

Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns

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Abstract: We investigated shoals of capelin (*Mallotus villosus*), the focal forage fish species in the Northwest Atlantic, in nearshore Newfoundland during spawning (2000–2003). Large shoals of maturing capelin were observed in warm ($>0^{\circ}\text{C}$), deep ($>240\text{ m}$) water. Smaller shoals of maturing fish were located in two specific areas closer to shore in shallower water (100–150 m). Shoals persisted in these staging areas in all years and moved into warm surface water during dark but remained in cold ($<0^{\circ}\text{C}$) deep water during daylight. These diel vertical movement patterns may reflect a trade-off between growth and survival, whereby cold, deep water allows reduced predation risk from visual, air-breathing predators while warm, surface water allows increased gonadal development. Shoals of spent capelin, mainly females, were also found in these areas. Sex-specific shoals were observed between staging areas and the coast. Closer to shore, mature, mixed-sex shoals revealed two previously undocumented demersal spawning sites (28–33 m). Suitable habitat for spawning and staging areas resulted in persistent aggregations of capelin shoals, reflecting key foraging areas for top predators and critical areas for conservation.

Résumé : Nous avons étudié les bancs de capelans (*Mallotus villosus*), l'espèce de poisson fourrage d'importance dans le nord-ouest de l'Atlantique, près des côtes de Terre-Neuve durant la fraye (2000–2003). De grands bancs de capelans en maturation s'observent dans les eaux chaudes ($>0^{\circ}\text{C}$) et profondes ($>240\text{ m}$). De plus petits bancs de poissons en maturation ont été trouvés dans deux sites spécifiques plus près de la rive en eau moins profonde (100–150 m). Les bancs se retrouvent dans ces sites de rassemblement à chaque année; ils se déplacent vers les eaux de surface chaudes pendant les heures d'obscurité, mais ils restent en eau profonde froide ($<0^{\circ}\text{C}$) pendant les périodes d'éclairement. Ces patrons de déplacement journalier représentent peut-être un compromis entre la croissance et la survie, dans lequel les eaux profondes et froides offrent un risque réduit de prédation de la part de prédateurs à repérage visuel et à respiration aérienne, alors que les eaux superficielles et chaudes permettent un développement accru des gonades. On trouve aussi dans ces sites des bancs de capelans, surtout de femelles, qui ont terminé leur fraye. Des bancs composés de poissons de même sexe se retrouvent entre les sites de rassemblement et la côte. La présence de bancs de poissons matures des deux sexes plus près de la côte révèle l'existence de deux sites encore non signalés de fraye sur le fond (28–33 m). Les habitats adéquats pour le rassemblement et la fraye déterminent des regroupements persistants de bancs capelans, qui représentent des sites de recherche de nourriture indispensables pour les prédateurs supérieurs et des sites essentiels pour la conservation.

[Traduit par la Rédaction]

Introduction

Focal forage species lie at the core of complex marine food webs and provide essential linkages for energy transfer among trophic levels (Lavigne 1996). Capelin (*Mallotus villosus*) is a pelagic shoaling fish and is an important planktivore that transfers energy up the food web to larger pisci-

vores, including fish, seals, whales, and birds (Lawson et al. 1998; Bundy et al. 2000; Montevecchi 2001). During the 1990s, capelin in the Northwest Atlantic underwent radical changes in their biology, behaviour, and distribution (Carscadden and Nakashima 1997). These changes include protracted and delayed spawning (~26 days), reduced size and age at maturity, reduced somatic condition (Carscadden and Frank

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2002), as well as shifts in horizontal and vertical distributional patterns (Mowbray 2002). Although the magnitude of the impact of these recent changes in capelin on marine food webs has yet to be fully realized, these changes have had direct consequences for the diets of Atlantic cod (*Gadus morhua*; Rose and O'Driscoll 2002) and the diets (Montevecchi and Myers 1996) and condition of seabird offspring (Davoren and Montevecchi 2003, 2005).

Capelin spend their winter near the edge of the continental shelf. During spring, they mature rapidly and undergo considerable migrations (100–200 km), typically from offshore feeding areas to inshore bays and then northward along the coast toward spawning areas (Nakashima 1992). Cross-shelf migration may occur along deep water trenches (>300 m), as evidenced by the inshore feeding migration routes of their primary piscivorous predator, Atlantic cod (Rose 1993). Trenches provide warm water refuges at depth relative to the typical cold shelf waters (Colbourne et al. 1997). This likely allows accelerated maturation rates during migration (Shackell et al. 1994a), although movement into warmer surface waters may serve the same purpose (Winters 1970). Prior to the 1990s, capelin generally exhibited diel vertical movement patterns, typically moving toward surface waters at night to disperse and then forming distinct shoals and moving toward the seabed during daylight (Bailey et al. 1977). Capelin feed on zooplankton, with diets consisting primarily of copepod species plus varying quantities of euphausiids and amphipods, among other species (e.g., O'Driscoll et al. 2001). Once maturation is complete, feeding becomes less of a priority (e.g., Vesin et al. 1981). Prior to spawning, mature capelin separate into sex-specific schools in coastal areas (Templeman 1948). Males form aggregations near suitable spawning sites, where they remain to ensure release of their milt over a number of spawning events (Fridgeirsson 1976). Alternately, shoals of female capelin move into these areas, release all of their roe in a single event, and then leave (Templeman 1948). Because spawning usually involves contact with the sediment, there is a higher incidence of injury and mortality for males compared with females (Fridgeirsson 1976), resulting in divergent life history characteristics (i.e., females: iteroparity; males: semelparity; Shackell et al. 1994b). Survivors actively feed after spawning, increasing their fat content by 20% before winter in offshore areas (Winters 1970; Vesin et al. 1981).

Before the 1990s, capelin consistently spawned during a 2- to 3-week period in June (Leggett et al. 1984). In Newfoundland, capelin are considered to be intertidal or subtidal beach spawners, with the exception of the demersal spawning area on the Southeast Shoal (Carscadden et al. 1989). The combination of both reproductive modes in one region is rare (Carscadden et al. 1989). Spawning locations are primarily determined by temperature and substrate particle size, favourable for the development of their demersal and adhesive eggs (Carscadden et al. 1989). Templeman (1948) hypothesized that capelin spawned intertidally on beaches until water temperatures became too warm, at which point they switched to subtidal, or demersal, spawning in areas immediately adjacent to suitable beaches. One study in coastal Newfoundland, however, showed that intertidal and demersal spawning occurred simultaneously (Nakashima and Wheeler 2002). Egg survival was negligible at these demersal sites,

leading to the conclusion that beaches are preferred spawning sites in coastal Newfoundland and that recruitment from demersal sites is not significant (Nakashima and Wheeler 2002). They also hypothesized that the 1-month delay in spawning of capelin during the 1990s could result in excessively warm beach temperatures during spawning, leading to a higher proportion of demersal spawning and subsequently lower recruitment into the spawning stock (Nakashima and Wheeler 2002).

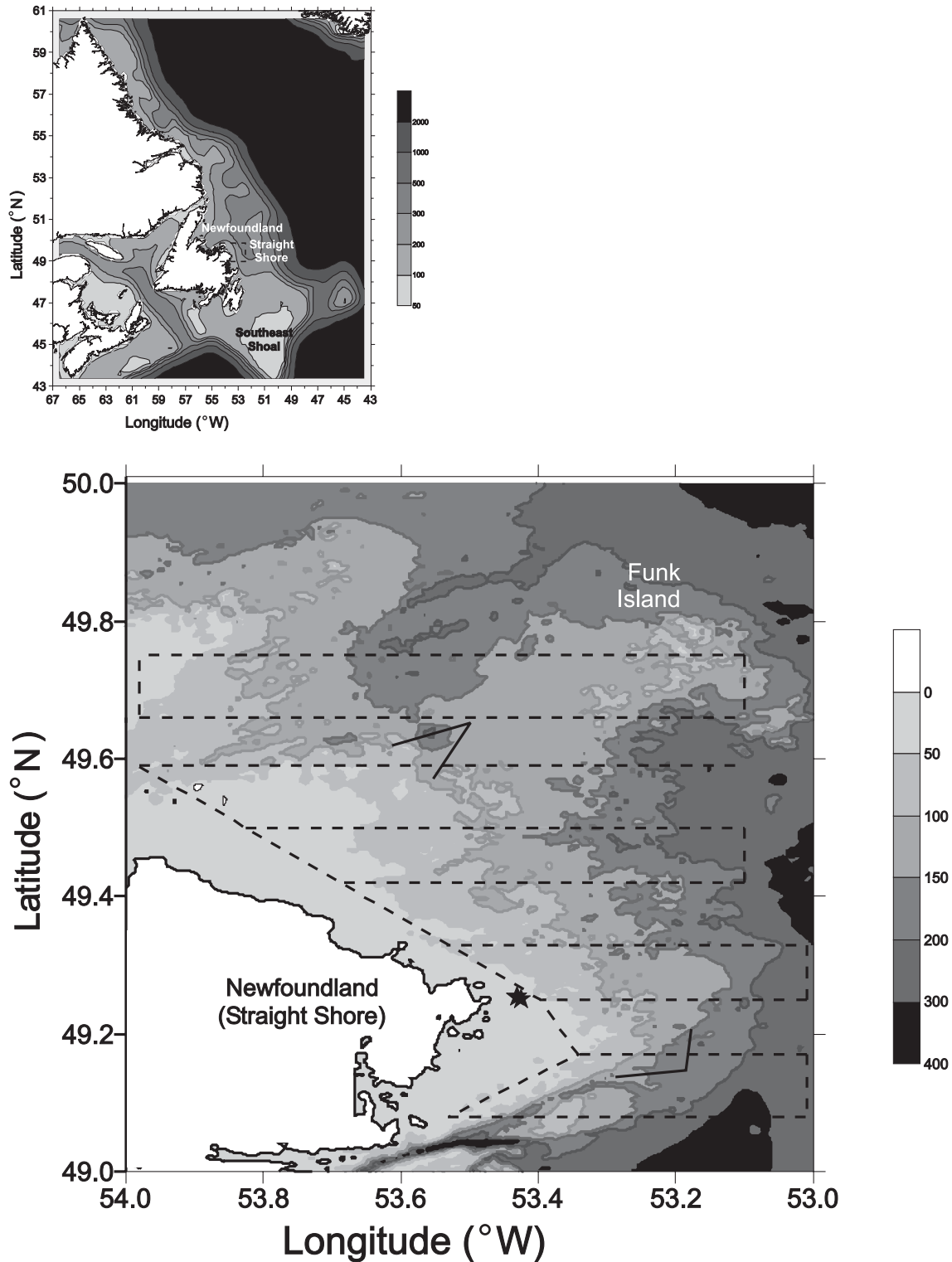
During research in 2000, we examined the consequences of capelin spawning dynamics on the foraging strategies of large vertebrate predators, primarily seabirds, in the area surrounding the Funk Island Seabird Ecological Reserve (see Davoren et al. 2003a). We quantified the meso-scale (>100 km) distribution, abundance, and spatial and temporal persistence of capelin to investigate the behavioural mechanisms used by the primary avian predator of capelin, the common murre (*Uria aalge*), to locate capelin at sea (Davoren et al. 2003a). In this study, behavioural patterns, sex and maturity composition, and distribution of nearshore capelin shoals during the spawning period began to emerge. Specifically, we found that aggregations of capelin persisted in particular locations (~2 km), and we hypothesized that persistence results from habitat selection for biophysical characteristics suitable for demersal spawning and for staging areas before and after spawning (Davoren et al. 2003b). The goals of the present study were to resolve these patterns and examine interannual variability by combining data from 2000 with similar data collected during 2001–2003. Specific objectives were to (i) categorize capelin shoals based on their vertical distribution in relation to available thermal habitats in the water column, (ii) describe the meso-scale distributional patterns of these shoals in relation to bathymetry, (iii) describe the composition of these shoals in regards to sex and maturity, and (iv) describe the behaviour of these shoals in regards to their persistence in specific locations. Areas where high abundances of marine fish and their predators aggregate allow the maximization of energy transfer among trophic levels and the maintenance of predator–prey interactions. Determining whether these aggregations are spatially persistent at an interannual scale, as well as the underlying biophysical habitat features that maintain their persistence, is vital for understanding trophic hotspots and for considerations of marine protected areas. Such investigations also elucidate the intricacies of predator–prey interactions and thus could increase our predictive capability of the ecosystem-level consequences of recent changes in the biology and behaviour of capelin in the Northwest Atlantic.

Materials and methods

Study area

The continental shelf along the northeast coast of Newfoundland (the Straight Shore) extends farthest from shore in our study area, out to and including Funk Island at its farthest extension (Fig. 1). The Funk Island Ecological Seabird Reserve lies approximately 60 km from the coast (49°45'N, 53°11'W), and it is the largest breeding colony of common murre in eastern North America, representing ~75% of the Northwest Atlantic population (Cairns et al. 1989). The other area of extensive shallow water is on the Southeast Shoal of

Fig. 1. Chart of the Northwest Atlantic region, indicating the location of the study area (Straight Shore) within the Newfoundland region, the meso-scale survey lines (broken lines), daylight–dark transect lines (bold, solid lines; northern line: 8.2 km; southern line: 10.3 km), and the two demersal spawning sites of capelin (stars). The shaded depth contours (m) are revealed in the legend.



the Grand Bank, the main demersal spawning location of capelin on the Newfoundland shelf (Carscadden and Frank 1989; Fig. 1). The seafloor off the Straight Shore is shallow and gradually sloping, with depths falling away regularly and with 150–200 m bathymetric depth contours running

parallel to the shoreline (Fig. 1). A deepwater trench cuts into the southern part of the study area, which is defined by a steep wall where depths drop sharply from 50 to ≥ 200 m and even reach ≥ 300 m. Another deeper water channel, bounded by the 150 m contour, cuts in southwest of Funk Is-

land. At the head of this channel is a deepwater depression that occurs just beyond the 100 m contour.

Survey design

To determine the meso-scale distributional patterns of capelin shoals in the study area, we conducted a survey during mid-late July in 2000, 2001, 2002, and 2003 off the east coast of Newfoundland (49°00'N–49°45'N, 53°30'W–54°00'W; Fig. 1). This survey was carried out during daylight aboard the 23 m Canadian Coast Guard research vessel *Shamook*, which operated 12 h·day⁻¹. Nine east–west (across shelf) hydroacoustic survey lines were conducted at a 5 nautical mile (9 km), north–south spacing (Fig. 1). The route deviated slightly among years, owing to different wind direction and speed conditions and because of time limitations; however, the same route template was followed in each year (see Fig. 1). A navigational software package (BIOPLOT version 2.0, 1991, BioSonics Inc., Seattle, Washington) continuously recorded the ship's position (cruise track) and Greenwich Mean Time (GMT) every minute. Periodically throughout the survey, we stopped at fixed stations to identify the species composition of acoustic signals via trawling and to describe both the biological (zooplankton biomass = capelin food density) and physical (temperature) characteristics of the water column.

After the meso-scale survey was completed in each year, the remaining ship time (range: 5–7 days·year⁻¹) was used primarily to study the fine-scale diel vertical movement patterns of capelin shoals. In 2000, we conducted transects during dark that were then repeated once during daylight (Fig. 1). Transects were conducted in areas where capelin shoals were persistently found (Davoren et al. 2003a), and acoustic estimates allowed the quantification of capelin biomass in different depth layers. During the survey in 2001, we collected capelin stomachs for dietary analysis and for comparison with zooplankton prey types available in the environment. In 2002, we investigated the diel vertical movement patterns of zooplankton by comparing biomass at different depths during daylight and dark. Additionally, we made direct observations of antipredator behaviour of capelin shoals using a remotely operated vehicle equipped with an underwater video camera deployed from a 15 m commercial seining vessel, the *Lady Easton II*. During these observations, we unexpectedly discovered two demersal spawning sites of capelin in close proximity to one another (Fig. 1; Davoren et al. 2003b). In 2003, we returned to these two sites aboard the *Lady Easton II* to describe the physical characteristics (temperature, seabed particle size composition) of these spawning sites.

Acoustic estimates

During the meso-scale survey in 2000, the distribution and density of capelin shoals in the water column were estimated using a Simrad EQ100 echosounding system (Simrad AS, Horten, Norway) that operated through a hull-mounted, single-beam transducer with a frequency of 38 kHz. This frequency is appropriate for observations of fish targets, and the distinct shape of capelin shoals allows them to be separated from other fish species (e.g., American sand lance (*Ammodytes americanus*), Atlantic herring (*Clupea harengus*)) within the study area (O'Driscoll et al. 2000). The

transducer had a 10° beam angle, and the echo sounder was operated at 1 ping·s⁻¹, a range of 150 m at one-tenth power, and a bandwidth of 0.3 ms. The transducer was at a depth of 3 m and the beam pattern would not form within a range of 5 m; therefore, acoustic signals were not reliable until 8 m. The sample depth of the acoustic system (8–250 m) and boat speed (14–16 km·h⁻¹) were held constant throughout the survey. Echograms were continuously printed during transects, and GMT was marked on the echograms every 10 min. Shoals were identified on each echogram based on a dark green colour corresponding to a volume backscattering coefficient (s_v) threshold of -70 dB.

During the meso-scale surveys in 2001–2003, a Biosonics DT-X 6000 (BioSonics Inc., Seattle, Washington) scientific echosounding system, calibrated with a tungsten carbide standard target, was used to determine the distribution and density of capelin shoals in the water column. This echo sounder operated through a 38 kHz split-beam transducer mounted in a towed body. The transducer was towed at a depth of 5 m, and acoustic signals were not reliable until 10 m. Vessel speed during acoustic transects was maintained between 11 and 14 km·h⁻¹. Raw, high-resolution acoustic data (s_v) were electronically recorded continuously. The transducer had a two-way beam angle of 22.671 dB, and the echo sounder was operated at 1 ping·s⁻¹, a bandwidth of 5.1 kHz, and a pulse duration of 0.4 ms. Data were acquired at a target strength threshold of -70 dB. During postprocessing of the data using CH2 (Simard et al. 1997), an s_v threshold of -68 dB was applied to the raw data prior to integration. A single capelin (100 mm) would exceed this threshold at the range of depths commonly encountered in this study (<200 m), while most other biological and nonbiological "noise" below this threshold would be filtered out (O'Driscoll et al. 2000).

Capelin shoals were identified by visually assessing each echogram, whether it was viewed on a printout (EQ100 in 2000) or on a computer screen (Biosonics DT-X 6000 in 2001–2003). Based on the appropriate and similar s_v thresholds used for both echosounding systems (-70 dB for the EQ100, -68 dB for the Biosonics DT-X 6000), in conjunction with the distinctive shape of capelin shoals and species composition determination from trawling, we identified a number of capelin shoals from surveys in each year. Four characteristics of each capelin shoal were estimated based on the depth gradations on each echogram and boat speed. These characteristics included the maximum horizontal (width, m) and vertical (height, m) distance that the shoal occupied in the water column, the minimum distance of the bottom of the shoal off the seabed (distance from seabed, m), and minimum distance of the top of the shoal from the surface (distance from surface, m; Maniscalco et al. 1998; Ostrand et al. 1998; LeFeuvre et al. 2000). A correlation analysis was performed to determine if these variables were independent ($r < 0.5$; Ostrand et al. 1998). The distance of the bottom of the shoal from the surface (maximum depth of the shoal, m) was also determined to quantify the ocean depth in which the shoal was located. An estimate of the area of each shoal was calculated by multiplying the vertical height by the width of the shoal. A proxy of capelin abundance in each year was calculated by multiplying the mean area of shoal in each year by the number of shoals observed, reflecting the approximate area occupied by capelin

shoals during a survey in a given year. Statistical significance was set at $\alpha = 0.05$, and all averages are reported as ± 1 standard error (SE).

Biological samples

A modified shrimp trawl was deployed from the *Shamook* (station) to identify the species composition of acoustic signals during the survey and was also deployed on many occasions while steaming between survey lines and toward port at the beginning or end of operational days when time permitted. Shoals with the greatest uncertainty of acoustic signal were targeted, and fishing was carried out primarily in areas where many shoals were observed (Ostrand et al. 1998). The trawl was used to primarily fish at the seabed, but occasionally in midwater, using a standard fishing duration (15 min). The trawl had a 3.5 m headrope and a 12 m footrope, resulting in an opening of 2 m by 8–9 m during both bottom and midwater tows. The mesh size of the body of the trawl was 80 mm and that of the codend was 40 mm. Parameters recorded during the tow included maximum trawl depth (m) and dimensions (m) using SCANMAR monitoring devices (Scanner AS, Åsgårdstrand, Norway), vessel speed ($\text{km}\cdot\text{h}^{-1}$), and distance traveled (km).

The total mass of the catch (kg) and the number of species were recorded immediately after each tow. Ten percent of the catch was randomly subsampled, and the mass each species contributed to the total catch was calculated. A sample of up to 200 capelin was randomly collected and frozen. In the laboratory, the sex, maturity index (1 = immature, 2 = maturing, 3 = ripe, 4 = partially spent, 5 = spent) and total length (snout to tip of tail, cm) of each fish were determined. We collapsed the maturity indices into four categories: immature (1), maturing (2), mature (3, 4), and spent (5). A length-stratified sample of two fish per sex per 0.5 cm length category was selected from each sample, and the total body mass (g), gonad mass (g), age (year), and stomach fullness index (0%, 25%, 50%, 75%, 100%) of each fish were recorded. During 2001–2003, random samples of 200 capelin were also collected from the catches of commercial purse seining vessels fishing capelin in the study area. Purse seine nets were $\sim 375 \text{ m} \times 75 \text{ m}$ in total size, with a mesh size ranging from 9.8 to 10.5 mm^2 .

The species composition and biomass of zooplankton prey available to capelin was sampled using a 0.232 mm Nitex mesh bongo net, with a 0.29 m^2 mouth opening. This net was towed obliquely at an average speed of $0.88 \pm 0.15 \text{ m}\cdot\text{s}^{-1}$ SE from either the seabed level or from a specified depth to the surface to target smaller zooplankton prey types of capelin. Nets were washed thoroughly into a 1 L sample jar and preserved in 5% formalin–seawater solution. In the laboratory, each sample was partitioned into two subsamples using a box type Motoda Plankton Splitter. One subsample was poured over a series of graded sieves: 0.232, 1, and 2 mm. The main zooplankton types (e.g., copepods, amphipods, euphausiids, etc.) present in each size fraction were recorded. Samples were then removed from each sieve and transferred to a preweighed tray and oven-dried at 75 °C for 48 h. Each dried sample was weighed to an accuracy of 0.001 g to calculate zooplankton biomass ($\text{g}\cdot\text{m}^{-3}$). The volume of water filtered during the

tow was estimated, based on flow meters and the diameter of the mouth of the net.

Temperature samples

Temperature profiles of the water column were measured using an Applied Microsystems STD-12+ (Applied Microsystems Ltd., Sidney, British Columbia) or a Sea-Bird SBE-25 (Sea-Bird Electronics Inc., Bellevue, Washington) at each station aboard the *Shamook* in all years. A Sea-Bird SBE-19 was deployed from the *Lady Easton II* in 2002–2003. Devices were deployed at $1 \text{ m}\cdot\text{s}^{-1}$, allowing data capture every 20–50 cm from the ocean floor to the surface. Temperature profiles collected during the surveys were used to characterize interannual variability in the thermal stratification of the water column. Historical oceanographic data (July: 1990–2000) obtained within the study area from Fisheries and Oceans Canada (courtesy of E. Colbourne, Northwest Atlantic Fisheries Centre, St. John's, NL A1C 5X1, personal communication) were used to determine the average thermal habitats available to capelin shoals.

Capelin daylight–dark transects (2000)

In 2000, daylight–dark transects were conducted to investigate the diel vertical movement behaviour of capelin. These transects varied in length (24 July, northern area, dark: 8.2 km, daylight: 6.6 km; 27 July, southern area, dark: 4.1 km, daylight: 10.3 km). These sites were chosen because capelin were persistently found there. During transects, the Biosonics DT-X 6000 echosounding system was used to quantify the mean biomass ($\text{g}\cdot\text{m}^{-2}$) in different depth layers. To determine mean capelin biomass, we first deleted acoustic signals near the bottom that could not be distinguished as biological or due to the ocean floor (dead zone, side-lobing; Lawson and Rose 1999). Shoals were identified as capelin on each echogram based on an s_v threshold of greater than -68 dB . We integrated s_v in each file to determine the average aerial backscattering coefficient (s_a) for capelin per 100 metres along the transect (MacLennan et al. 2002). Capelin density ($\text{fish}\cdot\text{m}^{-2}$) was calculated by dividing s_a by the average backscattering cross section (σ_{bs}), which is related to target strength. Target strength was estimated using the length-scaled relationship for capelin (Rose 1998). Capelin density ($\text{fish}\cdot\text{m}^{-2}$) was converted to biomass estimates ($\text{g}\cdot\text{m}^{-2}$) by multiplying fish density by the mean mass of capelin (g) caught in our study area. We compared capelin biomass estimates per 100 metres along each transect at two depth ranges in the water column (10–50 m, 50–200 m) during daylight transects with that found within these depth layers during dark transects using t tests.

Capelin stomach content analysis (2001)

During the 2001 survey, 50 capelin were randomly selected from each trawl and seine catch. The stomachs were immediately removed and placed in a 20 mL kimble vial with 5% formalin. In the laboratory, a length-stratified sample of one fish per 1.0 cm length category was selected for stomach content analysis. Stomachs were removed from the vials and dabbed on a paper towel to remove excess moisture. The stomach and contents were weighed to the nearest 0.001 g. Under a microscope, identifiable prey types were sorted into major taxonomic groups: copepods, euphausiids,

amphipods, pteropods, chaetognaths, invertebrate eggs, fish larvae, fish eggs, and crab. The damp weights of each of these prey type categories were measured by dabbing these contents on a paper towel and then were measured to the nearest 0.001 g. The percent by weight of each major zooplankton group was then determined for each stomach that was not empty.

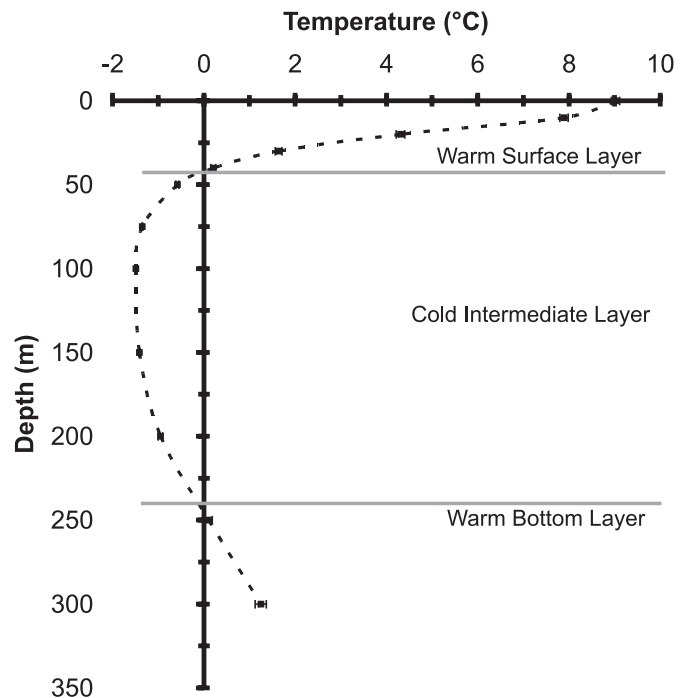
Capelin behavioural observations (2002)

In 2002, we used a remotely operated vehicle (ROV) equipped with an underwater video camera (VideoRay PRO; Video Ray LLC, Phoenixville, Pennsylvania) to make direct observations of antipredator behaviour of capelin shoals. This ROV was a small (35 cm × 22.2 cm × 21.6 cm) submersible, with the advantage of high portability, and thus was deployed from the *Lady Easton II*. With a maximum depth rating of 76 m, however, observations were constrained to shoals <50 m deep. The shallow area (<50 m) along the coast, where capelin shoals were consistently located during the meso-scale surveys in 2000–2003, was traveled until a capelin shoal was observed acoustically. The ROV was then deployed and observations were recorded with a VCR on a VHS tape. Video recordings were later viewed to quantify behavioural responses of shoals to predatory attacks. Predatory attacks by seabirds and whales were not observed. Instead, we used the ROV to simulate predatory attacks according to the following protocol. The ROV descended until the shoal came into sight, at which point descent was halted and the undisturbed shoal was observed for 5–10 min. After the initial observation period, the ROV descended to the seabed. The ROV was then thrust toward the shoal. Responses of the shoal were recorded, included vacuole, split, herd, etc., as defined in Axelsen et al. (2001), as well as lateral or vertical escape movements. During underwater observations, two demersal spawning sites of capelin were discovered.

Seabed particle size composition (2003)

In 2003, samples of the seabed were collected using a 0.3 m² Van Veen type benthic grab system at the two demersal spawning sites of capelin located in 2002 from the *Lady Easton II*. Samples were placed in a 40 L bucket, and a 250 mL representative subsample was removed and preserved in 10% formalin–seawater solution. In the laboratory, the samples were poured onto a 0.15 mm sieve and flushed with water. The remaining sample on the sieve was then scooped into a jar and soaked in a 2% KOH solution for 24 h to detach biological material (e.g., fish eggs) adhered to sediment particles. Biological matter was decanted off the top of the sample and preserved in 5% formalin–seawater solution. The sediments were oven-dried at 75 °C for 48 h. Once dried, samples were poured over a series of graded sieves: 0.15, 0.25, 0.5, 0.7, 1, 2, 4, 8, 11.2, 16.0, 22.4, and 31.5 mm. Size fractions were removed from each sieve, transferred to a preweighed plastic tray, and weighed to the nearest 0.001 g. Percentages of the size fractions in each sample were calculated and categorized according to the Udden–Wentworth scale of sediment–rock size classification (Wentworth 1922). We summarized these categories as <0.5 mm (silt and fine sand), 0.5–2.0 mm (coarse sand),

Fig. 2. The mean ± standard error temperature profile of the water column within the study area using historical data (1990–2000).



2.0–4.0 mm (pebble), 4.0–22.5 mm (small cobble), and >22.5 mm (large cobble).

Results

Over all years, we conducted 53 trawl stations (range: 11–17 trawls·year⁻¹), eight of which were empty (range: 1–5 trawls·year⁻¹). Fish were collected at 38 stations (range: 8–11 samples·year⁻¹), 28 of which contained capelin (range: 4–11 samples·year⁻¹). Over all years, capelin was the numerically dominant fish species caught (96.5%). Minimal numbers of other species (3.5%) were encountered, only 0.03% of which were Atlantic cod. Over all years, shrimp species were the numerically dominant invertebrate species caught (75.7%), followed by crab species (18.1%), and minimal numbers (3.2%) of other bottom-dwelling species. These results reflect the dominance of capelin in the study area. During 2001–2003, capelin were also sampled from 11 seine catches (range: 2–5 samples·year⁻¹). Over all years, 7317 capelin were sampled (female: 85–199 mm, $n = 5529$; male: 59–193 mm, $n = 1788$).

Temperature (available thermal habitat)

Historical temperatures in July in the study area were generally consistent with the temperature profiles measured throughout the study period. Using the mean historical temperature data, the water column was divided into three temperature layers: two warm (>0 °C) water layers (0–50 m, >200 m), separated by a cold intermediate water layer (<0 °C, 50–200 m; Fig. 2). The cold intermediate layer is a characteristic feature of the water column on the Newfoundland shelf throughout most of the year and is generally defined by the 0 °C isotherm, revealing the extent of the subzero water layer (Petrie et al. 1988). Using temperature

Table 1. Mean \pm standard error (SE) and range of depths at which the temperature of the water column first became $<0^\circ\text{C}$ and when the temperature of the water column first became $>0^\circ\text{C}$ over all stations within the study area from 2000 to 2003.

Year	Depth (m) of 1st temperature $<0^\circ\text{C}$			Depth (m) of 1st temperature $>0^\circ\text{C}$		
	<i>n</i>	Mean \pm SE	Range	<i>n</i>	Mean \pm SE	Range
2000	14	60.3 \pm 3.2	34.7–83.7	2	228.9 \pm 5.2	223.8–234.1
2001	6	35.3 \pm 3.1	24.5–47.2	0	—	—
2002	20	61.1 \pm 3.9	27.7–83.7	3	234.2 \pm 8.7	220.1–250.2
2003	14	51.8 \pm 3.3	33.9–79.2	2	215.2 \pm 4.0	211.3–219.1

Note: *n* indicates the number of stations at which temperature was measured in each year.

measurements obtained during surveys, we investigated the interannual differences in the extent of the warm surface layer by determining the depth from the surface at which the temperature of the water first became $<0^\circ\text{C}$. This depth differed significantly among years (analysis of variance, ANOVA: $F_{[3,50]} = 5.934$, $p = 0.002$), with the warm surface layer in 2001 being significantly shallower than that in 2000 (post hoc Scheffé's test: $p = 0.008$) and 2002 ($p = 0.004$) but not in 2003 ($p > 0.05$; Table 1). The depth at which the temperature became $>0^\circ\text{C}$ near the seabed was used to investigate interannual differences in the extent of the warm bottom layer. The extent of this layer did not differ significantly among years (ANOVA: $F_{[2,4]} = 1.634$, $p = 0.303$; Table 1); however, the sample size was limited ($n = 7$). Overall, the two measures combined revealed that the extent of the cold intermediate layer was larger in 2001 in the study area.

Shoal distribution (vertical and horizontal)

Over all years, 631 capelin shoals were identified (2000: $n = 204$; 2001: $n = 283$; 2002: $n = 69$; 2003: $n = 75$). The four shoal characteristics were independent (width–height: $r = 0.24$; width – distance from seabed: $r = -0.04$; width – distance from surface: $r = 0.28$; height – distance from seabed: $r = 0.09$; height – distance from surface: $r = 0.13$; distance from seabed – distance from surface: $r = -0.29$). The maximum depth of the shoal increased significantly with water depth ($r^2 = 0.858$, $F_{[1,613]} = 3694.039$, $p < 0.0001$), as did the distance from surface ($r^2 = 0.775$, $F_{[1,613]} = 2115.252$, $p < 0.0001$). Therefore, shoals were primarily associated with the seabed. Large shoals also occurred in deeper water, indicated by significant increases in height, width, and area of the shoals with water depth (height: $r^2 = 0.114$, $F_{[1,613]} = 79.016$, $p < 0.0001$; width: $r^2 = 0.087$, $F_{[1,613]} = 55.716$, $p < 0.0001$; area: $r^2 = 0.123$, $F_{[1,613]} = 86.029$, $p < 0.0001$).

We categorized the vertical distribution of each shoal in the water column according to the three thermal habitats: surface shoals, intermediate shoals, and bottom shoals. This categorization was based on the maximum depth of each shoal, the mean depth of the warm surface layer (depth from the surface at which the temperature of the water first became $<0^\circ\text{C}$), and the mean depth of the warm bottom layer (depth at which the temperature became $>0^\circ\text{C}$ near the seabed) for each year. Two-factor ANOVAs, with year and thermal habitat as factors, revealed different width and height characteristics of shoals found in these three thermal habitats. The width of shoals did not differ significantly among years ($F_{[3,617]} = 0.636$, $p = 0.592$), but shoals were signifi-

cantly wider in the bottom layer ($F_{[2,617]} = 17.417$, $p < 0.0001$; Table 2). There was a significant interaction between year and thermal habitat ($F_{[6,617]} = 2.185$, $p = 0.043$), indicating that shoals in the bottom layer were wider in 2002 and 2003 relative to other years (Table 2). As indicated previously, the height of the shoals increased significantly from the surface layer to the intermediate layer and then to the bottom layer ($F_{[2,617]} = 26.523$, $p < 0.0001$; Table 2). Shoal height also differed significantly among years ($F_{[3,617]} = 10.263$, $p < 0.0001$), and the interaction between thermal habitat and year was significant ($F_{[6,617]} = 8.930$, $p < 0.0001$), reflecting an increase in shoal height from 2000 to 2003 (Table 2). As expected, the distance of the shoals from the seabed in the surface layer was significantly higher relative to that of the shoals found in the bottom and intermediate layers ($F_{[2,617]} = 46.139$, $p < 0.0001$), but there was also a significant difference among years ($F_{[3,617]} = 7.528$, $p < 0.0001$), indicating that shoals in the surface layer were higher off the seabed in 2002 than in other years ($F_{[6,617]} = 9.992$, $p < 0.0001$; Table 2). Also as expected, the distance of the shoal from the ocean surface increased significantly from shoals in the surface to intermediate and then to the bottom layer ($F_{[2,617]} = 382.859$, $p < 0.0001$), but there was also a significant difference among years ($F_{[3,617]} = 7.528$, $p < 0.0001$) with the shoals in all temperature layers being closer to the surface in 2001 ($F_{[6,617]} = 14.030$, $p < 0.0001$; Table 2).

Overall, surface shoals were found in areas where water depth was shallow (49.2 ± 1.6 m, $n = 319$) relative to intermediate shoals (102.6 ± 2.7 m, $n = 238$) and bottom shoals (264.8 ± 4.9 m, $n = 27$; $F_{[2,617]} = 239.022$, $p < 0.0001$), but there was also a significant difference among years ($F_{[3,617]} = 8.701$, $p < 0.0001$) with shoals in all thermal habitats being in deeper water in 2002 and 2003 ($F_{[6,617]} = 9.708$, $p < 0.0001$; Table 2). To illustrate the distributional patterns, we categorized the horizontal location of each shoal type (surface, intermediate, bottom) into one of the three depth contour categories (0–50, 50–200, and >200 m) based on the three thermal habitats available in the study area. Shoals in the surface, intermediate, and bottom layers were not distributed randomly throughout the survey area (Fig. 3). Generally, bottom depth within the study area gradually increased with distance from shore (Fig. 1), and this, combined with the primary association of capelin shoals with the seabed, resulted in surface shoals primarily located close to shore within the 50 m depth contour in most years (Fig. 3). Similarly, intermediate shoals were primarily found in deeper water (50–200 m) farther from shore in all years (Fig. 3). These trends, however, were less obvious in 2002

Table 2. Mean \pm standard error characteristics of capelin (*Mallotus villosus*) shoals in the warm surface, cold intermediate (CIL), and warm bottom layers in all years.

Thermal habitat	n	Shoal location			Shoal characteristics			% of shoals in depth range			
		Bottom depth (m)	From surface (m)	Off bottom (m)	Width (m)	Height (m)	Area (m ²)	0–50 m	50–200 m	>200 m	
2000											
Surface	109	43.0 \pm 0.9	39.5 \pm 1.1	4.1 \pm 0.5	63.3 \pm 10.2	14.3 \pm 0.6	965.6 \pm 187.8	83.5	16.5	0	
CIL	93	124.9 \pm 4.5	118.4 \pm 4.4	1.6 \pm 0.6	94.6 \pm 7.6	16.3 \pm 1.1	1 578.1 \pm 396.3	5.4	94.6	0	
Bottom	2	230 \pm 0	210.0 \pm 20.0	0 \pm 0	100 \pm 25	15.0 \pm 5.0	1 625.0 \pm 875.0	0	0	100	
2001											
Surface	132	42.0 \pm 2.4	15.5 \pm 0.5	19.4 \pm 2.3	59.4 \pm 5.7	15.5 \pm 0.6	1 061.5 \pm 132.5	77.7	22.3	0	
CIL	150	84.4 \pm 3.2	58.1 \pm 3.1	10.9 \pm 1.6	66.0 \pm 2.9	22.7 \pm 0.8	1 633.3 \pm 120.9	24	76	0	
Bottom	1	219.7	190	0	250	40	10 000	0	0	100	
2002											
Surface	34	88.8 \pm 6.2	17.7 \pm 2.5	55.9 \pm 6.3	277.9 \pm 89.0	20.0 \pm 1.9	5 426.5 \pm 1900.9	20.6	79.4	0	
CIL	21	114.5 \pm 7.8	75.2 \pm 10.6	9.8 \pm 2.8	277.4 \pm 112.7	32.4 \pm 4.4	8 547.6 \pm 2597.6	0	100	0	
Bottom	14	285.3 \pm 2.1	255.0 \pm 3.7	10.4 \pm 1.9	178.6 \pm 43.4	27.8 \pm 2.8	5 607.1 \pm 1715.7	0	0	100	
2003											
Surface	46	54.6 \pm 5.0	15.0 \pm 1.1	28.5 \pm 4.7	91.3 \pm 17.8	17.6 \pm 1.1	1 907.6 \pm 505.0	56.5	43.5	0	
CIL	19	124.3 \pm 10.6	100.0 \pm 11.9	5.8 \pm 1.3	96.1 \pm 10.7	24.7 \pm 3.6	2 552.6 \pm 514.3	5.3	94.7	0	
Bottom	10	247.7 \pm 5.2	200.0 \pm 11.6	9.0 \pm 1.6	490.0 \pm 205.9	54.0 \pm 14.5	51 575.0 \pm 40 301.6	0	0	100	

Note: n indicates the number of shoals observed in each water layer in each year.

and 2003, when fewer shoals were observed in the study area and shoals tended to occupy deeper water. Bottom shoals, however, were always found farther from shore, where water depths reached >200 m (Fig. 3). Overall, the total capelin abundance, estimated as the area occupied by capelin shoals in each survey, was similar among years (2000: 272 000 m²; 2001: 395 123 m²; 2002: 442 500 m²; 2003: 652 000 m²; calculated from Table 2).

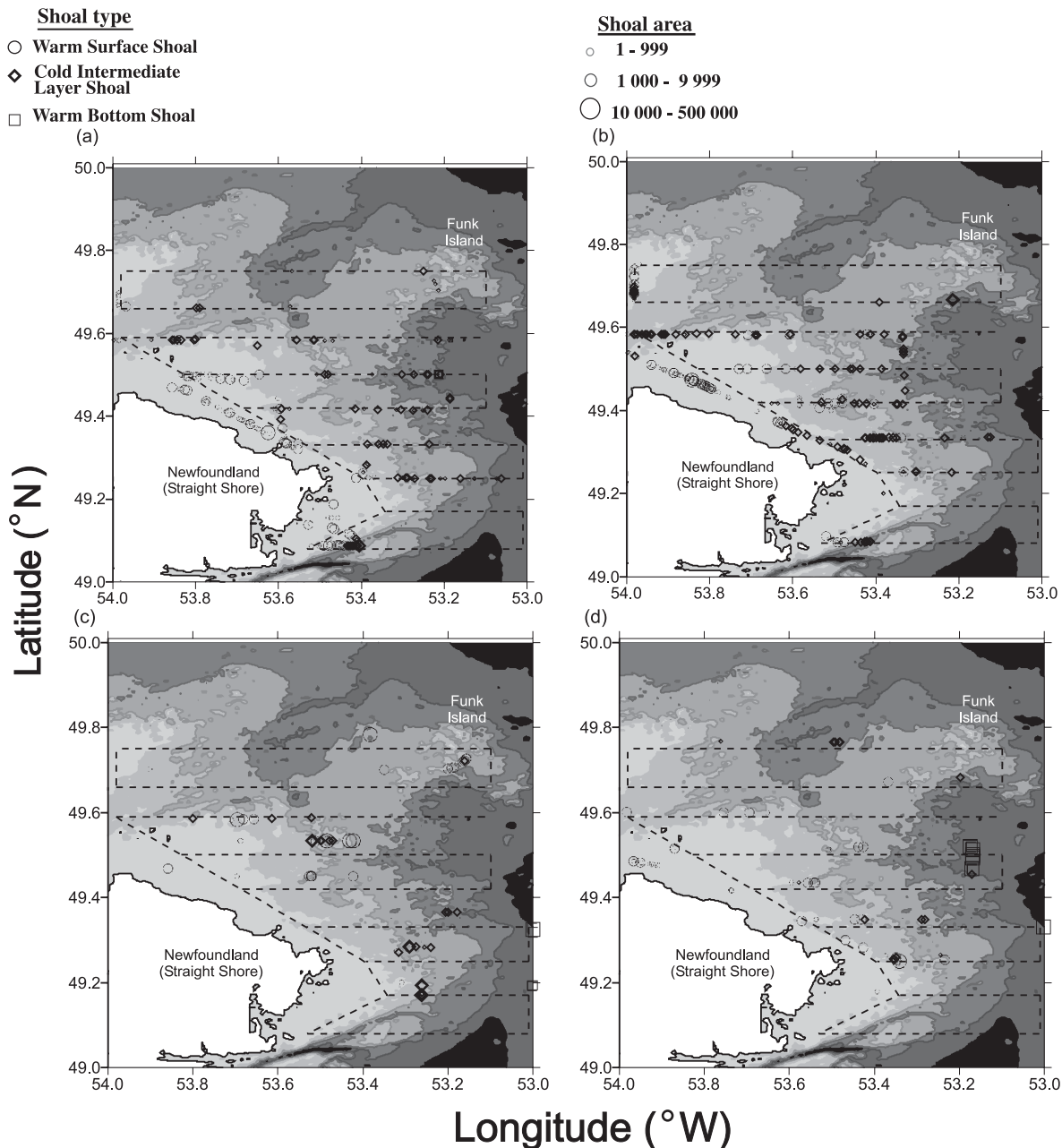
Composition of capelin shoals

We sampled shoals in the warm surface layer and the cold intermediate layer in all years but only those in the warm bottom layer in 2002 and 2003 (Table 3). Shoal types were categorized as either female ($\geq 75\%$ female) or a mixture of females and males ($< 75\%$ females) and by the dominant maturity stage (immature, maturing, mature, spent), based on data in Table 3. Using χ^2 tests, we investigated whether shoal types of varying sex and maturity differed in their use of thermal habitats, based on the frequency of each shoal type found in each habitat. The majority of surface shoals were primarily composed of females ($\chi^2_1 = 6.846$, $p < 0.01$) that were mature ($\chi^2_3 = 10.692$, $0.01 < p < 0.025$; Table 3), although maturing ($n = 2$) and spent ($n = 3$) shoals were also observed. The low percentage of males in these shoals were also mature ($\chi^2_3 = 19.308$, $p < 0.001$; Table 3). All mature shoals were sampled with purse seines, with only one mature shoal sampled with the trawl (station 16, Table 3). This was expected, as commercial seiners selectively fish mature capelin. The cold intermediate layer shoals were composed of a similar frequency of female shoals and male and female shoals ($\chi^2_1 = 0.040$, $p > 0.05$; Table 3). These shoals were composed of a higher frequency of either spent or maturing females, with very few immature and mature females ($\chi^2_3 = 21.560$, $p < 0.001$), combined with a mixture of immature, maturing, mature, and spent males ($\chi^2_3 = 5.696$, $p > 0.05$; Table 3). The frequency of spent female shoals relative to maturing shoals of males and females differed significantly among years of this study ($\chi^2_4 = 34.204$, $p < 0.0001$), with a higher percentage of spent female shoals in 2000 (70%, $n = 10$) and 2001 (100%, $n = 5$) relative to 2002 (0%; $n = 5$) and 2003 (50%, $n = 4$). Although only two of the warm bottom layer shoals were sampled, both were composed of nearly equal ratios of maturing male and female capelin (Table 3). All years combined, surface shoals of mature capelin ($n = 8$) were located closest to shore, whereas surface shoals of maturing ($n = 2$) and spent ($n = 3$) capelin were found farther from shore (Fig. 4). Shoals in the cold intermediate layer, composed of maturing or spent capelin, were found farther from shore (Fig. 4). Finally, bottom shoals were found farthest from shore (Fig. 4).

Composition of capelin stomachs

Of the capelin stomachs that were subsampled, 13% were empty, 68% were less than half full, and 19% were more than half full (female: $n = 993$; male: $n = 368$). A higher frequency of mature capelin had empty stomachs relative to other maturity categories (female: $\chi^2_6 = 385.744$, $p < 0.0001$; male: $\chi^2_6 = 94.477$, $p < 0.0001$), suggesting that feeding intensity declined immediately prior to spawning relative to maturing, immature, and spent fish (Fig. 5). A total of 9000 capelin stomachs were collected for dietary analysis at 12

Fig. 3. An expanding symbol plot of the size (area (m²) = vertical height × width) and distribution of capelin (*Mallotus villosus*) shoals in the warm surface, cold intermediate, and warm bottom layers during the meso-scale survey in 2000 (a), 2001 (b), 2002 (c), and 2003 (d) with the template survey route indicated (broken lines).



stations in 2001, out of which 66 stomachs were subsampled for dietary analyses (range: 4–8 fish-tow⁻¹; $n = 15$ empty stomachs). Dietary composition analysis revealed that copepods comprised the majority of the diet by weight, followed by euphausiid species, and then amphipod species (Table 4). The total length of capelin with stomachs removed varied (range: 119–188 mm), and the percentage of copepods in the diet (by weight) declined with increasing capelin length ($r^2 = 0.147$, $F_{[1,44]} = 7.560$, $p = 0.009$; $y = -0.977x + 200.719$), whereas the percentage of amphipod species increased with increasing capelin length ($r^2 = 0.204$, $F_{[1,44]} = 11.298$, $p = 0.002$; $y = 0.919x - 122.659$), and there was no trend for euphausiid species ($r^2 = 0.000$, $F_{[1,44]} = 0.010$, $p = 0.923$). Comparing the percent occurrence of each

prey type in the diet of capelin with those available in the environment (2000–2002) revealed a significant difference ($\chi^2_8 = 44.84$, $p < 0.0001$), likely due to a higher percentage of copepods and invertebrate eggs and a lower percentage of chateognath species in the diet relative to the percentages available in the environment (Table 4).

Behaviour of capelin shoals

During trawling, capelin shoals encountered in different thermal habitats were either ephemeral or persistent in space and time. Shoals in the warm surface layer sampled with the trawl were generally ephemeral in space on the temporal scale of minutes. When a shoal was encountered, the exact position was recorded and in the minutes it took to prepare

Table 3. The percent composition of each capelin (*Mallotus villosus*) shoal sampled with each gear type, broken down by sex and maturity stages.

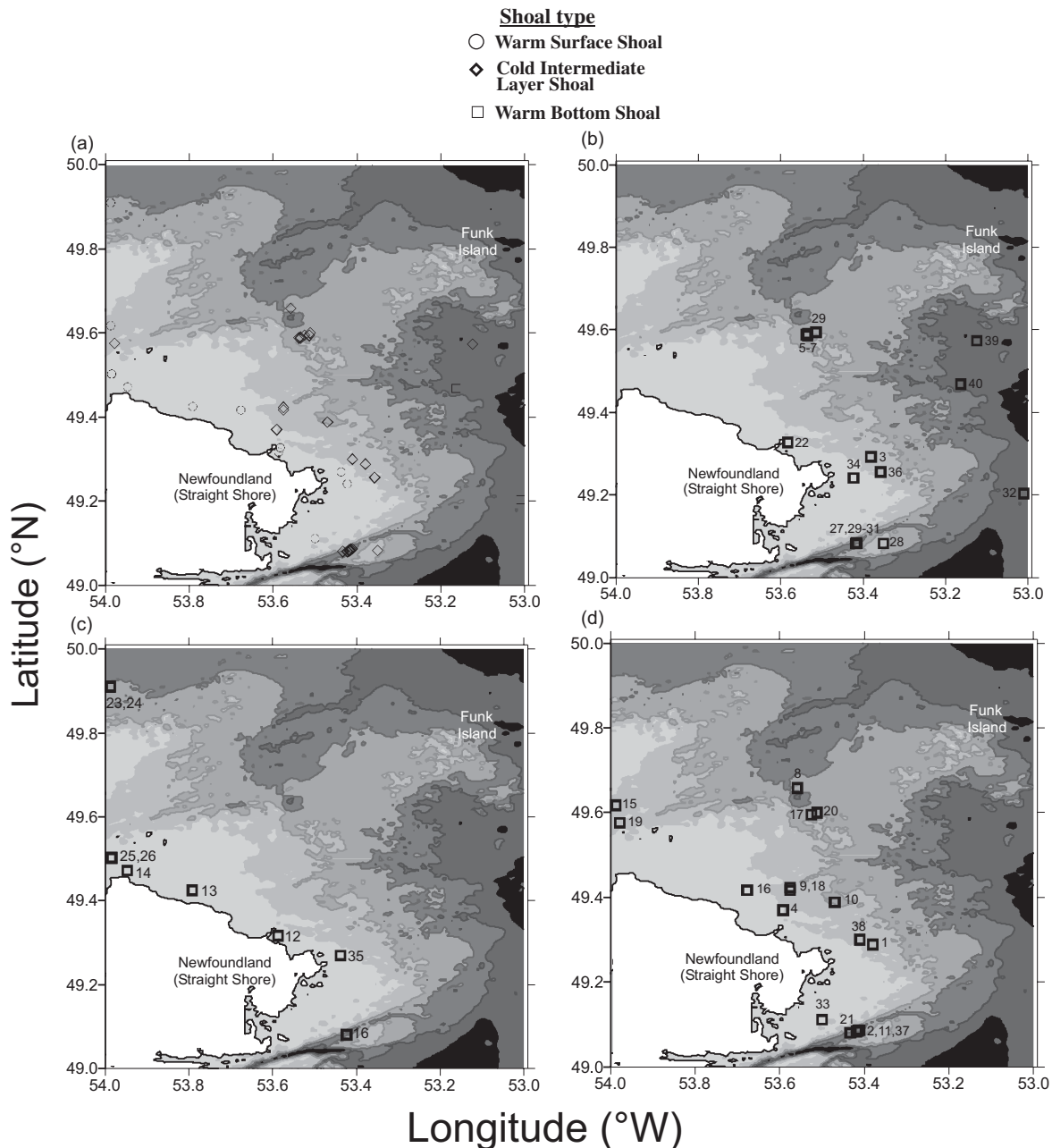
Thermal habitat	Station no.	Gear type	<i>n</i>	% females	Females				Males			
					Immature	Maturing	Mature	Spent	Immature	Maturing	Mature	Spent
2000												
Surface CIL	1	T	82	95.1	0	1.3	25.6	73.1	0	0	100	0
	2	T	200	98.5	0	0.5	1	98.5	0	0	33.3	66.7
	3	T	70	91.4	0	46.9	21.9	31.3	16.7	16.7	66.7	0
	4	T	200	91.5	0	1.1	33.3	65.6	5.9	17.6	76.5	0
	5	T	200	48.5	0	78.4	3.1	18.6	0	96.1	3.9	0
	6	T	200	64.0	0	79.7	0	20.3	0	100	0	0
	7	T	200	58.0	0	70.7	3.4	25.9	0	95.2	1.2	3.6
	8	T	200	91.5	0	6.0	1.1	92.9	64.7	35.3	0	0
	9	T	37	100.0	0	5.4	5.4	89.2	—	—	—	—
	10	T	199	97.0	0	6.7	0	93.3	66.7	33.3	0	0
	11	T	200	88.5	8.5	0	5.6	85.9	82.6	4.3	13.0	0
Bottom			—									
2001												
Surface CIL	12	S	200	33.0	0	1.5	92.4	6.1	0.7	0	69.4	29.9
	13	S	200	83.0	0	32.5	40.4	27.1	14.7	23.5	61.8	0
	14	S	200	58.5	0	0	99.1	0.9	0	0	100	0
	15	S	200	98.0	0.5	0	1.5	98.0	25.0	0	75.0	0
	16	T	200	64.0	7.6	0	49.4	43.0	76.0	0	23.1	0.8
	17	T	200	76.0	0	0.5	3.1	96.4	33.3	0	66.7	0
	18	T	200	70.5	0	0	0.5	99.5	100	0	0	0
	19	T	200	66.5	0	0	2.6	97.4	0	0	28.6	71.4
	20	T	200	46.0	0	0	3.6	96.4	0	0	100	0
	21	T	200	86.0	6.2	0.8	3.1	90.0	87.1	0	4.3	8.6
Bottom			—									
2002												
Surface CIL	22	S	200	64.5	0	96.9	2.3	0.8	0	100	0	0
	23	S	200	76.0	0	0.7	99.3	0	0	0	100	0
	24	S	200	75.0	0	0	100	0	0	0	98.0	2.0
	25	S	200	70.5	0	0	100	0	0	0	91.5	8.5
	26	S	200	70.5	0	0.7	99.3	0	0	0	93.2	6.8
	27	T	200	76.0	0	82.9	0.7	16.4	8.3	91.7	0	0
	28	T	200	70.5	0	98.6	1.4	0	3.4	96.6	0	0
	29	T	200	66.5	0	99.2	0.8	0	3.0	97.0	0	0
	30	T	200	46.0	0	92.4	0	7.6	4.6	93.5	1.9	0
	31	T	200	86.0	1.7	82.6	0.6	15.1	14.3	21.4	60.7	3.6
Bottom	32	T	200	64.0	1.6	98.4	0	0	4.2	95.8	0	0
2003												
Surface CIL	33	S	200	98.0	0	0.5	19.4	80.1	25.0	0	0	75.0
	34	S	200	82.0	0	97.0	1.2	1.8	0	100	0	0
	35	S	200	76.0	0	0.7	93.4	5.9	0	0	85.4	14.6
	36	T	200	46.0	0	98.9	1.1	0	0	100	0	0
	37	T	139	84.9	0	15.3	0	84.7	33.3	57.1	9.5	0
	38	T	135	100.0	0	1.5	8.9	89.6	—	—	—	—
	39	T	36	69.4	0	92.0	4.0	4.0	0	100	0	0
Bottom	40	T	200	59.0	0	99.2	0.8	0	0	98.8	1.2	0

Note: *n* represents the number of individual capelin subsampled per catch. CIL, cold intermediate layer; T, trawl; S, purse seine.

the net for trawling, the shoal always disappeared. Consequently, the duration of these tows were extended until another shoal was encountered to obtain an adequate sample of capelin. In contrast, the surface shoals sampled with the purse seine were more stationary, in that once a shoal was

located it could easily be sampled. The shoals sampled with the purse seine were primarily composed of mature capelin, which was expected, as commercial seiners selectively harvest mature capelin. In contrast, shoals sampled with the trawl were either spent or maturing capelin. These apparent

Fig. 4. The distribution of capelin (*Mallotus villosus*) shoals sampled (trawl, purse seine) in the warm surface, cold intermediate, and warm bottom layers during all years (2000–2003) of this study (a), indicating shoals that were maturing (b), mature (c), and spent (d). Numbers represent station numbers, as shown in Table 3.



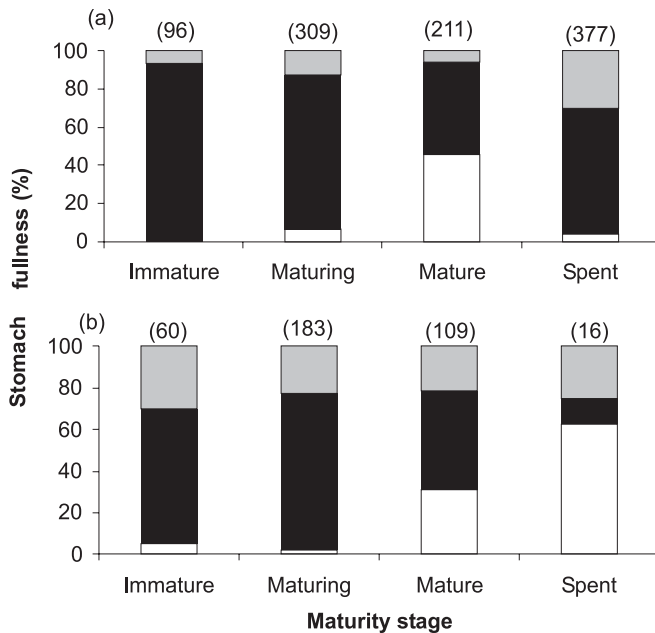
differences in “ephemerality” may have been due to varying avoidance behaviour of different capelin maturity stages to different vessels and (or) gear types.

In 2002, we observed four surface shoals of capelin with the ROV, which led to our discovery of the two demersal spawning sites within 1–2 km of these shoals. Fish in all four shoals formed tight balls and were associated with the seabed. Within the shoal, fish were oriented in different directions and were composed of female and male capelin having secondary sexual characteristics (e.g., elaborate anal fin). Samples of capelin obtained incidentally in the bottom grab when collecting sediment samples revealed that these fish were mature (females: $n = 4$; males: $n = 7$). During fur-

ther descent of the ROV toward the seabed, the shoal formed an increasingly tighter ball and moved closer to the seabed. As the ROV descended into the shoal, capelin formed a vacuole around it in all cases and did not move away from the ROV either laterally or vertically. Thrusting the ROV toward the shoal ($n = 11$, for 3 shoals) resulted in lateral movement of the shoal, but fish never dispersed completely from the site they were initially observed and could not be dispersed vertically upward in the water column.

Some shoals in the cold intermediate layer were located in the exact same two areas on different days within a year as well as among years (Fig. 4; northern area: stations 5–8, 17, 20, 29; southern area: stations: 2, 11, 21, 27–31, 37). These

Fig. 5. The stomach fullness (empty (open), <50% full (shaded), and >50% full (solid)) of each maturity stage of female (a) and male (b) capelin (*Mallotus villosus*) for all years combined (2000–2003).



shoals were consistently observed hydroacoustically during the meso-scale survey in 2000 and 2001 but not in 2002 and 2003, when fewer shoals were observed in the study area (Fig. 3). Nonetheless, bottom trawls in these same locations after completing the survey in these years always revealed the presence of capelin in these two areas (Fig. 4). Therefore, capelin were spatially persistent on the scale of hundreds of meters and temporally persistent over the 4 years of this study. Bottom shoals were also persistently found in the study area in 2002 and 2003. Bottom shoals could be predictably located in 2002 and 2003 farther from shore once water depths reached >200 m, although the exact location changed between these 2 years (Fig. 3).

Day–night comparisons

During 2000, shoals within the cold intermediate layer were found in the water column toward the surface during dark and associated with the seabed during daylight. This was evidenced by significantly higher fish biomass ($\text{g} \cdot \text{m}^{-2}$) per 100 metres of transect in the upper water column (10–49 m) during dark compared with daylight (24 July 2000: $t_{[146]} = 2.383$, $p = 0.018$; 27 July 2000: $t_{[245]} = 6.849$, $p < 0.0001$; Fig. 6) and higher fish biomass in the lower water column (50–200 m) during daylight compared with dark (24 July 2000: $t_{[146]} = 2.162$, $p = 0.032$; 27 July 2000: $t_{[245]} = 2.483$, $p = 0.014$; Fig. 6).

In all years, capelin were caught primarily during daylight, and thus, daylight–dark comparisons of stomach fullness ($n = 1116$) were difficult. The frequency of stomachs that were >50% full, however, differed significantly among four 4-h time periods throughout the day (0800–2350 Newfoundland Daylight Savings Time (NST) = GMT – 2.5 h; $\chi^2_6 = 296.875$, $p < 0.0001$), being highest in the daylight–

dark transition period (1700–2059 NST; Fig. 7). During 2002, the depth distribution of the three size fractions of zooplankton caught during daylight and during dark were investigated using two-way ANOVAs, with time of day (daylight, dark) and depth (surface: 0–50 m; bottom: >50 m) as factors. Analyses revealed that the dry biomass of all size fractions combined was significantly higher in the bottom layer relative to the surface layer ($F_{[1,16]} = 9.419$, $p = 0.0007$). Zooplankton biomass was not significantly different during daylight and dark ($F_{[1,16]} = 1.138$, $p = 0.302$); however, there was a significant interaction between time of day and depth, indicating higher biomass in the bottom during daylight relative to dark and higher biomass at the surface during dark relative to daylight ($F_{[1,16]} = 9.816$, $p = 0.0006$). The dry biomass of the 1 mm size fraction was significantly higher in the bottom layer relative to the surface ($F_{[1,16]} = 38.176$, $p < 0.0001$), but did not differ during daylight and dark periods ($F_{[1,16]} = 0.460$, $p = 0.507$). The dry biomass of the 2 mm size fraction did not differ significantly during daylight and dark periods ($F_{[1,16]} = 3.459$, $p = 0.081$) nor with depth ($F_{[1,16]} = 0.055$, $p = 0.818$); this was also true for the 0.232 mm size fraction (time of day: $F_{[1,16]} = 1.330$, $p = 0.266$; depth $F_{[1,16]} = 1.410$, $p = 0.301$).

Zooplankton may tend to avoid the net when visual cues are available. To investigate whether this biased our daylight–dark comparisons, we conducted single-factor ANOVAs to compare the biomass of zooplankton between daylight and dark periods in the bottom layer only, assuming that light is greatly reduced at depths >50 m and, thus, that dark and daylight periods would not differ significantly in light conditions. No significant differences in the biomass of zooplankton were observed between daylight and dark periods in water >50 m (total biomass: $F_{[1,8]} = 1.357$, $p = 0.278$; 2 mm: $F_{[1,8]} = 0.083$, $p = 0.781$; 1 mm: $F_{[1,8]} = 1.934$, $p = 0.202$; 0.232 mm: $F_{[1,8]} = 1.313$, $p = 0.285$). This suggests that these results were not biased because of avoidance behaviour of zooplankton and indicates that zooplankton biomass was higher in the bottom relative to the surface layer throughout the 24 h cycle, primarily driven by the 1 mm size fraction, with only a minor indication of diel movement toward surface waters during dark periods.

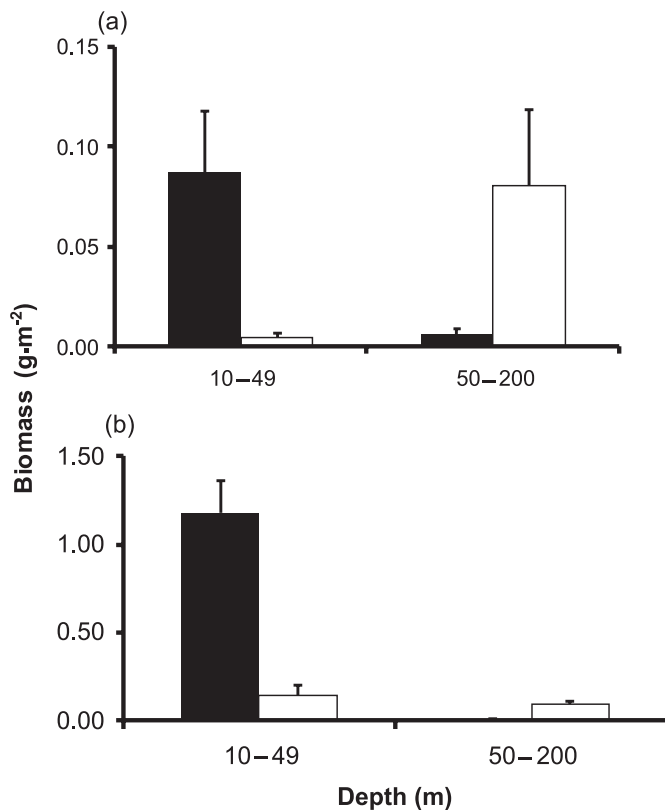
Demersal spawning sites

In 2002, two discrete patches of capelin eggs were found adhered to pebbles within the 50 m depth contour during observations of antipredator behaviour of shoals using the ROV. Eggs that adhered to the legs of the ROV were frozen and subsequently identified in the laboratory as capelin eggs. These two sites were visited in 2003, showing persistent use of demersal sites by capelin among years of this study. Physical characteristics were measured at each site on a number of occasions in 2003. In the first patch (49°15.55'N, 53°25.53'W), particles sizes sampled ($n = 8$) were primarily composed of coarse sand (48.5% \pm 7.2%), with less silt and fine sand (21.8% \pm 4.8%), small cobble (17.6% \pm 7.6%), pebble (7.4% \pm 3.2%), and large cobble (2.1% \pm 1.7%). The mean water depth was 33.0 \pm 0.6 m ($n = 7$), with a mean temperature of 4.3 \pm 0.3 °C ($n = 4$) and was located ~6.4 km from the coast. In the second patch (49°15.12'N, 53°25.95'W), particles sizes sampled ($n = 7$) were primar-

Table 4. The percentage by mass of each zooplankton prey type in the diet of capelin (*Mallotus villosus*, 2001), along with the percentage of occurrence of each prey type in the diet and net samples in each year.

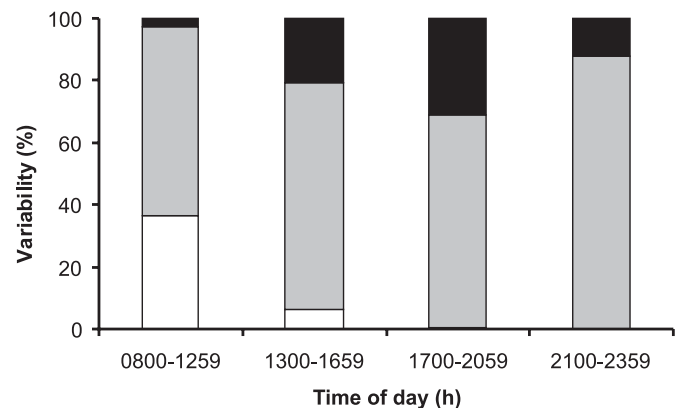
Category	% by weight	% occurrence			
	Stomachs 2001 (n = 51)	Nets 2000 (n = 8)	Nets 2001 (n = 6)	Nets 2002 (n = 38)	Stomachs 2001 (n = 51)
0.232–1 mm					
Copepod species	63.8±5.4	100	100	100	92
>1 mm					
Amphipod species	14.0±4.5	25	50	92	25
Euphausiid species	16.4±3.4	50	67	87	49
Chaetognath species	0.9±0.4	100	33	63	10
Pteropods	0	0	0	13	4
Invertebrate eggs	4.2±2.7	0	0	0	20
Fish larvae	0.5±0.5	0	50	8	2
Fish eggs	0	0	0	0	4
Crabs	0.1±0.1	38	0	21	2

Fig. 6. Mean + standard error of densities of capelin (*Mallotus villosus*; g·m⁻²) in the upper (10–49 m) and lower (50–200 m) water column during dark (solid) and daylight (open) in the northern staging area on 24 July 2000 (a) and in the southern staging area on 27 July 2000 (b). Note the different scales on the y axes.



ily composed of coarse sand (75.1% ± 3.1%), with less pebble (20.1% ± 3.6%), silt and fine sand (2.8% ± 1.0%), small cobble (1.2% ± 1.0%), and no large cobble. The mean water depth was 28.0 ± 0.4 m, with a mean tempera-

Fig. 7. The variability in stomach fullness (empty (open), <50% full (shaded), and >50% full (solid)) with time of day for all capelin (*Mallotus villosus*; n = 1116) in all years combined (2000–2003).



ture of 7.0 ± 0.9 °C and was located ~5.7 km from the coast.

Discussion

We hypothesize that capelin shoals of varying maturity stages used habitat on a meso-scale in the following manner in our study area. Capelin likely migrated inshore toward the study area from eastern, overwintering areas near the shelf edge, pausing in large shoals at the offshore boundary of our study area in warm, deep (>240 m) water. Capelin appeared to split into smaller shoals and move closer to the coast, where they paused in shallower water (100–150 m) in two specific areas. Shoals were persistently present in these two areas among years of this study, suggesting that they are important staging areas for mixed shoals of maturing male and female capelin completing gonadal development. These shoals moved into warm surface waters at night but remained at depth in subzero water temperatures during daylight, possibly for reasons discussed below. When gonadal development was complete, we further hypothesize that sex-specific shoals moved toward both beach and demersal spawning sites within the 50 m depth contour. Capelin that survived

spawning attempts, mainly females, moved back into the two staging areas, returning to regular diel vertical movement patterns. The primary association of capelin shoals with the seabed, along with warmer water in deeper areas, may lead to a preference for bathymetric channels and trenches during residence in coastal areas. This is supported by the persistent association of capelin shoals with the deepwater trench in the southern portion of our study area and has been demonstrated for Atlantic cod during their inshore foraging migrations (Rose 1993).

The findings of this study are consistent with previous literature accounts. Spent and maturing fish appeared to be actively feeding (Winters 1970; Vesin et al. 1981), while mature male and female capelin of surface shoals had a higher frequency of empty stomachs, showing that feeding was much less of a priority for these fish (e.g., Vesin et al. 1981). The frequency of occurrence of zooplankton prey types in capelin stomachs that were not empty were similar to recent reports (e.g., O'Driscoll et al. 2001), with the majority of stomachs containing copepods (90%) and the importance of copepods declining in larger capelin (O'Driscoll et al. 2001). The low numbers of spent male capelin encountered during our study also support the divergent life history characteristics of semelparous male and iteroparous female capelin (Fridgeirsson 1976; Shackell et al. 1994b).

Interannual comparisons

Temperature regimes differed within the study area over the years of this study. The extent of the cold intermediate layer is known to vary interannually (Colbourne et al. 1997). It appeared to be larger in 2001, resulting in a smaller extent of the warm surface layer and all shoals being nearer the surface in 2001, which was also exemplified by cold intermediate layer shoals occurring within the 50 m depth contour. Differences among shoal size, distribution, and composition mainly occurred between the first (2000, 2001) and later two (2002, 2003) years. Fewer but larger shoals were observed in 2002 and 2003 compared with 2000 and 2001. As estimated capelin abundance (total surveyed area occupied by capelin shoals) was similar among years, these differences do not appear to be due to density-dependent effects on behaviour.

The cold intermediate layer shoals remained in deeper water in 2002 and 2003 and were composed primarily of maturing male and female capelin compared with shoals primarily composed of spent females in shallower water in 2000 and 2001. Additionally, there were more bottom shoals observed in offshore regions (>200 m) in the later 2 years relative to the first 2 years. As the timing of the survey was held constant among years, these interannual differences suggest that the timing of spawning varied among years in our study area, with capelin in 2000 and 2001 spawning earlier relative to those of the later 2 years. This finding lends further support to the hypothesis that the ratio of spent to maturing capelin in the study area, revealed by analysis of seabird diets during the same time period each year, reflects the timing of spawning of capelin (Davoren and Montevicchi 2003, 2005).

Interannually persistent cold intermediate layer shoals

Why did persistent shoals of maturing and spent capelin in the two staging areas occupy the cold intermediate water

layer? Capelin do not produce substantial amounts of antifreeze proteins and thus are thought to avoid water temperatures that are considerably below the freezing point of their body fluids (-0.4 to -0.8 °C; Raymond and Hassel 2000). Despite this, capelin can supercool and thus have been caught in even colder waters (-1.6 °C; Raymond and Hassel 2000). Atlantic cod, however, generally occupy temperatures between -0.5 and 8.5 °C (Rose and Leggett 1990), and capelin may avoid encounters with this predator by occupying colder waters. Although few cod were caught in the study area ($n = 25$; range: 3–9 per year), this species was the dominant predator of capelin prior to stock decline and collapse during the mid to late 1980s (Hutchings 2000). Capelin shoals in the cold intermediate layer may have historically used this layer to avoid cod (Mowbray 2002), likely reflecting important thermal refuges for avoiding predation by their primary piscivorous predator (Rose and Leggett 1990). Zooplankton may be higher at these depths, as suggested by the considerably higher zooplankton biomass in the lower (>50 m) versus the upper water column (<50 m) in the southern portion of the study area during both daylight and dark periods in 2002.

Why did shoals of maturing and spent capelin move into warmer surface waters at night? The mechanisms influencing vertical movement in fish have been explained using a combination of three hypotheses: foraging, bioenergetic, and predator avoidance (Clark and Levy 1988; Neilson and Perry 1990). There is an exponential decay of light with increasing water depth, resulting in a reduction in the visual range of predators with increasing depth (Clark and Levy 1988). Therefore, remaining under low light conditions throughout the diel cycle, by remaining at depth during daylight and moving into surface waters during dark periods, would likely minimize the risk of encountering and being attacked by visual predators. Currently, the numerically dominant predators in the study area are diving marine birds (see Davoren et al. 2003a). Most avian predators observed in the study area are incapable of diving to the depths occupied by these shoals during the day, except common murre. Although murre are the numerically dominant endothermic predator, the biomass and subsequent consumption rate of one whale observed in the study area (numerically dominant species: humpback whale *Megaptera novaeangliae*, Davoren et al. 2003a) would greatly overshadow all murre combined. Consequently, occupying depths >100 m is likely ineffective to avoid predation but may reduce the risk of predation by visual endothermic predators, as well as reduce the time available to air-breathing predators to locate and capture prey. Remaining under low light conditions throughout the diel cycle, however, also reduces the foraging efficiency of capelin. The higher frequency of full stomachs in the daylight–dark transitions relative to other daylight periods suggests that movement of capelin into surface waters at night is important for feeding. The higher feeding intensity at dusk is consistent with the hypothesis that diel vertical movements reflect a trade-off between maximizing food intake rates and minimizing predator encounter rates (Clark and Levy 1988). There was little evidence, however, for the diel vertical movement patterns of zooplankton in the southern portion of the study area. This suggests that movement of capelin shoals into warmer surface waters at night may be

more important to enhance metabolic rates, allowing higher rates of digestion and, thus, high rates of fat reserve replenishment in spent capelin or gonadal development in maturing capelin, as suggested by previous studies (e.g., Winters 1970).

Overall, we hypothesize that these capelin shoals occupy the subzero water during daylight periods because they provide higher zooplankton biomass while allowing a reduced risk of predation from visual, air-breathing predators. We also hypothesize that movement into warm surface waters at night, either to accelerate rates of recovery or gonadal development, reflects a trade-off between growth and survival, as suggested by Clark and Levy (1988).

Warm surface layer shoals and demersal spawning sites

Mature capelin are known to separate into sex-specific schools prior to spawning (Templeman 1948). The ephemeral nature of shoals of maturing or spent capelin in the 50 m contour suggests that these fish were traveling among regions within the study area. Capelin may not remain in these shallow areas for long periods, owing to their presumably higher vulnerability to visual, air-breathing predators. We hypothesize that these shoals represent fish moving toward (maturing) and away from (spent) both beach and demersal spawning sites, as observed in other studies ("pelagic migratory schools"; Saetre and Gjosaeter 1975). The shoals of mature male and female capelin observed with the ROV within the 50 m contour near demersal spawning sites appeared to be more stationary. Mature males and females aggregate for only a short period immediately prior to spawning (Templeman 1948). Therefore, we hypothesize that the shoals of mature male and female capelin, sampled with the purse seine within the 50 m contour, represent spawning shoals at or near demersal spawning sites and that further investigation of sites may reveal additional demersal spawning areas.

Sediment size range is considered to be the ultimate factor determining demersal spawning site location on the Southeast Shoal, Newfoundland (Carscadden et al. 1989). Sediment sizes at the demersal spawning sites in this study were within limits previously reported for capelin (range: 0.1–25 mm, Nakashima and Taggart 2002), primarily ranging 0.5–2.0 mm. Carscadden et al. (1989) concluded that capelin appear to prefer temperatures $>2^{\circ}\text{C}$ at demersal sites on the Southeast Shoal, which is consistent with temperature ranges at other demersal spawning sites in Newfoundland (1.4–12.1 $^{\circ}\text{C}$, Nakashima and Wheeler 2002; 4–7 $^{\circ}\text{C}$, this study). Observations on the Southeast Shoal also revealed that there was little interannual variation in spawning locations (Carscadden et al. 1989), as found during the 2 years of this study (water depth: 28–33 m). We hypothesize that demersal spawning sites will be persistent among years, depending on the rate of substrate disturbance, and that additional demersal spawning sites will be restricted to <35 m, based on the historical temperature data for our study area.

The mature shoals of male and female capelin near demersal spawning sites appeared to have an affinity to the location they were first observed. Fish were oriented in different directions and could not be dispersed either laterally or vertically off the seabed under simulated predatory attacks. Similar shoal behaviour has been observed at

demersal spawning sites in Norway (Saetre and Gjosaeter 1975), as well as offshore (Carscadden et al. 1989) and coastal Newfoundland (Nakashima and Wheeler 2002). This behaviour provides capelin predators with an abundant food resource that is persistent in time and space on a fine spatial scale, allowing the use of time and energy-efficient strategies to both locate and capture prey (Davoren et al. 2003a, 2003b). In the context of human fishing, however, this behaviour makes spawning capelin highly susceptible to harvest and makes suitable demersal spawning habitat vulnerable to disturbance from fishing gear.

Future research

Diel vertical movements of capelin were a typical behaviour exhibited before the 1990s but has since become irregular among regions and seasons (Mowbray 2002). We observed regular diel vertical movements of maturing and spent capelin shoals in the two staging areas; however, this behaviour was not investigated in other regions of our study area. Erratic migratory patterns likely result from a combination of factors that differentially affect capelin at various maturity levels or capelin exposed to varying levels of predation and predator types (Mowbray 2002). Mowbray (2002) provided evidence that irregular vertical movement patterns were primarily a result of shifting prey availability, and thus, future investigations should focus primarily on foraging behaviour and dietary analyses of capelin. Combining data on dietary composition and feeding intensity (e.g., stomach fullness) throughout the 24 h daylight–dark cycle (e.g., Darbyson et al. 2003) with light extinction curves and unbiased measures of vertical movements of zooplankton (e.g., acoustic Doppler current profiler) appears critical. This integrated approach is essential to determine appropriate timing and design of hydroacoustic surveys (e.g., Neilson et al. 2003) and may elucidate the relationship between the precipitous decline in hydroacoustic-derived biomass estimates of capelin in the early 1990s (Carscadden and Nakashima 1997), coincident with the breakdown of regular diel vertical movement patterns (Mowbray 2002).

Testing the predictions and hypotheses outlined by Nakashima and Wheeler (2002) will be critical for future stock assessments of capelin in Newfoundland, as well as revealing whether capelin are sensitive indicators of climate change. Comparing the reproductive success and possible recruitment of capelin at known beach and demersal sites throughout coastal Newfoundland will be essential to these investigations. An underlying assumption is that capelin select spawning habitat based on the assessment of local environmental conditions, as hypothesized by Templeman (1948), rather than being reproductively isolated populations of obligatory demersal and beach spawners (Dodson et al. 1991). The investigation of maternal (e.g., size-specific fecundity) and early life history traits (e.g., egg size; Chambers et al. 1989), combined with morphometric and genetic investigations (e.g., microsatellites; Gordos et al. 2005), will help test the hypothesis of whether capelin exists as locally adapted subpopulations. Additionally, determining the potential spatial extent of demersal spawning in coastal Newfoundland is important and may be possible using available data on bathymetry, historical temperature, and substrate types and distribution in coastal Newfoundland.

The presence of suitable biophysical habitat characteristics for demersal spawning and staging areas for maturing and spent capelin resulted in the persistent aggregations of capelin among the years of this study, which were consistently used by marine predators, primarily seabirds and whales (Davoren et al. 2003a). Owing to the reliance of top predators on capelin in the Northwest Atlantic (Lavigne 1996), these persistent aggregations of capelin will likely influence the foraging strategies and distribution patterns of most upper trophic level consumers. Overall, such aggregations likely play an important role within the Northwest Atlantic ecosystem, owing to the concentration of predators and prey in a particular location where energy transfer among trophic levels is maximized. The large aggregations of animals along with their persistent behaviour within these areas also make them highly vulnerable to human activities and thus should be considered as key management areas where fishers and researchers work together to minimize the negative interactions between humans and marine organisms (Hyrenbach et al. 2000).

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