mid tide (MT), and low tide (LT) regions of the intertidal zone at the beach using a 6.5 cm internal diameter steel corer (Frank and Leggett 1981) and preserved in 5% formalin solution buffered with sodium borate for determination of egg density. Egg depth did not exceed the depth of the core. In 2004, three egg samples were taken from each tidal zone, whereas in 2005, two egg samples were taken from each tidal zone owing to limited beach spawning in the study area. Subsamples were taken because of variability in egg densities over the spawning bed (Frank and Leggett 1981). In both years, Stockard's samples were also collected at the beach near each of the core samples for determination of egg development and mortality. Egg samples at demersal sites were collected using a 0.3 m² Van Veen Benthic Grab System. A core and Stockard's sample was collected from each of three replicate grab samples on each sampling day (See Chapter 2 for details).

A random sample of 50 eggs from each Stockard's 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 (Table 3.1). I determined the approximate timing and duration of spawning events, as indicated by the presence of Stage I-II eggs. Dead eggs were distinguished from live ones on the basis of a cloudy or opaque appearance and the number of dead eggs per sample was recorded.

Table 3.1: Key visual characteristics of stages in the embryonic development of capelin (modified from Fridgeirsson 1976).

Developmental Stage Index	Characteristics
I-II	Includes the formation and cleavage of the blastodisk, ends with formation of the blastula
III	Gastrulation; formation of the endo-, meso-, and ecto-derm
IV	Organogenesis I; the head and part of the embryonic body are formed, as well as the rudimentary organs of the Central Nervous System
V	Organogenesis II; marks the full development of main organs, with the exception of the tail
VI	Includes the formation of the mouth, preparation for independent feeding, and intense pigmentation

A central measure of egg development was calculated for each day using the following equation (Frank and Leggett 1981):

$$WMDSI = \frac{\sum_{i=1}^6 s_i e}{\sum_{i=1}^6 e_i}$$

where $WMDSI$ is the weighted mean developmental stage index, s_i is the developmental stage index, and e_i is the average proportion of eggs in each developmental stage over all replicate samples. Tidal zones were pooled to calculate the average proportion of eggs on each day at the beach. Time to hatch was estimated by extrapolating WMDSI plots to Stage VII (hatching).

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

$$\text{Egg mortality} = \left[\left(\sum_{i=1}^k d_i / \sum_{i=1}^k x_i \right) \right] * 100$$

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.

A standard egg abundance estimate (mean number of eggs·cm⁻²) was calculated to allow comparisons of egg abundance within a standard area between sites and years. The average daily egg abundance for each tidal zone was calculated as a mean of the two (2005) or three (2004) replicate samples. Tidal zones were pooled to calculate the average daily egg abundance at the beach. The average daily egg abundance at the demersal site was calculated as the mean of the three replicate samples. Trapezoidal integration was used to interpolate between point estimates of the average daily egg densities at the beach and demersal sites, calculating the total annual deposition of eggs at

each site. See Chapter 2 for details on the methodology of egg counting and calculation of trapezoidal integration.

Physical Samples (Temperature)

At the beach, water temperature was measured on each sampling day using a handheld thermometer at waist-height during low tide (2004-2005). Temperature profiles of the water column were measured using a Sea Bird SBE-19 at demersal spawning sites (2003-2004). Vemco Miniloggers (Vemco 8-bit Minilog-TR) that recorded temperature every 20 min throughout the incubation period were used to characterize the mean daily incubation temperature experienced at the beach and demersal spawning sites. Loggers were buried 6 cm in the sediment at each region of the intertidal zone (HT, MT, and LT) at the beach in 2005 and were anchored near the seabed at demersal spawning sites in 2004-2005.

Statistical Analysis

To test the prediction that egg densities are higher at demersal sites in warmer years, I compared average daily egg densities (no. eggs·cm⁻²) throughout the incubation period between sites and years using a two-factor ANOVA. The factors included in the model were location (beach and demersal), and year (2004 and 2005). Multiple comparisons were made using the Tukey-Kramer adjustment method. The total annual production of eggs was compared between sites and years. These are single values and, thus, were not statistically analyzed.

I used a two-factor ANOVA to examine differences in incubation temperature between sites and between years. Comparisons of temperature at the beach in 2004 were limited to the daily point measurements taken during sampling at low tide. Data at the beach in 2005 and at the demersal site in both years are average daily incubation temperatures calculated from thermister data.

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 fertilization) between the beach and demersal sites and years. 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 ($F = [(SS_{site} + SS_{site*year})/2]/MS_{error}$). If this hypothesis was rejected, the relationships were tested for parallelism (same slope but different intercept) and equality of intercepts (but different slopes).

To examine differences in time to hatch between beach and demersally spawned capelin, analysis was extended beyond the two site comparison. Data available from all beach and demersal spawning sites in the Straight Shore study area (2003-2005) were used where site-specific average incubation temperatures were available (See Chapter 2). Additionally, I used published data on capelin egg development, separating these sources into beach spawned eggs in the field (Fig. 4: Frank and Leggett 1981) and in the laboratory (Jeffers 1931, Sleggs 1933), and demersal spawned eggs in the laboratory (Fridgeirsson 1976, Gjosaeter and Gjosaeter 1986).

To determine if the relationship between average incubation temperature and time to hatch differed between beach and demersally spawned eggs, I performed a linear regression analysis using $\ln(x+1)$ transformed average incubation temperatures and time to hatch (days) for each source as per Frank and Leggett (1981). Observed time to hatch for Straight Shore beach and demersal sites was determined by extrapolating the WMDSI plots to the hatching period. If a relationship existed between time to hatch and average incubation temperature, I pooled all data sources into beach and demersal to test if the observed time to hatch at a given temperature was as predicted in the literature by Frank and Leggett (1981). Predicted values were obtained from the documented relationship between time to hatch and temperature for capelin ($\ln y = 4.27 - 0.63 \ln(x+1)$, $r^2=0.85$, $p<0.001$; Frank and Leggett 1981). A Chi-squared goodness of fit test (Zar 1999) was performed to compare observed and predicted values.

To test the prediction that mortality would be higher at the beach than demersal spawning sites, I compared average daily mortality (the average proportion of dead eggs in replicate Stockard's samples) throughout the incubation period between sites and years using a two-way ANOVA. The factors included in the model were location (beach and demersal) and year (2004 and 2005). Multiple comparisons were made using the Tukey-Kramer adjustment method. All average proportions of dead eggs were arcsine and square root transformed prior to analysis. To examine the influence of abiotic and biotic factors on egg mortality, I performed a two-way ANOVA. The factors included in the model were egg density (biotic) and average incubation temperature (abiotic).

Prior to all analyses, data were tested for normality and homogeneity of variance to meet the assumptions of linear models.

3.3. Results

Timing and Duration of Spawning

In both years, beach spawning was earlier and shorter in duration than demersal spawning. In 2004, spawning at the beach began on July 10 and lasted for approximately 3-4 d. Spawning at the demersal spawning site in 2004 began 17 d later on July 27 and lasted for 12 d. In 2005, spawning at the beach began on July 3 and lasted for 2 d. I missed initial spawning at the demersal site in 2005 but it was predicted to have begun on July 13 and lasted for 8 d.

Water Temperature

Water temperatures were higher at the beach than at the demersal site in 2004 ($p<0.0001$) and 2005 ($p<0.0001$; Fig. 3.2). Water temperatures during the incubation period were warmer in 2005 than 2004 at both sites ($p<0.0001$). At the beach in 2005, daily temperature fluctuations ranged from 0.8-26°C. At the demersal site in 2004, daily temperature fluctuations ranged from 1.0-5.7°C and were only slightly higher in 2005 (1.2-7.3°C) when temperatures were significantly warmer.

Egg Density

Average daily egg densities throughout the incubation period (i.e. fertilization to hatch) were higher in 2004 than in 2005 ($F_{1,90}=5.66$, $p=0.0195$) and were higher at the demersal site relative to the beach site ($F_{1,90}=4.79$, $p=0.0312$). These relationships were driven by lower egg densities at the beach in 2005 ($p=0.0003$) because there was a significant

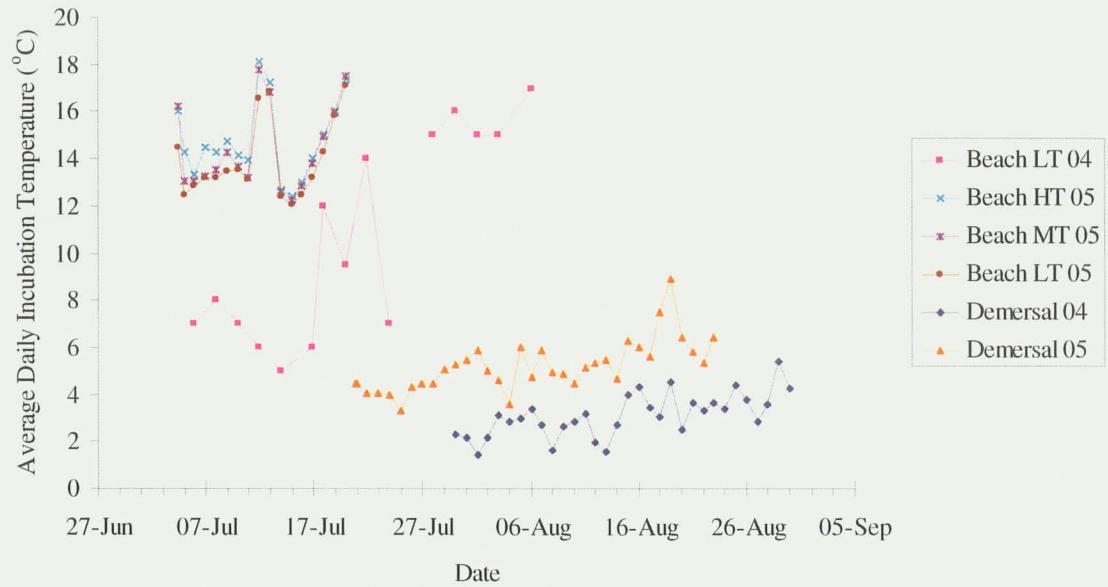


Figure 3.2: Capelin egg incubation temperatures at the beach (Lumsden) and demersal (Gull Island I) sites in 2004 and 2005. Temperatures indicated are daily averages with the exception of Beach 04 when water temperature was recorded at low tide during sampling.

second-order interaction between location and year ($p=0.03$) and post-hoc multiple comparisons revealed that egg densities were not significantly different between years at the demersal site ($p=0.999$). Egg densities were significantly higher at the demersal relative to the beach site in 2005 ($p=0.01$) but not in 2004 ($p=1.00$).

In 2004, the total annual egg deposition per standard core estimate at the beach ($3494 \text{ eggs}\cdot\text{cm}^{-2}$) was similar to deposition at the demersal site ($2901 \text{ eggs}\cdot\text{cm}^{-2}$). In 2005, deposition at the beach ($22 \text{ eggs}\cdot\text{cm}^{-2}$) was lower than at the demersal site ($1484 \text{ eggs}\cdot\text{cm}^{-2}$). Overall, the total annual egg deposition per standard core estimate was higher in the study area in 2004 than in 2005.

Developmental Rates

There was no significant difference in developmental regression slopes between years at the beach site (ANCOVA, $F_{1,8}=0.33$, $p=0.7283$) and the demersal site (ANCOVA, $F_{1,14}=0.558$, $p=0.5846$; Fig. 3.3). Developmental rates were significantly different between beach and demersal spawning sites in 2004 ($F_{1,15}=9.23$, $p=0.0044$) and 2005 ($F_{1,11}=9.08$, $p=0.0047$) with equality of intercepts but different slopes (Fig. 3.3).

Analysis of all published and Straight Shore beach (Andrews 2005, Reinfort 2006) and demersal data available revealed that with the exception of Straight Shore beach sites, the relationship between time to hatch and average incubation temperature (Fig. 3.4A) was significant for beach and demersal data (Table 3.2). More than 80% of the variation in time to hatch was explained by average incubation temperature in published sources of lab and field beach data, as well as in published demersal data. At

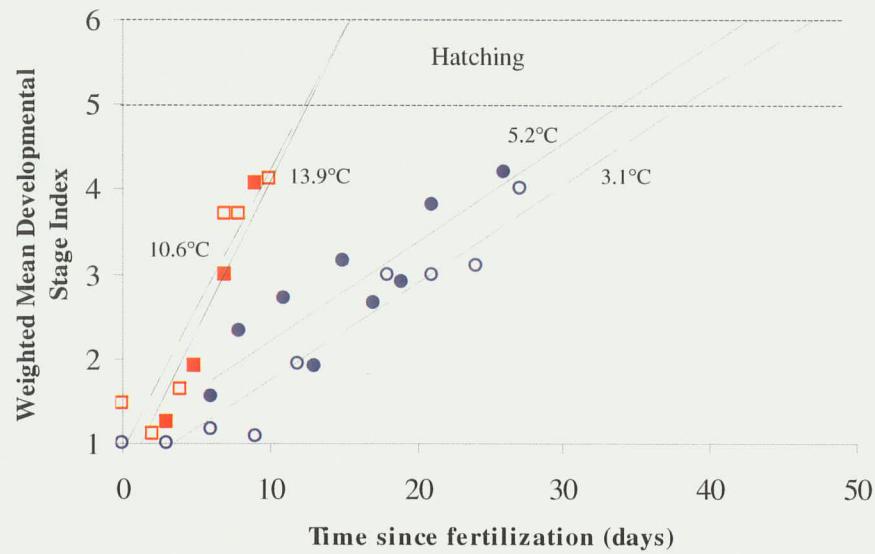


Figure 3.3: Capelin egg development rate determined from core samples at beach (square-Lumsden) and demersal sites (circle-Gull Island I) in 2004 (open symbol, dotted line) and 2005 (closed symbol, solid line). Average incubation temperature is indicated. Dotted horizontal lines indicate the hatching interval. (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: $y=0.1171x+0.0353$, $r^2=0.78$).

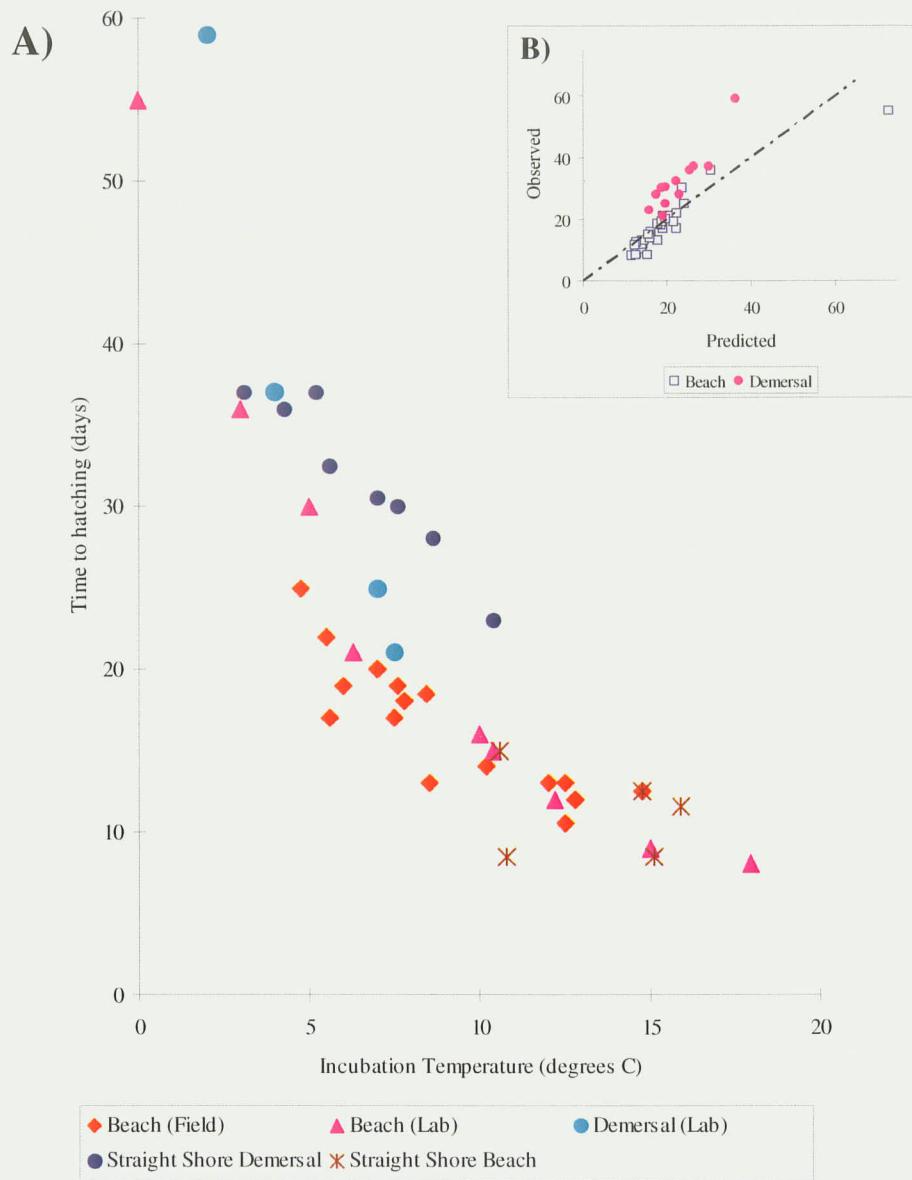


Figure 3.4: (A) Relationship between time to hatch and mean daily incubation temperature (redrawn from Frank and Leggett (1981), including data points from Straight Shore beach (2004-2005) and Straight Shore demersal (2003-2005) spawning sites in the study area), and (B) observed versus predicted time to hatch for beach and demersal capelin eggs. Predicted values were obtained from the beach (Field) relationship in (A) ($\ln y = 4.27 - 0.63 \ln(x+1)$, $r^2=0.85$, $p<0.001$; Frank and Leggett 1981). The dotted line has a slope equal to one (observed=predicted values).

Table 3.2: Regression equations showing the relationship between ln (x+1) transformed average incubation temperature and ln transformed time to hatch (ln y) for data from beach and demersal spawning capelin.

Data Source ^a	Experiment Type	Regression Equation	R ²	p
Frank and Leggett	Field	ln y = 4.12 - 0.63 ln (x+1)	0.81	<0.00001
Published Beach	Lab	ln y = 4.29 - 0.67 ln (x+1)	0.89	<0.00001
Straight Shore Beach (2004-2005)	Field	ln y = 2.86 - 0.18 ln (x+1)	0.02	0.810
Published Demersal	Lab	ln y = 5.12 - 0.94 ln (x+1)	0.99	0.006
Straight Shore Demersal (2003-2005)	Field	ln y = 3.90 - 0.28 ln (x+1)	0.55	0.022

^aData Sources of Beach and Demersal Data: Beach=Frank and Leggett 1981, Jeffers 1931 and Slegg 1933, and Straight Shore Beaches Appendix A. Demersal=Fridgeirsson 1976 and Gjosaeter and Gjosaeter 1986, and Straight Shore Demersal Appendix B.

the Straight Shore demersal spawning sites, however, only 55% of this variation was explained by average incubation temperature (Table 3.2).

Observed and predicted time to hatch were similar for all sources (published field and lab, and Straight Shore) of beach spawning data ($\chi^2=0.94$, d.f.=32, p=1.00; Fig. 3.4B). At demersal spawning sites (published and Straight Shore), observed time to hatch was 8-10 days later than predicted (Fig. 3.4B) but the observed and predicted values were not significantly different ($\chi^2=4.89$, d.f.=11, p=0.9364).

Mortality

The mean daily proportion of dead eggs, or egg mortality, at beach and demersal sites was higher in 2004 than in 2005 (Table 3.3) and was higher at the beach relative to the demersal site (Table 3.3). Post-hoc pairwise comparisons revealed that egg mortality between years was not significantly different at the demersal site (p=0.7128), so the above relationship was driven by higher egg mortality at the beach in 2004 (range: 4-90%, Appendix A) relative to 2005 (range: 4-76%, p=0.0795; Appendix A).

These results suggested that the effects of average incubation temperature and egg density on mortality be evaluated at the demersal site, combining years, and at the beach site in each year. Egg density (ANOVA, $F_{1,11}=14.89$, p=0.0027) and average incubation temperature (ANOVA, $F_{1,11}=51.20$, p<0.0001) were significant in explaining the variation in mortality at the beach site only in 2004. Higher temperatures and egg densities caused higher mortality, as there was a significant interaction between egg density and average incubation temperature (ANOVA, $F_{1,11}=11.31$, p=0.0063). Egg

Table 3.3: Two-factor Analysis of Variance and *a posteriori* means test on the daily average (\pm SE) proportion of dead eggs. The factors were location (beach, Lumsden and demersal, Gull Island I) and year (2004, 2005). Note: > indicates significant differences at $p<0.05$.

Source	df	p
Model	3	<0.0001
Location (L)	1	<0.0001
Year (Y)	1	0.0274
L*Y	1	0.6287
Error	87	
Corrected Total	90	

Tukey-Kramer adjustment for multiple comparisons
Level of alpha=0.05

Between Years

Year	2004	>	2005
Mean	29.3 \pm 3.3%		13.8 \pm 2.9%
n	54		37

Between locations

Location	Beach	>	Demersal
Mean	31.9 \pm 2.7%		1.9 \pm 0.7%
n	64		27

density and average incubation temperature did not significantly influence egg mortality at the beach site in 2005 (ANOVA, $F_{3,16}=0.23$, $p=0.8731$) or at the demersal site in both years (ANOVA, $F_{3,21}=0.29$, $p=0.2839$).

3.4. Discussion

Capelin exhibit two spawning modes within my study area on the Northeast coast of Newfoundland. Spawning was both spatially and temporally separated between beach and demersal habitats, which had markedly different thermal regimes. Temperature was higher and more variable at beach sites relative to demersal sites. Two distinct developmental strategies were observed: high mortality and rapid development at the beach versus low mortality and slow development at demersal sites, likely owing to the divergent thermal regimes between the two habitats. Overall, based on these investigations of one of the critical early life history stages of capelin, results suggest that demersal spawning is a viable reproductive tactic on the Northeast coast of Newfoundland.

Mortality

Owing to the higher mortality of eggs at the beach, I hypothesize that the demersal spawning environment is a higher quality habitat for egg survival relative to the beach. Temperature has been shown to be a major regulator of survival of the early life history stages of marine fish, with higher temperatures causing higher mortality (Pepin 1991). Higher temperatures offer the advantage of faster development, which comes at the cost

of a higher frequency of developmental abnormalities and higher energy requirements for basic metabolic and physiological activities (Pepin 1991). When incubation temperature is high, metabolic rates increase and may cause oxygen availability to become limited, especially when egg densities are high. This is especially true at beach sites, as oxygen is replenished and metabolic wastes removed from the egg layer only during periodic exposure to water. In comparison, the thermal incubation environment at demersal sites is characterized by low water temperatures, resulting in slower metabolic rates, and current velocities sufficient to continuously replenish oxygen to the egg layer (Chapter 2). This presumably results in the lower mortality observed at the demersal site relative to the beach.

The beach is a highly dynamic environment and is subject to large fluctuations in temperature due to the changes in inundation with water as the tide comes in and out, as well as the direct effects of daily solar radiation. I hypothesize that large fluctuations in temperature also contribute to higher egg mortality at the beach, as this results in thermal stress especially when fluctuations exceed physiological tolerance limits (Cossins and Bowler 1987). Pepin (1991) reported that development of marine teleost eggs, and thus mortality, was sensitive to variations in temperature. At the beach, temperature was significant in explaining the observed egg mortality only in 2004. Temperatures at the beach were more variable in 2004 relative to 2005 and egg densities were much higher in 2004. At demersal sites, mortality was low in both years, presumably due to lower and less variable temperatures and similar egg densities in both years.

One single factor is not sufficient to explain egg mortality but rather, there is likely an interaction between biotic and abiotic factors. My data support the findings of

previous studies on egg mortality at the beach that reported a combination of both temperature (determined by inundation with water and solar radiation) and density as significant factors explaining egg mortality in capelin (Frank and Leggett 1981). I propose that other major factors that were not quantified but could contribute to the observed differences between beach and demersal egg mortality in capelin include, but are not limited to, desiccation and oxygen availability through an interaction between egg density and hours of sunlight at the beach, as found by Frank and Leggett (1981). These environmental factors do not contribute to mortality at demersal sites and, thus, I propose that the observed mortality at these sites is likely due only to natural genetic defects. Further study of the causes of mortality at beach and demersal spawning sites should include investigation of these and other variables.

Developmental Rates

Developmental rates of beach and demersally spawned capelin in the study area were significantly different, with slower development occurring under the cooler water temperatures at demersal sites. This was expected based on the negative relationship between time to hatch and temperature in capelin (Frank and Leggett 1981). Additionally, the relationship between incubation temperature and time to hatch at demersal sites was predicted by the linear relationship that is characteristic of the Newfoundland beach spawning population (Frank and Leggett 1981). The observed trend of time to hatch, however, was 8-10 d longer at demersal sites than predicted. Later than expected time to hatch was also reported in investigations of demersally spawned capelin in Trinity Bay, Newfoundland (Nakashima and Wheeler 2002). This led to the conclusion that

demersally spawned eggs were not viable and did not contribute to the reproductive success of capelin in Newfoundland (Nakashima and Wheeler 2002).

In my investigations on the Straight Shore, incubation temperature explained less of the variation in time to hatch than published sources included in the analysis. The relationship between time to hatch and temperature at the beach in the study area was not significant. This was likely due to a combination of low statistical power ($n=5$) and low variability in incubation temperatures experienced at the beach during this study. Only 55% of the variation in time to hatch was explained by average incubation temperatures at demersal sites in my study area. This result suggests that factors other than incubation temperature are responsible for the unexplained variation at demersal spawning sites.

Additional factors that were not investigated in this study but could potentially contribute to differences in developmental rates include maternal effects and oxygen levels. For instance, the 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) and, thus, the possibility exists that eggs deposited at demersal sites are larger than at the beach. If egg size is not a factor, observed differences in developmental rates could be due to oxygen that is limiting for growth in fish (Wootton 1998), or other factors, such as salinity.

Implications and Future Study

Egg deposition per unit area at the demersal spawning site in the study area was similar to or greater than the beach site in the study area. Additionally, mortality was higher at the beach relative to the demersal site. As such, I conclude that based on investigations of

the egg stage, demersal spawning is a viable reproductive tactic on the Northeast coast of Newfoundland and may make a significant contribution to recruitment. This contrasts with previous research on beach and demersally spawned capelin that concluded that high egg mortality at demersal spawning sites indicated that demersal spawning made little or no contribution to the reproductive success of capelin in Newfoundland (Nakashima and Wheeler 2002). Recruitment of capelin, however, is determined by the relative survival of larvae during the first four months of post-hatch dispersal (Leggett et al. 1984) and survival of post-hatch capelin larvae is determined by the amount of energy reserves available upon hatching (Chambers et al. 1989). Therefore, the spawning strategy that results in the highest number of larvae with high energy reserves upon hatch will be likely contribute more to recruitment.

In species whose survival of early life history stages depends on unpredictable environmental conditions, cohort survival can be increased through the expression of a greater diversity of life history traits (Benoit and Pepin 1999), thereby reducing variation in year-class strength (Shackell *et al.* 1994). An interesting question is whether these two tactics represent phenotypic responses to divergent thermal regimes or genetic divergence of locally adapted sub-populations. Embryos that experience different thermal regimes throughout incubation are expected to adapt, resulting in genetic divergence (Hebert *et al.* 1998, Hendry *et al.* 1998). This, however, depends on reduced gene flow between reproductive modes, which would essentially result in obligate beach and demersal spawning capelin. The temporal and spatial segregation of beach and demersal spawning capelin in the study area and evidence of rapid evolution of fish in the wild (Reznick *et*

al. 1997, Hendry and Kinnison 1999, Hendry *et al.* 2000), suggests that adaptive divergence is a possibility and should be investigated in future studies.

Demersal spawning appears to be a persistent spawning tactic in coastal Newfoundland, given its continual presence since at least 2002 (Davoren *et al.* 2006). This suggests that there is some selective advantage to demersal spawning in the study area. Owing to the demonstrated viability of this reproductive tactic, future research should investigate the spatial extent of demersal spawning and differential survival rates of beach and demersally spawned larvae in this and other regions of Newfoundland to quantify the relative contribution of beach versus demersal spawning to recruitment of this focal forage fish in the Northwest Atlantic. This is critical as current abundance indices used during stock assessments of capelin in Newfoundland are based on beach spawning, with research conducted at a single beach (Bellevue Beach, Trinity Bay).

Chapter 4. Mechanisms of larval emergence at demersal spawning sites of capelin (*Mallotus villosus*) on the Northeast coast of Newfoundland: implications for larval survival.

4.1 Introduction

Cushing's (1990) Match-mismatch hypothesis predicts that spawning in marine fish is timed so that peaks in hatching of larvae "match" peaks in the abundance of its planktonic prey, resulting in high survival and recruitment (Cowan and Shaw 2002). Evidence of this hypothesis has largely been described in temperate species spawning annually in either spring or fall at a time when the ocean environment regulates seasonal plankton blooms (Carscadden *et al.* 1997). This phenomenon has also been demonstrated within a spawning season for beach spawning capelin in Newfoundland, whereby emergence of capelin into food-rich and predator-poor environments is stimulated by wind events (Frank and Leggett 1982). The synchronous response of larvae to environmental cues is thought to be adaptive, offering fitness advantages to the early life history stages of fish (Frank and Leggett 1983).

In capelin, factors that operate during the immediate post-hatching period are hypothesized to be largely responsible for year-class strength (YCS) (Carscadden, *et al.* 1989). Upon hatching at the beach, larvae remain in the sediment ('pre-emergent larvae'). This represents a critical stage in larval survival with mass mortalities often occurring due to starvation after depletion of the yolk sac when larvae remain in the sediment for extended periods (Houde 2002). Frank and Leggett (1983) reported that emergence of capelin larvae from the sediment is active, stimulated by sharp increases in

temperature in the absence of sediment disturbance. Therefore, strong cohorts are produced by the frequent, synchronous emergence of larvae in good condition from beach sediments (Leggett *et al.* 1984), allowing the determination of YCS as early as 6-8 weeks after spawning when fish are still in the larval stage (Dalley *et al.* 2002). Frank and Carscadden (1989) demonstrated that these same environmental factors stimulate larval emergence for demersal spawning capelin on the Southeast Shoal.

The oceanographic mechanism underlying the temperature cue that triggers larval emergence from sediments has been studied extensively (i.e.. Carscadden *et al.* 2000). Templeman (1966) proposed that winds could have a dramatic influence on the bio-physical characteristics of near shore waters in Newfoundland, causing Coastal Water Mass Replacement. Offshore (135-315°) winds dominate on the eastern coast of Newfoundland where capelin spawn during the summer. These winds blow warm surface water seaward, resulting in the upwelling of deep, colder waters and its associated fauna. These conditions are not optimal for larval survival due to high abundances of chaetognaths and jellyfish, which are cold-water predators of capelin larvae (Frank and Leggett 1982a). In contrast, less frequent occurrence of onshore winds (0-90°) drive warm surface waters toward the coast, causing downwelling of warm surface waters and resulting in sharp but short increases in bottom temperature and sediment disturbance at coastal beaches. This favourable Coastal Water Mass Replacement causes a shift in the cold-water predator field away from the larvae and simultaneously brings warm surface water rich with prey of larval capelin, including copepod eggs and nauplii. Frank and Leggett (1982a) estimated a 3- to 20- fold decrease in the abundance of predators and a 2- to 3- fold increase in the biomass of suitable prey with an onshore wind event of 18-hour

duration. Similarly, emergence of capelin larvae on the Southeast Shoal is stimulated by storms that destratify the water column, increasing water temperatures and currents near the seabed (Frank and Carscadden 1989).

In this study, I investigated the effects of Coastal Water Mass Replacement on the patterns of capelin emergence and larval condition at demersal sites on the Northeast coast of Newfoundland during the spawning season (July-August) in 2004 and 2005. My first objective was to test if Coastal Water Mass Replacement occurs and, thus, is applicable to larval emergence at demersal spawning sites on the Northeast coast of Newfoundland. To do this, I determined whether wind speed and direction, integrated into a vector component, caused destratification of the water column at demersal spawning sites and, if so, whether this produced a temperature cue for larvae to emerge from sediments. My second objective was to determine if this Coastal Water Mass Replacement caused synchronous release of larvae at demersal spawning sites. To do this, I determined if increased larval densities in the water column were associated with increased temperatures near the seabed due to destratification. I also determined if the condition of larvae in the water column was associated with time since last destratification, which would indicate that larvae had remained in the sediment until a temperature cue triggered emergence.

4.2 Methods

Study Design

This study was conducted at demersal spawning sites along the exposed Northeast coast of Newfoundland (Fig. 2.1 in Chapter 2) during July-August in 2004-2005 aboard the *Lady Easton II*, a 13.4 m commercial fishing vessel which operated 12 h·d⁻¹ during daylight. In both years, biological sample collection was focused at three sites (Turr Island, Cracker's Rock and Gull Island I) in the southeast section of the study area. In each year, ship time constraints resulted in sampling intervals primarily based on requirements for analysis of egg development data and, thus, occurred every third day in 2004 and every second day in 2005 due to higher temperatures in 2005 (see Chapter 3). Larval tows were initiated at each site based on predicted hatching times (see Chapter 3) and were conducted from 14 - 30 August in 2004 and 25 July to 23 August in 2005. In 2004, hatching did not occur at Gull Island I before the end of the study period so larval emergence patterns in 2004 are based on Turr Island and Cracker's Rock sites only. Earlier spawning in 2005 relative to 2004 (Chapter 2) resulted in a longer period of larval collection, including all three sites.

Physical Samples

Vemco Miniloggers (Vemco 8-bit Minilog-TR) that recorded temperature every 30 min throughout the incubation period were anchored near the seabed at demersal spawning sites in both years to characterize the temperature experienced by incubating eggs and larvae remaining in the sediment. Temperature profiles of the water column were

measured at demersal spawning sites on each sampling day in 2004 using a Sea Bird SBE-19 to characterize the thermal properties of the water column in relation to thermister data. The device was deployed at $0.2 \text{ m}\cdot\text{s}^{-1}$, allowing data capture every 10-30 cm from the surface to the demersal spawning bed.

Hourly wind speed and direction during the study period in both years were obtained from daily summaries published by Environment Canada for the local meteorological station located in Pool's Island, 13.5 km southeast of the demersal spawning sites.

Biological Samples

In each year (2004-2005), emergent larvae were collected at demersal spawning sites beginning on predicted dates of hatching using a 0.44 m^2 cone net with a 0.270 mm Nitex mesh. In both years, larvae were collected in surface tows because it has been shown that recently hatched capelin larvae are confined to the upper 20 m of the water column (Frank and Carscadden 1989). The larval net was towed in the upper 5-10 m of the water column at ~2 knots for 15 min (~2 km). Vessel speed, direction and net depth were recorded for each tow. Additionally, time, latitude and longitude were recorded at the beginning and end of each tow. In 2004, one tow was conducted against the current across each spawning site. In 2005, three tows were conducted in a triangular grid around the spawning site. The net was rinsed with seawater and the entire contents of the codend were preserved with a 5% formalin solution buffered with sodium borate in a 1 L sample jar.

In the laboratory, samples were poured over a 0.270 mm sieve and rinsed with water for ~20 min. Samples were sub-sampled using a 1 L capacity Motoda splitter (Motoda 1959) and the final split (~300-500 larvae) was placed into a petrie dish. Capelin larvae were identified and counted using a dissecting microscope. Larvae in the final split were categorized as good or bad based on a modification of Frank and Leggett's (1981a) description of larval condition (Table 4.1). Good larvae are expected to have high chances of survival and bad larvae are in deteriorated condition, with low probability of survival (Frank and Leggett 1982). Densities of larvae were expressed as the number of larvae·m⁻³ based on the volume of water filtered through the net. The volume of water filtered was estimated using the radius of the opening of the net (r) and the distance (d) that the net was towed ($V=\pi r^2 d$).

Analysis of Physical Data

Hourly temperature data from all three demersal spawning sites were smoothed using a 24-h running mean filter to emphasize the daily trends. To determine if temperature trends were coherent among the three demersal spawning sites, a correlation analysis of the smoothed temperature data was performed for data collected in both years. If temperature trends were coherent, I examined the Coastal Water Mass Replacement hypothesis using a single site, Turr Island. To determine if sharp but short increases in bottom temperatures were associated with the thermal destratification of the water column, I compared temperature profiles of the water column on dates when bottom temperatures peaked and when they were low.

Table 4.1: Key visual characteristics of good and bad larvae (modified from Frank and Leggett 1981a).

Category	Characteristics
Good	Robust larvae obviously in good condition Body transparent or developing a whitish appearance No spinal curvature
Bad	Body more white than transparent or white Slight or extreme spinal curvature Obvious loss of muscle integrity, thinning

I examined the effect of wind on bottom temperature at Turr Island using a two-factor ANOVA. The factors included in the model were wind speed and direction. To prepare the data for analysis, I first determined if a pattern appeared to exist between bottom temperature and wind direction. I graphed both of these variables together against date. Using these graphs, I visually determined the time lag, or the time required for wind events to destratify the water column as indicated by peaks in temperature, in each year. Second, I quantified the specific range of wind directions that caused destratification of the water column at my demersal sites. Previous studies on wind events causing emergence of capelin larvae have neglected to do this (Mertz *et al.* 1994), opting instead arbitrarily to use onshore winds, defined by the orientation of the study area (Frank and Leggett 1981, Frank and Carscadden 1989, Carscadden *et al.* 2000). To determine the wind direction that causes destratification of the water column at demersal spawning locations in my study area, I plotted average temperature (y) against wind direction (x) during the post-hatching period in each year. The range of wind directions that was consistently associated with high average lagged bottom temperatures with low variation was used to define wind directions that cause destratification at my demersal sites.

Finally, I determined if wind speed and direction were both responsible for the observed patterns in lagged bottom temperature using a 2-way ANOVA (wind speed and direction). If both components of wind were significant in explaining the observed patterns in temperature, I transformed wind into a vector component by integrating wind speed and direction. Wind speed and direction were integrated using indicator (dummy) variables. The speeds of destratifying wind directions were multiplied by +1 and

stratifying wind speeds were multiplied by -1. This produced an integrated measurement of the meteorological data used to simultaneously analyze the effects of wind speed and direction on bottom temperature in a linear regression analysis.

Analysis of Biological Data

To examine the prediction that high larval densities in surface waters are associated with destratification of the water column, I used linear regression analysis to test the relationship between larval abundance and bottom temperature at all three sites where larval samples were collected. I tested this hypothesis using two temperature measurements, the mean and the fluctuation, to investigate whether capelin cue to small, gradual increases or large fluctuations in temperature. To investigate this relationship across all sites where temperature patterns varied, I standardized the temperature data by calculating the mean bottom temperature during the post-hatching interval for each spawning site in each year and expressed each hourly bottom temperature as a deviation from the mean. The mean temperature anomaly for each site in each year was calculated for 12, 24, 36, and 48 h prior to sampling the larvae to ensure that if a pattern existed but was lagged at a particular temporal scale, the pattern would be observed. To standardize the fluctuation in temperature measurement, I subtracted the minimum from the maximum temperature for 12, 24, 36 and 48 h periods and divided by the average temperature during post-hatching.

If destratification did not cause the release of larvae into the water column, I tested the alternative hypothesis that larvae emerge continuously into surface waters upon hatching. To test this prediction, I used a correlation analysis to examine the relationship

between the sequential order of the proportion of total eggs spawned per day and the proportion of total larvae collected per day. As a result of the sampling interval, I was limited to investigating this hypothesis at a resolution of every third day in 2004 and every second day in 2005. The proportion of eggs spawned at each site was calculated for each sampling day during spawning by dividing the average daily density of newly spawned eggs (Stage I-II; see Chapter 2) by the total number of eggs spawned at each site during each year. I then correlated this with the daily average proportion of larvae collected, which was calculated by dividing the average daily density of larvae collected by the total number of larvae collected at each site during each year. For the analysis, the proportion of eggs spawned during the spawning period was correlated with the proportion of larvae collected during the post-hatching period. For instance, the proportion of eggs spawned on day three of the spawning period was correlated with the proportion of larvae collected on day three of the post-hatching period.

Throughout analyses, data were tested for normality and homogeneity of variance. Larval abundance data were \log_{10} transformed, egg and larval proportions were square root arcsine transformed and temperature measurements were square root transformed to meet the above assumptions of linear models.

4.3 Results

Coastal Water Mass Replacement

Correlation analysis revealed that smoothed (24-h) temperature series were coherent among demersal spawning sites in 2004 ($p<0.0001$; Fig. 4.1; Table 4.2) and 2005 ($p<0.0001$; Fig. 4.1; Table 4.2). As such, all subsequent analyses of the Coastal Water Mass Replacement hypothesis were based on hydrographic and meteorological data from a single site (Turr Island) with the most complete data set. In 2004, when thermal profiles of the water column were collected, the water column was thermally stratified (Fig. 4.2). When bottom temperatures had short but sharp increases, the water column became thermally destratified (Fig. 4.2).

The relationship between wind and temperature was visually examined to determine if a time lag between wind events and temperature data existed. Hourly temperature data were smoothed with a 6-h running mean filter. A time lag existed in both years (Fig. 4.3). In 2004, the response of temperature was approximately 26 h after wind events (Fig. 4.3A) and only 19 h in 2005 (Fig. 4.3B). Wind speed and direction were significant in explaining the variability in lagged bottom temperature at the demersal site throughout the time series in 2004 and 2005 (Table 4.3). Wind events oriented from $270^\circ - 20^\circ$ were associated with higher temperatures in both years, as inferred from plots of average temperature during different wind directions (Fig. 4.4). In 2004, wind speed and direction was significant ($p<0.0001$) in explaining 38% of the variation in temperature (Fig. 4.5).

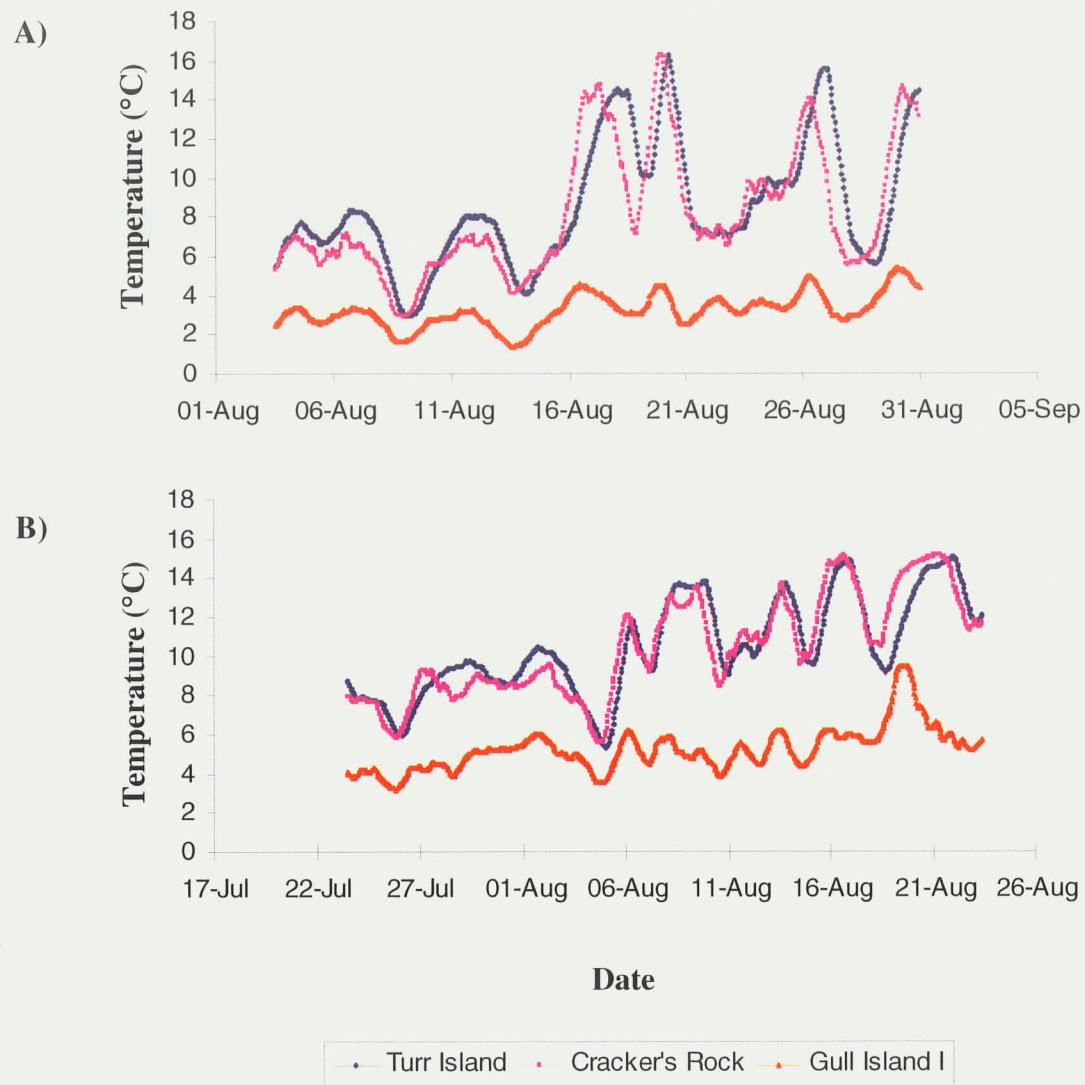


Figure 4.1: Smoothed (24-h) incubation temperatures at three demersal spawning sites in (A) 2004 and (B) 2005.

Table 4.2: Correlation analysis of hourly temperatures at demersal spawning sites in 2004 (n=659) and 2005 (n=743). Pearson correlation coefficients and p values are reported below.

Year								
2004			2005					
	Turr	Crackers	Gull Is I		Turr	Crackers	Gull Is I	
Turr	1.0000	0.8434	0.6084		Turr	1.0000	0.9153	0.5735
		<0.0001	<0.0001				<0.0001	<0.0001
Crackers		1.0000	0.8303		Crackers		1.0000	0.7476
			<0.0001					<0.0001
Gull Is I			1.0000	Gull Is I				1.0000

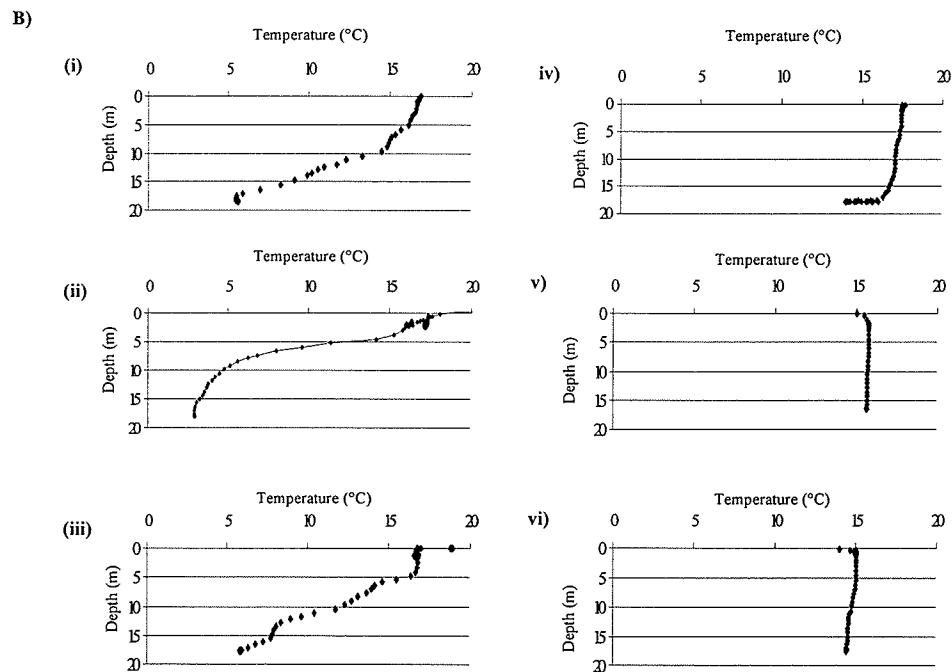
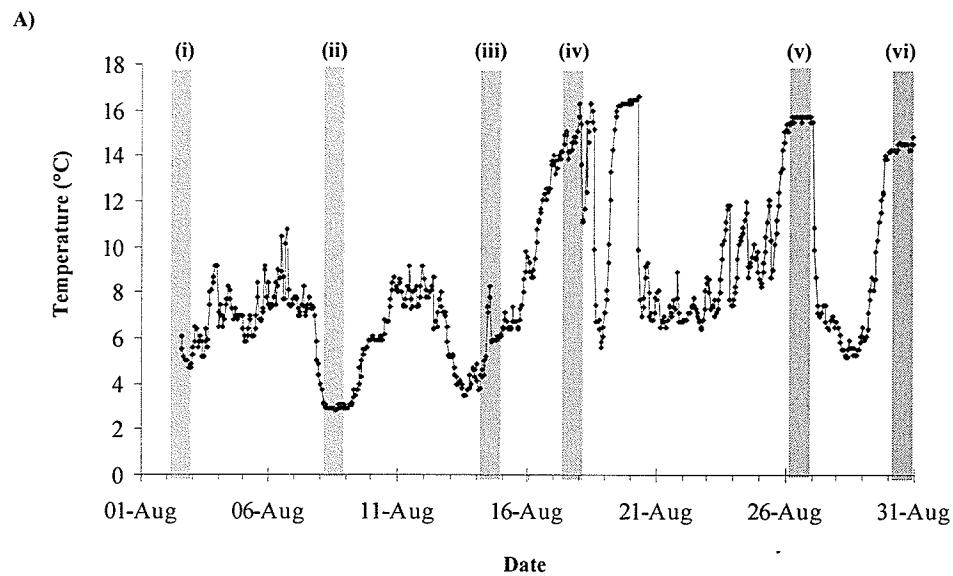


Figure 4.2: Hydrographic data at Turr Island in 2004 showing (A) time series of water temperatures near the seabed (shaded areas denoted by roman numerals correspond to thermal profiles in B), and (B) thermal profiles of the water column when bottom temperatures were low on (i) August 2, (ii) August 8, and (iii) August 14, and when bottom temperatures were high on (iv) August 17, (v) August 26, and (vi) August 30..

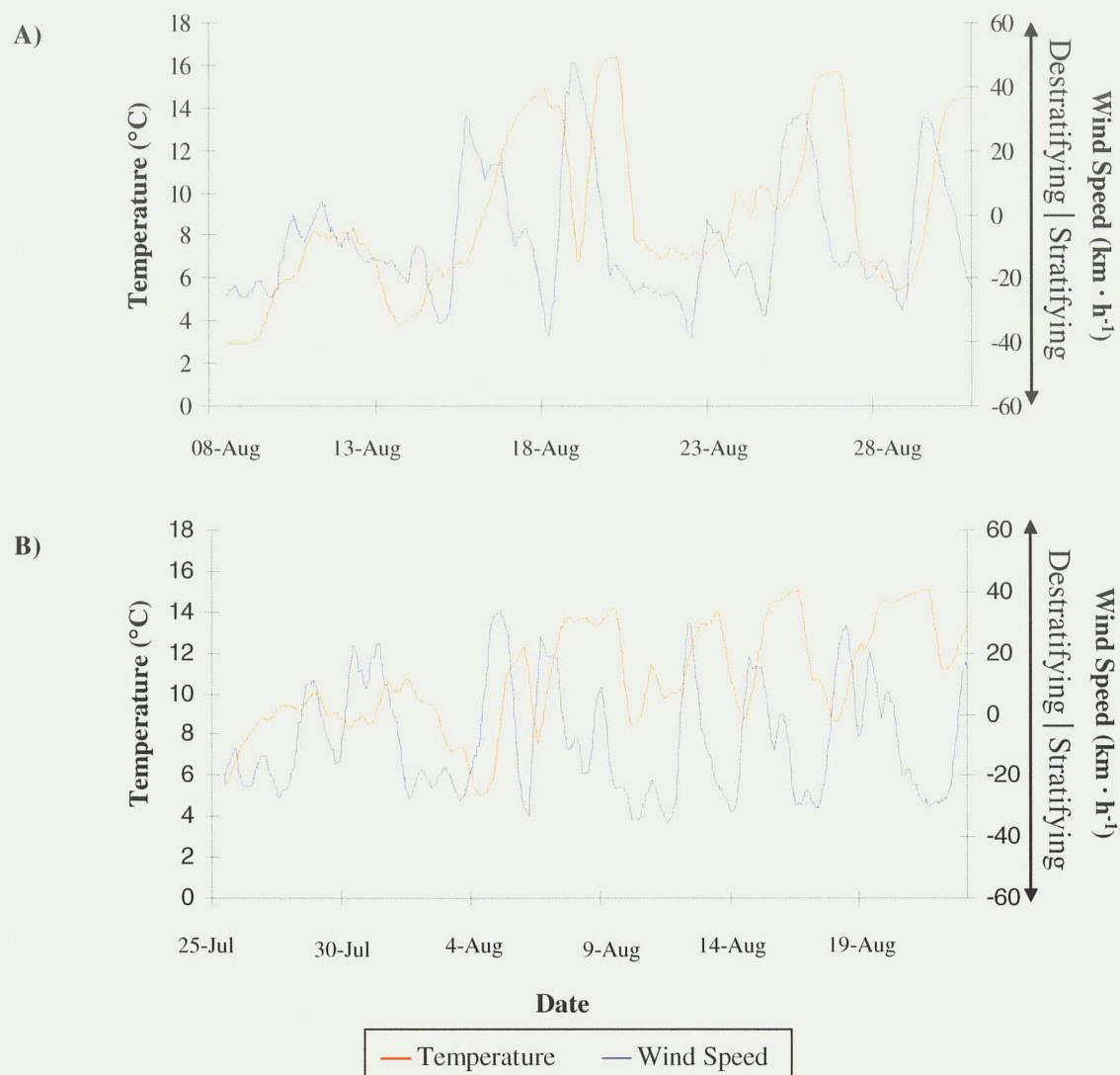


Figure 4.3: Smoothed (12-h) wind and temperature time series data at Turr Island in (A) 2004 and (B) 2005.

Table 4.3: Two-factor Analysis of Variance examining the effect of wind speed, wind direction and an interaction between the two factors (S*D) on bottom temperature at Turr Island in 2004 and 2005.

YEAR					
2004			2005		
Source	df	p	Source	df	p
Model	3	0.0007	Model	3	0.0001
Wind Speed	1	0.6583	Wind Speed	1	0.0002
Wind Direction	1	0.4327	Wind Direction	1	<0.0001
S*D	1	0.0668	S*D	1	<0.0001
Error	543		Error	697	
Corrected Total	546		Corrected Total	700	

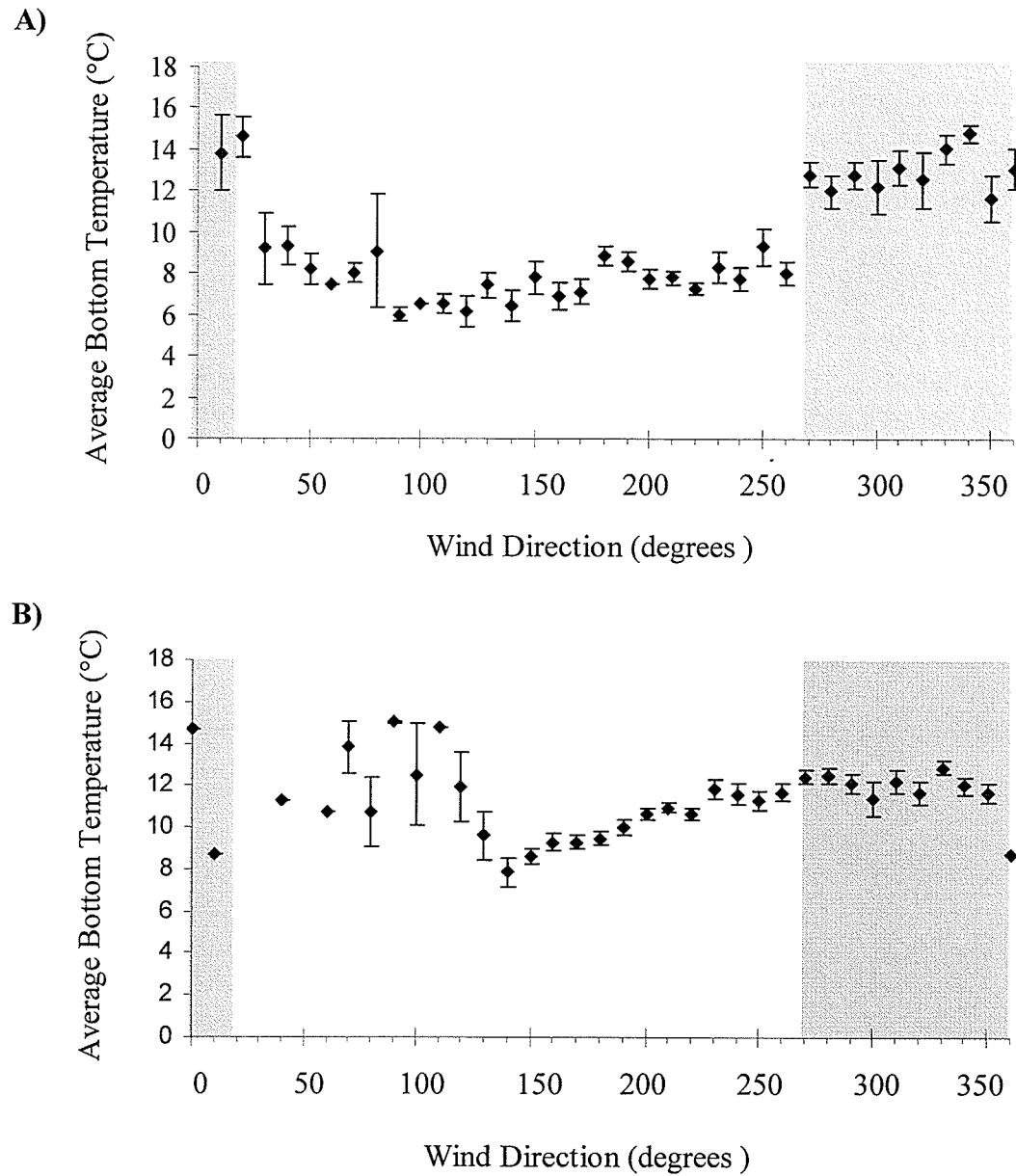


Figure 4.4: Average bottom temperature at Turr Island during different wind directions in (A) 2004 and (B) 2005, with shaded areas indicating the range of wind directions that are associated with higher temperatures.

Larval Emergence and Condition

Regression analyses of larval densities and mean temperature and temperature fluctuation at different temporal scales were not significant ($p>0.05$; Table 4.4). Similarly, larvae collected at all demersal spawning sites in both years were in good condition ($90.4 \pm 0.03\%$, $n=50$), indicating that there was no variation in the daily proportion of good and bad larvae throughout the time series in both years. Correlation analysis revealed, however, that the larval emergence patterns sequentially coincided with the egg deposition patterns during the spawning period ($p<0.0001$; Fig. 4.6), suggesting that larvae emerged continuously from the sediment upon hatching.

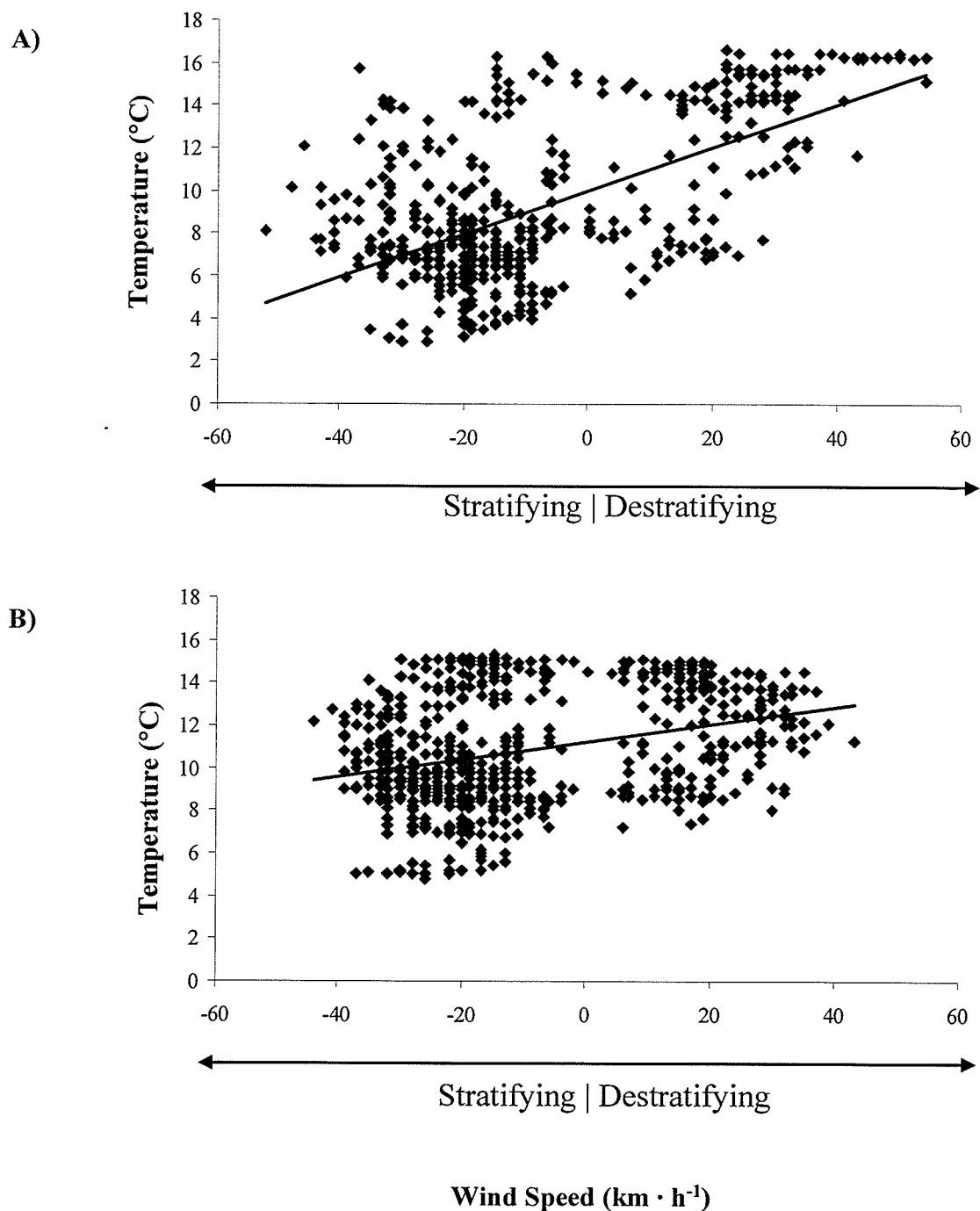


Figure 4.5: Relationship between lagged hourly temperature and wind speed of destratifying and stratifying wind events in (A) 2004 and (B) 2005. 2004 (26 h time lag): $y=0.1019x+10.019$, $r^2=0.3798$; 2005 (19 h time lag): $y=0.0407x+11.233$, $r^2=0.1126$.

Table 4.4: Regression analysis showing the relationship between \log_{10} transformed larval densities and square root transformed measures of temperature (12, 24, 36, and 48 h lag of mean temperature deviation and fluctuation).

Time Lag	Measurement of Temperature	F	d.f.	r ²	p
12h	deviation	0.21	30	0.0069	0.6513
	fluctuation	0.24	40	0.0061	0.6238
24 h	deviation	0.84	27	0.0303	0.3667
	fluctuation	0.04	40	0.0010	0.8409
36 h	deviation	0.47	24	0.0191	0.5013
	fluctuation	0.00	40	0.0001	0.9540
48 h	deviation	0.66	27	0.0237	0.4248
	fluctuation	0.50	40	0.0124	0.4828

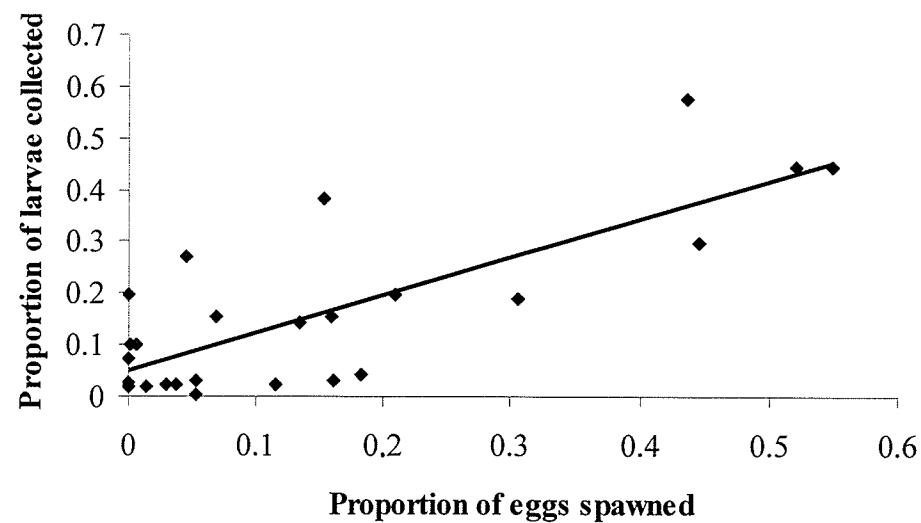


Figure 4.6: Relationship between the daily proportion of the total number of eggs spawned per site per year during the spawning period and the daily proportion of larvae collected per site per year during the post-hatching period both years combined.
 $y=0.7345x+0.05$, $r^2=0.6191$.

4.4 Discussion

Coastal Water Mass Replacement occurs at demersal spawning sites (18-33 m) along the northeast coast of Newfoundland, with wind events (range: 270° – 20°) causing destratification of the water column and increased water temperature near the seabed at time lags of ~1 d (19-26 h). Increased bottom temperatures associated with Coastal Water Mass Replacement, however, did not appear to stimulate larval emergence. Rather, larvae in good condition appeared to emerge continuously from the sediment upon hatching, resulting in asynchronous emergence of larvae from demersal spawning sites.

Coastal Water Mass Replacement

I determined that Coastal Water Mass Replacement on the exposed northeast coast of Newfoundland applies to coastal areas at least up to 33 m in depth, caused by wind directions oriented 270° to 20°. This supports Templeman's (1966) hypothesis that the influence of wind on the warm surface layers in the summer significantly alters the thermal properties of the water column in coastal areas. The range of onshore wind directions that caused changes in the thermal properties of the water column was different, however, from those reported in previous studies (Frank and Leggett 1981, Leggett *et al.* 1984). Wind directions in these studies, however, were arbitrarily set as those that were oriented onshore to the coastline being studied. Mertz *et al.* (1994) suggested that determining destratifying wind directions was not simple due to the complexity of coastal oceanography. These researchers further suggested that future

studies of the Coastal Water Mass Replacement should test whether winds in a specific range of directions cause destratification (Mertz *et al.* 1994).

After defining the range of wind directions that caused short but sharp increases in temperature at demersal spawning sites, I found that the effect on bottom temperatures at the demersal spawning site investigated was time delayed. The time required to cause an increase in temperature was determined primarily by the thermal structure of the water column when it was stratified. This is evidenced by the colder bottom water temperatures in 2004 relative to 2005, resulting in a longer period of time for the wind to alter temperature at depth. I also found that wind events causing destratification occurred relatively frequently during the post-hatch period (2004: n=5, range: 1.5-4 d duration; 2005: n=6, range: 1-3 d duration) throughout August in both years of this study. This suggested that Coastal Water Mass Replacement could act as an appropriate environmental cue to stimulate the emergence of capelin from the sediment at demersal spawning sites.

Larval Emergence and Condition

Despite the definite presence of a temperature cue at depth, larvae did not appear to respond to it. Synchronous responses to environmental cues cause high variability in recruitment due to unpredictability of environmental factors but can be adaptive if they increase fitness through decreased risk of predation and/or increased food supply (Frank and Leggett 1983, Fortier *et al.* 1987). This suggests that selective pressures do not shape emergence behaviour or an alternative environmental cue may be responsible for larval emergence at demersal spawning sites in the study area.

In the beach spawning capelin population of Newfoundland, Coastal Water Mass Replacement is hypothesized to be largely responsible for year-class strength (Leggett *et al.* 1984, Carscadden *et al.* 2000). Onshore winds have been shown to cause Coastal Water Mass Replacement, resulting in a shift in the predator field away from the larvae (Frank and Leggett 1982). In my study of coastal demersal spawning locations, capelin larvae appeared to emerge continuously upon hatching. This may indicate that predation pressure on larvae emerging from demersal spawning sites is not strong enough to elicit an adaptive behavioural response. Video recordings of transects across egg beds in a preliminary study revealed that fish predators (*i.e.*, sculpin, flounder) were scarce at these demersal sites (Davoren unpubl. data). Alternatively, it is also possible that the decreased predator and increased prey field that is reported to be associated with the Coastal Water Mass Replacement (Frank and Leggett 1981, Frank and Carscadden 1989) does not occur in our study area. If this were true, there would be no selective advantage for larvae to emerge synchronously in a destratified water column. Instead, equal or higher survival probability would be associated with emergence upon hatching.

The possibility exists that larvae at demersal spawning sites in my study area respond to an alternative environmental cue that stimulates emergence. In support of this, Fortier *et al.* (1987) found that capelin larvae did not emerge from the beach sediment in the St. Lawrence estuary due to a temperature cue, but rather actively emerged during low light intensities from dusk to dawn. In this capelin stock, emergence at dark was thought to be an adaptation to emerge when visibility is low, thereby reducing predation by visual predators (Fortier *et al.* 1987). Although such a mechanism of emergence is possible, low light levels at the depth of demersal sites (18-33 m) would

result in a much reduced cue relative to beach sites. Additionally, because larval emergence patterns appeared to correspond with the timing of spawning, it seems unlikely that an environmental cue was responsible for emergence. In support, an environmental cue to stimulate larval release has not been found for the demersal spawning stocks in the Icelandic and Barents Sea, although this has not been well studied for these stocks (Vilhjalmsson 1994). At these locations, larvae are thought to simply emerge from the sediment upon hatching.

Stimulation of emergence by unpredictable environmental cues causes large variability in recruitment because of the survival risks of remaining in the sediment due to depleting yolk-sac reserves (Fortier *et al.* 1987). Trippel *et al.* (1997) proposed that protracted spawning and, thus, continuous trickling of larval emergence, had the potential to be selectively advantageous to the early life history stages of fish. Utilizing this mechanism of emergence, rather than a single synchronous emergence peak, would ensure a higher probability that at least some larvae emerging in good condition would match high prey and low predator abundances necessary for survival (Trippel *et al.* 1997). Therefore, I hypothesize that because capelin continuously emerge in good condition, there may not be a selective advantage to emerging in response to environmental cues at demersal spawning sites in my study area.

Implications and Future Study

For capelin, divergent mechanisms of emergence have been used to imply genetically distinct sub-populations (Fortier *et al.* 1987). Larval emergence at demersal sites in my study area occurs where Coastal Water Mass Replacement is applicable, but in contrast to

emergence mechanisms proposed for beach spawning populations in Newfoundland, larvae do not synchronously emerge when this environmental cue is present. Instead, larvae in good condition continuously emerge in the water column upon hatching. Further study of emergence mechanisms at demersal spawning sites should investigate whether changes in predator-prey fields occur, as reported for the Coastal Water Mass Replacement theory. If predator and prey fields do not change with destratification of the water column in my study area, continuous larval emergence may be selectively advantageous at demersal spawning sites relative to at the beach.

Chapter 5. General Discussion

Spawning habitat selection is critical to the fitness of individual fish because it determines not only the environment in which progeny develop, but also the risks experienced by the early life history stages. Capelin, the key forage fish in the North Atlantic, uses two reproductive tactics in Newfoundland, spawning primarily on beaches but also spawning demersally far offshore. Recent discoveries of demersal spawning in coastal Newfoundland (Nakashima and Wheeler 2002; Davoren *et al.* 2006), however, suggest that demersal spawning may be a result of major environmental changes in the in the 1990s that caused a cold water event in the Northwest Atlantic (Nakashima and Wheeler 2002). Recent investigation of the early life history stages of demersally spawned capelin led to the conclusion that demersal spawning is not a viable reproductive mode in Newfoundland (Nakashima and Wheeler 2002). I investigated this hypothesis by examining the factors influencing the early life history stages, mainly eggs and larvae, of capelin that are considered to be important to recruitment. These factors include physical characteristics of spawning sites (Nakashima and Taggart 2002), egg densities (Frank and Leggett 1981) and larval emergence mechanisms (Frank and Leggett 1981, Carscadden *et al* 2000).

Beach and demersal spawning in Newfoundland result in divergent temperature regimes experienced by eggs and larvae, which influences their development and survival. In my investigations of the influence of temperature on the egg stage of both spawning tactics, egg development was faster at the beach relative to demersal sites likely due to warmer temperatures (Chapter 3). Development at the beach was as predicted by

the equation for capelin egg development and, thus, is considered normal for capelin in Newfoundland (Frank and Leggett 1981). The slower development and later time to hatch of demersally spawned eggs, although still within the normal range reported for capelin, is considered to be detrimental to the survival of this forage species (Nakashima and Wheeler 2002). In drawing this conclusion, researchers neglected to consider that optimum developmental rates are not fixed and are a result of adaptation to conditions that are conducive for survival. As such, the optimum developmental rate is not necessarily one that is the fastest, but, rather, the rate at which mortality is the lowest (Cossins and Bowler 1987). At the beach, egg development is rapid in response to warmer temperatures, but at the cost of significantly higher mortality. The beach spawning mode is proposed to be selectively advantageous by reducing predation pressure on this critical early life history stage (Fortier *et al* 1987). This is accomplished through both spawning in the intertidal zone, away from fish predators such as winter flounder (*Pseudopleuronectes americanus*), and rapid developmental rates that reduce the amount of time eggs are exposed to predation (Fortier *et al* 1987). Although predation pressure at demersal spawning sites was not quantified, transects across egg beds revealed scarce fish predators (Davoren unpubl. data). I suggest, then, that the slower developmental rates at the demersal spawning sites in my study area do not result in higher predation pressure experienced by eggs.

Coastal Water Mass Replacement, caused by wind events, is known to drastically influence the properties of the nearshore water column caused by wind events. This has been proposed to be an important regulator of larval survival and recruitment in capelin (Frank and Leggett 1981, 1982, 1983, Leggett *et al* 1984, Carscadden *et al* 2000).

Synchronous emergence stimulated by environmental cues is considered to be a strategy that is maintained by natural selection due to the fitness benefits to larvae (Frank and Leggett 1983). This behaviour, however, can result in large variations in recruitment and, thus, year-class strength due to the unpredictability of environmental cues (Fortier *et al* 1987). The large fluctuations in year-class strength that are characteristic of the beach spawned capelin in Newfoundland are thought to be due to the deterioration of larvae prior to emergence from the beach gravel because larval condition upon emergence into the water column is a negative function of beach gravel residence time (Frank and Leggett 1982, Leggett *et al* 1984). Coastal Water Mass Replacement occurred at demersal spawning sites in the study area, causing drastic changes in the water column properties (Chapter 4). Larvae did not respond to this environmental cue, however, suggesting that the fitness benefits of this behaviour at the beach were not applicable to demersally spawned capelin.

Implications for Stock Structure

Results from this study of the early life history stages of capelin indicate the possibility of genetic divergence of beach and demersal spawning capelin in Newfoundland. Adaptive divergence is known to occur where gene flow is restricted between populations in time and space. Restriction in gene flow is accomplished if fish are philopatric and home to natal areas, or if differences in spawning times lead to divergent spawning habitats (Hendry and Day 2005). A temporal restriction in gene flow may arise due to different spawning times (isolation-by-time, IBT; Hendry and Day 2005). Hendry and Day's (2005) adaptation-by-time (ABT) hypothesis predicts that if fish experience different

environmental conditions due to spawning at different times (IBT), they will adapt to these conditions. If these adaptations offer fitness advantages and can be inherited, then selection will lead to adaptive divergence (Hendry *et al* 1998). Divergent timing, location and thermal habitat of spawning in fish have been suggested to result in locally adapted and genetically distinct populations (Hendry *et al* 2002).

Capelin in the study area exhibit differences in the timing and location of spawning by spawning at beach sites earlier in the season and at demersal spawning sites later in the season. My study provides unequivocal evidence that survival at the egg stage is higher at demersal spawning sites than at the beach (Chapter 3), suggesting that there are fitness advantages to spawning in cooler water. Egg development was significantly different at demersal spawning sites relative to the beach and could not be attributed to incubation temperatures alone. This indicates that other factors, such as maternally-linked traits (i.e. egg size) or genetic divergence, may be the source of the unexplained variation. The fitness differences between beach and demersal spawning capelin on the northeast coast of Newfoundland reported in this study suggest a possibility for adaptive divergence. Additionally, the different larval emergence mechanism of demersally spawned capelin in the study area, relative to that at the beach, likely reflects local adaptation and genetically divergent sub-populations (Fortier *et al* 1987). This, however, cannot be concluded with any certainty without further study. I suggest that common garden experiments where beach and demersally spawned eggs are raised at a range of controlled temperatures would provide substantial evidence as to whether beach and demersally spawned eggs are genetically divergent or if they are simply expressions of phenotypic plasticity along a developmental reaction norm that is

common for capelin. Genetic studies investigating selectively neutral microsatellite loci of beach and demersal spawning capelin is also important to resolve this question.

Implications for Recruitment

Results of this study provide evidence that does not support the hypothesis that demersal spawning does not contribute to reproductive success of capelin (Nakashima and Wheeler 2002). I propose that the conflicting results of those reported in the previous investigation of demersal spawning (Nakashima and Wheeler 2002) and my results may be due to the differences in the environmental features of demersal spawning grounds. My investigations were conducted along the Straight Shore of Newfoundland, an area that is directly exposed to the hydrographic properties of the Labrador Current (Chapter 2). Capelin research conducted by Fisheries and Oceans Canada has occurred at a single location, Bellevue Beach in Trinity Bay since 1990. This area, located at the bottom of a large embayment, is considered to be one of the largest capelin spawning beaches on the east coast of Newfoundland (Nakashima and Wheeler, 2002). The meteorological and hydrographic parameters that are considered to be essential to egg and larval survival in capelin, then, would be very different between these two locations. Researchers reported that egg mortality was higher at demersal spawning sites in this study area, presumably due to anaerobic conditions in deep water (Nakashima and Wheeler 2002). This study provides evidence that due to its exposure to the open ocean, circulation through the egg layer at demersal spawning sites is sufficient to replenish oxygen to incubating eggs (Chapter 2).

The observed differences in the results of this study and in Trinity Bay (Nakashima and Wheeler 2002) could also stem from the context in which questions were framed. Although not directly investigated in this study, I propose that two major theories pertaining to recruitment in fisheries science can explain the success and retention of the two spawning tactics in the Northwest Atlantic. Cushing's (1990) Match-mismatch hypothesis predicts that spawning in marine fish is timed so that hatching of larvae "matches" peaks in the abundance of its planktonic prey, resulting in successful survival and recruitment (Cowan and Shaw 2002). This hypothesis has been proposed to be critical to beach spawning capelin of Newfoundland, whereby emergence of capelin into food-rich and predator-poor environments is stimulated by onshore wind events (Frank and Leggett 1982). Larvae at demersal spawning sites, however, emerged continuously into the water column and did not respond to Coastal Water Mass Replacement (Chapter 4). I propose that an alternate hypothesis considered essential to recruitment in marine fishes can provide explanation for the observed results.

Developmental rates at demersal spawning sites were slower relative to beach sites due to lower incubation temperatures and time to hatch was 8-10 d later than predicted (Chapter 3), with larvae emerging continuously into the water column (Chapter 4). Growth efficiency (mm growth per unit energy) is maximum at low temperatures (Frank and Leggett 1982) and extended time to hatch results in larger larvae upon hatching (Chambers *et al* 1989). The Bigger-is-better hypothesis predicts that smaller larvae are subject to more intense predation and, thus, the production of larger larvae would result in higher recruitment potential (Cowan and Shaw 2002). Increased size presumably lowers predation risk and larger yolk-sacs at hatch prolong the time period of

exogenous feeding when food supply is unpredictable. I propose that due to higher growth efficiency at lower temperatures and prolonged time to hatch relative to the beach, demersal spawning has the potential to produce larger larvae that have yolk sacs equal to or larger than at the beach upon hatching and, thus, have a higher potential for survival. As such, recruitment indices using the early life history stages of capelin should incorporate demersal spawning. This will be critical for incorporation into stock assessment models, thereby improving their ability to quantify year class strength and ultimately an appropriate total annual allowable catch. This is timely, as budgetary restrictions at Fisheries and Oceans Canada have limited the number of indices used for year class strength predictions of capelin, despite a continuing inshore purse seine and trap capelin fisheries during the spawning season.

Reference List

- Andrews, D.W. Beach spawning of capelin (*Mallotus villosus*) on the northeast coast of Newfoundland. B.Sc. (Hons) thesis, Memorial University of Newfoundland, St. John's, Newfoundland.
- Bakke, S. and Bjørke, H. 1973. Diving observations on Barents Sea capelin at spawning grounds off Northern Norway. *FiskDir.Skr.Ser.HavUnders.* **16:** 140-147.
- Balon, E.K. 1984. Patterns in the evolution of reproductive styles in fishes. In *Fish Reproduction: Strategies and Tactics*. Edited by G.W.Potts and R.J.Wootton. Academic Press, London pp. 35-54.
- Beacham, T.D., Withler, F.C., and Morley, R.B. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). *Can.J.Zool.* **63:** 847-850.
- Beacham, T.D. and Murray, C.B. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of Chum salmon (*Oncorhynchus keta*) in British Columbia. *Can.J.Fish.Aquat.Sci.* **44:** 244-261.
- Benoit, H.P. and Pepin, P. 1999. Individual variability in growth rate and the timing of metamorphosis in yellowtail flounder *Pleuronectes ferrugineus*. *Mar.Ecol.Prog.Ser.* **184:** 231-244.
- Brannon, E.L. 1987. Mechanisms stabilizing salmonid fry emergence timing. *Can.Spec.Publ.Fish.Aquat.Sci.* **No. 96:** 120-124.

Carscadden, J., Nakashima, B.S., and Frank, K.T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Can.J.Fish.Aquat.Sci. **54** : 781-787.

Carscadden, J., Frank, K.T., and Leggett, W.C. 2000. Evaluation of an environment-recruitment model for capelin (*Mallotus villosus*). ICES J.Mar.Sci **57**: 412-418.

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**: 1743-1754.

Carscadden, J.E. and Nakashima, B.S. 1997. Abundance and changes in distribution, biology and behavior of Capelin in response to cooler waters of the 1990s. Proceedings-Forage Fish in Marine Ecosystems.

Carscadden, J.E., Frank, K.T., and Leggett, W.C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Can.J.Fish.Aquat.Sci. **58**: 73-85.

Carscadden, J.E. and Vilhjalmsson, H. 2002. Capelin - What are they good for? ICES Journal of Marine Science **59**: 863-869.

Chambers, C., Leggett, W.C., and Brown, J.A. 1989. Egg size, female effects, and the correlations between early life history traits of Capelin, *Mallotus villosus*: An appraisal at the individual level. Fishery Bulletin, U.S. **87**: 515-523.

- Chambers, C. and Trippel, E.A. 1997. Early life history and recruitment: legacy and challenges. *In* Early life history and recruitment in fish populations. Edited by C.Chambers and E.A.Trippel. Chapman and Hall, London pp. 515-543.
- Clutton-Brock, T.H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press.
- Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970-1993. ICES Mar.Sci.Symp. **198**: 311-322.
- Conover, D.O. and Schultz, E.T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends in Ecology and Evolution **10**: 248-252.
- Cossins, A.R. and Bowler, K. 1987. Temperature biology of animals. Chapman and Hall, New York.
- Cowan, J.H. and Shaw, R.F. 2002. Recruitment. *In* Fishery Science: The Unique Contributions of Early Life Stages. Edited by L.A.Fuiman and R.G.Werner. Blackwell Science Ltd., Oxford pp. 88-111.
- Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology **26**: 250-293.

- Cushing, D.H. 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, New York.
- Dalley, E.L., Anderson, J.T., and deYoung, B. 2002. Atmospheric forcing, larval drift, and recruitment of capelin (*Mallotus villosus*). ICES J.Mar.Sci **59**: 929-941.
- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecological Monographs. **73**: 463-481.
- 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**: 268-284.
- Dietrich, G. 1957. General oceanography. John Wiley & Sons, New York.
- 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.
- Einum, S. and Fleming, I.A. 2004. Does within-population variation in egg size reduce intraspecific competition in Atlantic Salmon, *Salmo salar*? Functional Ecology **18**: 110-115.

Fortier, L., Leggett, W.C., and Gosselin, S. 1987. Patterns of larval emergence and their potential impact on stock differentiation in beach spawning capelin (*Mallotus villosus*). *Can.J.Fish.Aquat.Sci.* **44**: 1326-1336.

Frank, K.T. and Leggett, W.C. 1981a. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meterological, hydrographic, and biological Factors. *Can.J.Fish.Aquat.Sci.* **38**: 1327-1338.

Frank, K.T. and Leggett, W.C. 1981b. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). *Can.J.Fish.Aquat.Sci.* **38**: 215-223.

Frank, K.T. and Leggett, W.C. 1982a. Coastal Water Mass Replacement: Its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Can.J.Fish.Aquat.Sci.* **39**: 991-1003.

Frank, K.T. and Leggett, W.C. 1982b. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the Match/Mismatch Hypothesis. *Can.J.Fish.Aquat.Sci.* **39**: 691-699.

Frank, K.T. and Leggett, W.C. 1983. Survival value of an opportunistic life-stage transition in capelin (*Mallotus villosus*). *Can.J.Fish.Aquat.Sci.* **40**: 1442-1448.

Frank, K.T. and Carscadden, J.E. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. *J.Cons.int.Explor.Mer.* **45**: 146-164.

Frank, K.T. and Leggett, W.C. 1994. Fisheries ecology in the context of ecological and evolutionary theory. *Annu.Rev.Ecol.Syst.* **25**: 401-422.

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

Fuiman, L.A. 2002. Special considerations of fish eggs and larvae. In *Fishery Science: The Unique Contributions of Early Life Stages*. Edited by L.A.Fuiman and R.G.Werner. Blackwell Science Ltd., Oxford pp. 1-32.

Gjosaeter, H. and Gjosaeter, J. 1986. Observations on the embryonic development of capelin (*Mallotus villosus* Muller) from the Barents Sea. *FiskDir.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**: 2048-2057.

Hendry, A.P., Hensleigh, J.E., and Reisenbichler, R.R. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Can.J.Fish.Aquat.Sci.* **55**: 1387-1394.

Hendry, A.P. and Kinnison, M.T. 1999. Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* **53**: 1637-1653.

Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., and Quinn, G.P. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. *Science* **290**: 516-518.

Hendry, A.P. and Day, T. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology* **14**: 901-916.

Hendry, M.A., Wenburg, J.K., Myers, K.W., and Hendry, A.P. 2002. Genetic and phenotypic variation through the migratory season provides evidence for multiple populations of wild Steelhead in the Dean River, British Columbia. *Transactions of the American Fisheries Society* **131**: 418-434.

Hjulstrom, F. 1939. Transportation of detritus by moving water. In *Recent Marine Sediments*. Edited by P.D.Trask. Dover, New York pp. 5-31.

Hoffmann, A.A. and Parsons, P.A. 1997. Extreme environmental change and evolution. University Press, Cambridge.

Houde, E.D. 2002. Mortality. In *Fishery Science: The Unique Contributions of Early Life Stages*. Edited by L.A.Fuiman and R.G.Werner. Blackwell Science Ltd., Oxford pp. 64-87.

Huse, G. 1998. Sex-specific life history strategies in capelin (*Mallotus villosus*)? *Can.J.Fish.Aquat.Sci.* **55**: 631-638.

Jangaard, P.M. 1974. The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition. *Bull.Fish.Res.Board Can.* **186**: 1-70.

Jeffers, G.W. The life history of the capelin (*Mallotus villosus*) (O.F. Muller). PhD thesis, University of Toronto.

King, C.A.M. 1962. An introduction to oceanography. W and J Mackay & Co. Ltd., Chatham.

Krebs, C.J. 2001. Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, San Francisco.

Leggett, W.C., Frank, K.T., and Carscadden, J.E. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can.J.Fish.Aquat.Sci. **41**: 1193-1201.

Leggett, W.C. and Frank, K.T. 1990. The spawning of the capelin. Scientific American **262**: 102-107.

Mann, R.H.K., Mills, C.A., and Crisp, D.T. 1984. Geographical variation in the life-history tactics of some species of freshwater fish. In Fish Reproduction: Strategies and Tactics. Edited by G.W.Potts and R.J.Wootton. Academic Press, London pp. 171-186.

Martin, K.L.M. and Swiderski, D.L. 2001. Beach spawning in fishes: phylogenetic tests of hypotheses. Amer.Zool. **41**: 526-537.

Mertz, G., Helbig, J.A., and Colbourne, E. 1994. Revisiting Newfoundland capelin (*Mallotus villosus*) recruitment: Is there a wind effect? J.Northw.Atl.Fish.Sci. **17**: 13-22.

Mertz, G. and Myers, R.A. 1994. Match/Mismatch predictions of spawning duration versus recruitment variability. *Fish.Oceanogr.* **3**: 236-245.

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 pp. 25-58.

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

Nakashima, B.S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth, and early life history of capelin (*Mallotus villosus*). *NAFO Sci.Coun.Studies* **24**: 55-68.

Nakashima, B.S. and Wheeler, J.P. 2002. Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters-the interaction between beach and demersal spawning. *ICES Journal of Marine Science* **59**: 909-916.

Nakashima, B.S. and Taggart, C.T. 2002. Is beach-spawning success for capelin, *Mallotus villosus* (Muller), a function of the beach? *ICES Journal of Marine Science* **59**: 897-908.

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.Fish.* **22**: 261-271.

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**: 503-518.

Pepin, P., Orr, D.C., and Anderson, J.T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). *Can.J.Fish.Aquat.Sci.* **54(Suppl. 1)**: 2-10.

Potts, G.W. 1984. Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. In *Fish Reproduction: Strategies and Tactics*. Edited by G.W.Potts and R.J.Wootton. Academic Press, London pp. 223-244.

Railsback, S.F. and Harvey, B.C. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* **83**: 1817-1830.

Reinfort, B. Biotic and abiotic factors affecting egg and pre-emergent larval mortality of capelin (*Mallotus villosus*) on a Northeast Newfoundland Beach. B.Sc. (Hons) thesis, University of Manitoba.

Reznick, D.N., Shaw, F.H., Rodd, F.H., and Shaw, R.G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275** : 1934-1937.

Roff, D.A. 2002. Life history evolution. Sinauer Associates Inc., Massachusetts.

Saetre, R. and Gjosæter, J. 1975. Ecological investigations on the spawning grounds of the Barents Sea capelin. *FiskDir.Skr.Ser.HavUnders.* **16**: 203-227.

Shackell, N., Carscadden, J., and Miller, D.S. 1994. Migration of pre-spawning capelin (*Mallotus villosus*) as related to temperature on the northern Grand Bank, Newfoundland. *ICES J.Mar.Sci* **51**: 107-114.

Shackell, N., Shelton, P.A., Hoenig, J.M., and Carscadden, J. 1994. Age- and sex-specific survival of Northern Grand Bank capelin (*Mallotus villosus*). *Can.J.Fish.Aquat.Sci.* **51**: 642-649.

Shepherd, T.D. and Litvak, M.K. 2004. Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. *Fish and Fisheries* **5**: 141-152.

Sleggs, G.F. 1933. Observations upon the economic biology of the capelin (*Mallotus villosus* O.F. Muller). *Rep.Newfoundland Fish.Resource Comm.* **1**: 1-66.

Stergiou, K.I. 1989. Capelin, *Mallotus villosus* (Pices: *Osmeridae*), glaciations, and speciation: a nomothetic approach to fisheries ecology and reproductive biology. *Mar.Ecol.Prog.Ser.* **56**: 211-224.

Templeman, W. 1948. The life history of capelin (*Mallotus villosus* O.F. Muller) in Newfoundland waters. *Bull.Fish.Res.Board Can.*

Templeman, W. 1966. Marine Resources of Newfoundland. *Bull.Fish.Res.Board Can.*

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

Trippel, E.A., Kjesbu, O.S., and Solemial, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In Early Life History and Recruitment in Fish Populations. Edited by C.Chambers and E.A.Trippel.* Chapman & Hall, London pp. 29-62.

Vilhjalmsson, H. 1994. The Icelandic capelin stock. *Rit Fiskideildar* **13**.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**: 377-392.

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

Zar, J.H. 1999. *Biostatistical analysis.* Prentice-Hall Inc., New Jersey.

Appendix A: Tidal zone and temporal changes in the mean \pm SE % dead eggs and number of eggs \cdot cm $^{-2}$ with date and average incubation temperature at Lumsden beach in 2004 and 2005.

Year	Day	LOCATION									
		HT			MT			LT			Avg. Inc. Temp
		Mortality	Density	Avg. Inc. Temp	Mortality	Density	Avg. Inc. Temp	Mortality	Density	Avg. Inc. Temp	
2004	06-Jul	—	16 \pm 15	—	6	74 \pm 29	—	9.4 \pm 1.2	94 \pm 14	7	
	08-Jul	12.1 \pm 3.0	26 \pm 9	—	23.0 \pm 11	163 \pm 14	—	12.0 \pm 5.3	53 \pm 33	8	
	10-Jul	—	1	—	14.1 \pm 7.4	488 \pm 144	—	7.1 \pm 1.7	295 \pm 97	7	
	12-Jul	11.3 \pm 6.4	322 \pm 162	—	4.1 \pm 1.1	1399 \pm 717	—	8.1 \pm 1.2	77 \pm 76	6	
	14-Jul	6.8 \pm 4.8	1344 \pm 162	—	8.0 \pm 5.0	1418 \pm 542	—	6.7 \pm 1.8	821 \pm 341	5	
	17-Jul	60.0 \pm 19.0	74 \pm 74	—	44.3 \pm 20.1	476 \pm 54	—	31.3 \pm 11.4	1632 \pm 1500	6	
	18-Jul	48.0 \pm 0	122 \pm 122	—	40.0 \pm 20.1	964 \pm 108	—	38.0 \pm 10.0	223 \pm 101	12	
	20-Jul	84.0 \pm 8.1	293 \pm 146	—	47.6 \pm 4.3	1045 \pm 536	—	32.7 \pm 5.2	1925 \pm 491	9.5	
	22-Jul	67.3 \pm 18.0	426 \pm 140	—	62.7 \pm 9.8	740 \pm 303	—	25.3 \pm 2.9	1085 \pm 159	14	
	24-Jul	85.0 \pm 15.0	291 \pm 189	—	50.0 \pm 3.1	568 \pm 137	—	26.9 \pm 4.9	921 \pm 326	7	
	26-Jul	43.3 \pm 20.2	181 \pm 45	—	32.7 \pm 9.7	967 \pm 306	—	41.3 \pm 7.7	557 \pm 345	15	
	28-Jul	36.0 \pm 3.1	203 \pm 45	—	34.0 \pm 11.0	155 \pm 77	—	38.0 \pm 11.5	491 \pm 328	16	
	30-Jul	36.7 \pm 16.5	60 \pm 49	—	28.7 \pm 8.5	397 \pm 133	—	30.7 \pm 5.2	565 \pm 366	15	
	01-Aug	46.0 \pm 4	24 \pm 18	—	45.1	26 \pm 25	—	54.9 \pm 6.0	204 \pm 103	15	
	03-Aug	—	19 \pm 8	—	90	47 \pm 23	—	56.0 \pm 12.0	606 \pm 363	17	
	06-Aug	—	5 \pm 3	—	—	56 \pm 29	—	60	114 \pm 105	—	
2005	04-Jul	59.0 \pm 31.0	8 \pm 2	16.0	8.0 \pm 8.0	13 \pm 1	16.2	4 \pm 0	26 \pm 16	14.5	
	06-Jul	45.0 \pm 9.0	14 \pm 3	13.3	21 \pm 1	4	13.1	19 \pm 11	9 \pm 5	12.8	
	08-Jul	76.0 \pm 6.0	—	14.3	11 \pm 9	13 \pm 3	13.6	8	9 \pm 2	13.2	
	10-Jul	28.0 \pm 2.0	11 \pm 6	14.1	28 \pm 16	38 \pm 27	13.7	16	12	13.5	
	12-Jul	22	27	18.1	11 \pm 1	4 \pm 1	17.8	11 \pm 9	4 \pm 1	16.6	
	14-Jul	24.0 \pm 16	13	12.7	18 \pm 8	10 \pm 3	12.6	36 \pm 10	4 \pm 0	12.4	
	16-Jul	22.0 \pm 14.0	8	13.0	—	—	—	—	—	—	
	18-Jul	16	12	15.0	—	—	—	—	—	—	
	20-Jul	12.0 \pm 12.0	23	17.4	—	—	—	—	—	—	

Appendix B: Temporal changes in the mean \pm SE % dead eggs and number of eggs \cdot cm $^{-2}$ with date and average incubation temperature at Gull Island I in 2004 and 2005.

Year	Day	Age	Mortality	Density	Avg. Inc. Temp
2004	27-Jul	0	7.4 \pm 5.8	331 \pm 250	—
	30-Jul	3	0.6 \pm 0.6	243 \pm 57	2.3
	02-Aug	6	0.5 \pm 0.5	381 \pm 115	2.1
	05-Aug	9	2.6 \pm 1.1	—	2.9
	08-Aug	12	2.6 \pm 1.4	635 \pm 281	1.6
	14-Aug	18	1.1 \pm 0.6	764 \pm 173	2.7
	17-Aug	21	2.5 \pm 1.2	301 \pm 195	3.4
	20-Aug	24	2.1 \pm 1.3	509 \pm 52	2.5
	23-Aug	27	17.5 \pm 16.8	234 \pm 50	3.6
	26-Aug	30	1.2 \pm 1.2	517 \pm 53	3.8
2005	30-Aug	34	0	612 \pm 13	4.3
	20-Jul	7	0.6 \pm 0.6	1121 \pm 254	4.4
	22-Jul	9	5.3 \pm 3.4	359 \pm 108	4.0
	25-Jul	12	0	224 \pm 3	3.3
	27-Jul	14	1.1 \pm 0.6	91 \pm 13	4.4
	29-Jul	16	1.0 \pm 0.5	372 \pm 54	5.1
	31-Jul	18	0.5 \pm 0.5	254 \pm 166	5.4
	02-Aug	20	2.2 \pm 1.7	188 \pm 72	5.0
	04-Aug	22	0	303 \pm 101	3.6
	09-Aug	27	0	689 \pm 520	4.8
	11-Aug	29	1.4 \pm 1.4	205 \pm 18	5.1
	13-Aug	31	0	1757 \pm 1594	5.5
	15-Aug	33	0.7 \pm 0.7	420 \pm 78	6.2
	17-Aug	35	0	377 \pm 175	5.6
	19-Aug	37	0	133 \pm 66	8.9
	21-Aug	39	0	356 \pm 167	5.8
	23-Aug	41	1.4 \pm 0.7	211 \pm 84	6.4

Note: egg age calculated from predicted date of spawning start (July 13) based on WMDSI