DISTRIBUTION AND MOVEMENTS OF ATLANTIC COD
IN PLACENTIA BAY, NEWFOUNDLAND

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by

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Abstract

This study investigates spatial and temporal variability in the distribution and movements of Atlantic cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland, Canada, and consists of three components. First, a combination of acoustic and submersible surveys is used to reveal systematic variation in acoustic density estimates resulting from diel behavioural patterns of cod vertical movements and habitat associations. Second, acoustic measures of cod distribution demonstrate that cod spawn repeatedly at well-defined grounds in coastal Newfoundland, that the timing and intensity of spawning vary inter- and intra-annually, and that gender and age-related behaviours affect the composition of spawning shoals over time. Third, the within-year distribution and movement patterns of cod in Placentia Bay are studied using acoustic methods and mark-recapture experiments, documenting substantial migrations and a shift in depth-related distribution from the spring spawning to fall feeding period. This thesis reveals strong spatial and temporal trends in coastal cod distribution, demonstrating that acoustics can be effectively employed in the Newfoundland coastal environment. The observations provide evidence for the existence of a Placentia Bay cod stock.

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Introduction and Overview

The Newfoundland cod fishery has shaped the social and economic character of the province since the 1500s. Historically, much scientific attention has focused on the once highly abundant and productive 'Northern' cod stock of the Grand Bank and Labrador and northeast Newfoundland continental shelves (reviewed in Taggart et al. 1994). With the collapse of the Newfoundland cod stocks and the imposition of general moratoria on fishing in 1992-93, increasing evidence has accumulated to suggest that a large proportion of the remaining biomass of cod in Newfoundland waters is concentrated in coastal regions (Rose 1996a; Taggart 1997). Although cod have been shown both to over-winter and spawn in coastal Newfoundland waters (Hutchings et al. 1993; Goddard et al. 1994; Wroblewski et al. 1994; Smedbol and Wroblewski 1997), and various mark-recapture experiments have been performed to investigate cod movements in coastal areas (summarized in Taggart et al. 1995), much of the fundamental ecology of these coastal populations remains to be understood.

The distribution of fish, particularly how it varies in space and time and its underlying causes, is an element of fish behaviour too often overlooked by fisheries science. Distributional dynamics can bring about selective fishing mortality, affect catchability, and have important consequences to the assessment of stock abundance (Godø 1994). Movements of fish often violate management assumptions that fish are uniformly distributed within stock units and do not move between units (Templeman 1983).

Understanding fish distribution and movements is therefore critical to effective fisheries management.

In 1997, NAFO sub-division 3Ps on the south coast of Newfoundland became the first Newfoundland cod stock to re-open to commercial fishing since the imposition of moratoria.. Placentia Bay constitutes a substantial proportion of coastal 3Ps, and now supports a thriving fishery. Prior to the present study, however, the seasonal distribution and movements of Placentia Bay cod had not been investigated. Similarly, no previous work had addressed the questions of whether cod spawn in Placentia Bay and where and when any possible spawning takes place within the bay. Understanding the timing and location of cod spawning is important to the study of recruitment, and to ensuring the long-term sustainability of any fishery.

Several methods have been used to study the distribution and behaviour of adult marine demersal fishes. Experimental or assessment trawl surveys have been commonly employed, but are limited by low spatial resolution, an inability to sample the entire water column, and bias introduced by gear selectivity (Godø 1994). In addition, bottom trawls cannot be employed in many coastal regions because of rough bottoms and steep slopes. Data from commercial fisheries can be used to infer fish distribution, but may be biased towards areas of high abundance (Rose and Kulka in press). Fisheries acoustics allow direct, precise, and relatively accurate observations of fish abundance and distribution

over the entire water column, and increasingly are being used in fisheries research and the study of marine fish behaviour (Misund 1997). By sampling along continuous transects, rather than at discrete points, acoustic techniques also allow surveys at high spatial resolution and intensity (MacLennan and Simmonds 1992). However, a major source of error in acoustic surveys stems from an inability to detect all fish within the sampled volume, especially when fish are located very close to the surface or bottom. This problem of 'detectability' is further exacerbated by rough bottoms and steep slopes, which are commonplace in coastal Newfoundland, and by vertical or horizontal movements of target species in and out of areas of low detectability. Exploratory acoustic surveys for cod in Placentia Bay (Rose 1996b) have suggested that acoustics can be successfully employed in this region, but further experiments must be conducted to verify their accuracy and ability to reliably detect cod.

I therefore examine the distribution of cod in Placentia Bay, Newfoundland, Canada, in 1996 - 1998, using acoustic methods in combination with submersible surveys and mark-recapture experiments. This study is divided into three components. I first examine the consequences of behaviourally-mediated systematic variation in detectability to acoustic surveys for cod. This aspect of the study allows an assessment and validation of the acoustic methods and demonstrates the feasibility of their application in Placentia Bay. Having established this feasibility, the second component of this thesis employs acoustics to ascertain whether cod spawn in Placentia Bay, and to investigate the distribution of cod

during this period of their life history. Specifically, I examine inter- and intra-annual variability in the temporal and spatial distribution of cod spawning, as well as effects of gender- and age-related behaviours on spawning shoal composition. The third component addresses cod distribution on a broader temporal scale, by examining the distribution, movements, and habitat associations of cod in Placentia Bay over the entire year. I then discuss some of the implications of my results to the management of the Placentia Bay cod fishery.

All manuscripts in this thesis were co-authored with George Rose. In all instances, I was the principal contributor to project design and proposal, implementation of the field research component, analysis of data, and preparation of manuscripts.

Chapter 1 of this thesis has been published in volume 56(3) of the ICES Journal of Marine Science, Chapter 2 has been submitted to the Canadian Journal of Fisheries and Aquatic Sciences, and Chapter 3 to Fisheries Research. Some aspects of my data have appeared in Canadian Stock Assessment Secretariat Research Documents 98/24, 98/68, 99/30, 99/41, and 99/43.

Chapter 1: The importance of detectability to acoustic surveys of semi-demersal fish

1.1 Introduction

The accuracy and precision of acoustic measurements of fish abundance may be affected by several factors, including vessel noise, equipment sensitivity, calibration, target strength, and species identification (MacLennan and Simmonds 1992). Several reviews have focused on the quantification and standardization of these variables (e.g., Foote et al. 1987; Rose 1992; Mitson 1995; Ona 1995; Scalabrin et al. 1996). A major additional source of bias stems from the inability of echosounders to detect all fish actually present. Acoustic surveys typically assume that the detection of fish is constant or varies at random within and between surveys, and hence may be a source of imprecision, but not bias. The likelihood that not all fish can be detected has been regarded as a positive characteristic of acoustic surveys because estimates of abundance will be conservative (Shotton and Bazigos 1984). However, few experiments have tested the absolute degree of detectability or its variability within and between surveys.

I define detectability as the proportion of the true abundance of a target species within the ensonified volume (surface to bottom) that is detected by an echosounder and included in integration. The term 'detectability' is drawn from sampling theory (Thompson and Seber 1996), where it is used to denote the common problem of not being able to detect all population members within a sampling unit. Detectability better describes the problem

than 'availability' which has been used in the acoustic literature (e.g., Godø and Wespestad 1993), but which is often used in a broader sense in fisheries science. Furthermore, fish may be un-available because they are located outside the ensonified volume (e.g., in unsurveyed areas), while detectability is specific to the detection of fish within the ensonified volume.

Detectability is determined primarily by physical properties of the acoustic beam and pulse, characteristics of the substrate, and how these relate to the distribution and behaviour of the fish. Detectability is reduced near bottom as a consequence of the acoustic shadow- or dead-zone: a region immediately above the bottom in which the echoes of fish overlap with that of the bottom (Mitson 1983; Ona and Mitson 1996). In Ona and Mitson's (1996) terminology, echoes from fish in the deadzone may be 'detected,' but not 'discriminated' from the bottom echo, and therefore can not be integrated. In my terminology, fish that are detectable must also be integrated. Deadzone height is set by the half pulse length and beam geometry, and increases with bottom roughness and slope (Mitson 1983). An acoustic blindzone also exists at the water's surface, and is determined by transducer depth, the blanking range, acoustic beam forming factors, and surface noise (Rose 1992). Detectability may introduce substantial bias and imprecision to acoustic surveys of areas having rough bottoms or steep slopes and where fish are distributed in close or variable proximity to the substrate or surface.

Behavioural patterns, such as vertical movements of fish into or out of the bottom and surface blindzones, can lead to bias through temporal and spatial variation in detectability (e.g., Fréon et al. 1993b; Demer and Hewitt 1995; Michalsen et al. 1996). Habitat selection for substrates of high or low detectability may also bias acoustic estimates (Fréon et al. 1993a). Detectability may vary with differences in age composition and local density where these factors affect vertical distribution (Godø and Wespestad 1993).

A key problem in quantifying detectability is that the true abundance of fish present typically is not known. Comparisons of acoustic density estimates with net catches cannot be used to quantify absolute detectability because traditional net catches provide relative indices of density subject to their own biases (Godø 1994). Submersibles may enable independent and less biased *in situ* observations of fish behaviour, distribution, and abundance, allowing estimates of absolute detectability.

Detectability is of particular importance for semi-demersal fishes such as Atlantic cod (*Gadus morhua* L.) which are frequently concentrated in close proximity to the bottom. In addition, vertical movements of bottom-dwelling fish are often complex and variable (Rose et al. 1995; Michalsen et al. 1996). Resultant variations in detectability may be especially acute in inshore shallow-water acoustic surveys, where rocky bottoms and steep bathymetry are commonplace.

In this paper I assess the detectability of Atlantic cod to inshore acoustic surveys in Placentia Bay, Newfoundland, Canada. I use surface acoustic density estimates in conjunction with submersible-based acoustic and visual measurements to test within-survey variation in detectability. This variation is considered in relation to diel behavioural patterns of vertical movements and bottom type associations. I then examine the consequences of variations in detectability to the accuracy of acoustic abundance estimates.

1.2 Methods

Study area

The study took place in Placentia Bay, Newfoundland, Canada (NAFO sub-division 3Ps; Fig. 1.1), at a study site bounded by 54° 10.20′ to 54° 10.70′ W and 47° 43.75′ to 47° 43.20′ N. The area was chosen for its steep slopes and variety of bottom types, in order to test my acoustic techniques under a range of conditions that are thought to affect detectability. Most of the experimental work was conducted on two transects running along the parallels 54° 10.50′ (Transect 1) and 54° 10.60′ W (Transect 2), from 47° 43.65′ to 47° 43.30′ N. Depths along these lines ranged from 35 to 80 m. A related survey was performed in the spring of 1998, covering both the inshore site and an offshore transect in 3Ps (along 45° 05.00′ N, from 55° 34.21′ to 55° 33.55′ W; Fig. 1.1).

Surface acoustic protocol

Over the course of 27, 28, 31 October and 1 November 1996, 17 acoustic transects were run on a north-south axis across the study site. On each of 27 September, and 2 and 7 October 1997, a 24 hour survey was conducted, in which Transects 1 and 2 were both run from one to three times per hour. The timing of these three surveys was chosen to span the full range of tidal phases. Two BioSonics single beam digital DT4000 echosounders were used in this study (38 and 120 kHz; 6° half-power beam widths, pulse durations 0.4 ms, 42 kHz digital sampling rates, pulse rates 2 pings s[-1]). Transducers were mounted on a 'dead weight' body towed at a depth of 1.5 m alongside either the MV Innovation or MV Mares (Marine Institute of Memorial University of Newfoundland research vessels, < 14 m). All transect runs were performed at a constant speed of 4 knots (7.4 km h^{-1}). Calibrations were performed *in situ* with a 38 mm tungsten carbide standard target according to standard practices (Foote et al. 1987). Handlines were used to collect fish at the study site to supplement acoustic interpretations and provide biological samples.

The acoustic signal consisted mostly of large and sometimes overlapping single targets (e.g., Fig. 1.2). A 30 cm vertical offset from the detected bottom was used, equivalent to approximately one half pulse length. Background and system noise levels experienced during the surveys were less than -100 dB. Acoustic data from the 38 kHz echosounder on each pass of an acoustic transect were integrated using FASIT software (Fisheries Assessment and Species Identification Toolkit; LeFeuvre et al. in press) to produce a mean transect areal backscatter (Sa). Mean Sa was scaled to areal density (fish m[-2]) using

mean target strengths of -31.0 dB per fish (for 1996) and -31.2 dB (1997). These target strengths were calculated for mean cod lengths of 56.5 cm (1996; n = 39 fish sampled, std error = 1.4) and 55.0 cm (1997; n = 46, se = 0.9) from the relationship: $TS_{(dB)}$ at 38 kHz = $20 \log_{10}$ Length - 66 (Rose and Porter 1996). Volumetric densities (fish m^{-3}) were also calculated for each transect over the entire water column and transect length, in bins of 1 m depth and 10 m horizontal length. Integration was referenced from the surface, so bin depth was subtracted from bottom depth to yield the height off the bottom of each volumetric integration bin.

For the 1996 surface acoustic data, a Kolmogorov-Smirnov one-way ANOVA on ranks tested whether daytime density estimates differed from those made at night. A three-way ANOVA tested the effects of whether the transect was run during day or night, survey date, and transect on the 1997 estimates of cod density. 'Day' was defined as the period from the start of nautical twilight in the morning (i.e., the appearance of first light as seen from the sea) to the end of nautical twilight in the evening.

Submersible surveys

Submersible surveys were conducted in 1996 with the Canadian Navy submersible SDL-1, supported by the HMCS Cormorant. The SDL-1 is a free-diving submersible with a maximum operating depth of 610 m. One large (ca. 1 m diameter) forward facing viewport permits visual observations. The crew of four was comprised of two pilots and

two scientists. A 120 kHz BioSonics DT4000 digital transducer was mounted on a moveable forward arm, connected through the submersible hull to the transmitter, receiver, and data storage computer. Four dives were made: one on each of 29 and 30 October (14:00-21:00h), and two on 31 October (08:00-11:00h and 13:30-16:30h). Position was determined by visually and radar-tracking a buoy attached to the submersible. The Cormorant remained approximately 0.5 nautical miles (ca. 900 m) from the buoy and was in constant radio contact with the SDL-1 during deployment. Once the transect starting point was attained and a run begun, the submersible's position was checked approximately every five minutes until it reached the end of the transect.

A strict protocol was observed during each submersible survey. One of transects 1 or 2 was first run acoustically at a constant speed of 0.5 knots (0.93 km h^{-1}) and a height of 20 m off the bottom. The submersible then descended and re-ran the transect in the opposite direction as a visual line census, at a height of 2 m off the bottom (following SCUBA survey techniques for coral reef fishes: Brock (1982); with modifications for submersible application after Zaferman (1981)). An external low-light sVHS camera with VCR recorded in a forward-facing direction continuously along the visual transect. External lighting was provided during both day and night from three 1000 W and two 500 W quartz lights. The radius of the field of view of the camera was not measured, but was judged by experienced Navy submariners to be constant because the submersible maintained a fixed height off the bottom.

Cod were the only large (> 30 cm) fish observed. Small redfish (< 30 cm; *Sebastes spp.*) were also present but remained down amongst rocks and boulders (and thereby in the acoustic deadzone). Cod were easily visible and identifiable at a distance of approximately 10 m in advance of the approaching submersible. There was no evidence of cod avoidance behaviour outside of the zone of observation. In general, changes in cod movement patterns were not evident unless the submersible approached within 1 - 2 m of the fish, by which point they had already been counted. Even at this close range, cod most often simply swam slowly out of the path of the approaching submersible.

An index of cod density was calculated by dividing the number of cod observed on the videotape of each transect by transect length. Transect length was calculated as the sum of the distances between subsequent position fixes. The height of the observed volume was set at 5 m, the approximate top of the camera's field of view. Transect width was the constant width of field of view. As a consequence of the inability to quantify this width, the video measure is expressed as a relative density index (fish m^{-1}).

Acoustic data collected from the submersible with the 120 kHz echosounder were echo-integrated to yield cod density (fish m^{-2}) using a mean target strength of -31.0 dB, calculated for a mean length of 56.5 cm (see above) from: $TS_{(dB)}$ at 120 kHz = $20 \log_{10}$

Length - 65 (Rose and Porter 1996). Data were integrated from the bottom (with the 30 cm vertical offset) to 5 m above bottom, for comparison to video density indices.

Cod habitat associations

The bottom type occupied by each observed cod was identified from the video record. Bottom types were defined in terms of the presence of rocks and sediment size: no cover denoted areas of sand, silt, and fine gravel; low cover areas had some rocks, but were mostly sand or gravel; high cover comprised areas with many large rocks and boulders. The time spent by the submersible over each bottom type was calculated for the visual transects. The expected number of cod in each bottom type was obtained by multiplying the total number of fish seen on the video by the proportion of total transect time spent over each substrate type. A chi-square test determined whether the observed distribution of cod differed from that expected if fish were distributed randomly relative to the proportional abundance of bottom types.

Analysis of cod associations with particular substrates was undertaken only for fish estimated to be within 1 m of the bottom, based on the assumption that only these fish could be selecting for bottom type. It was also noted whether the fish was in the acoustic lee of any rocks. A fish must be at least one half pulse length above the height of any rock within the footprint of the acoustic beam to be discriminated from the bottom echo (Mitson 1983). The approximate half-power footprint of a surface DT4000 at the range of

depths censused by the submersible (35 to 80 m) is between 3.5 and 8 m. A fish observed on video was therefore conservatively defined as being outside the 'acoustic lee' of rocks if it was located either more than ten metres away from, or clearly above, any rock.

1.3 Results

Surface acoustics

In fall of 1996, acoustic areal density estimates of cod at the survey site were higher during the day than at night (Kolmogorov-Smirnov test statistic $Z = 1.61$, $p = 0.01$, Fig. 1.3). Only four transects were performed during darkness and only two in the early morning, so a full day-night comparison is not possible. Nevertheless, this initial result led to the hypothesis of a substantial diel change in detectability.

Transects spanning the full daily cycle in 1997 showed acoustic areal densities increasing sharply at sunrise, remaining high but quite variable during the day, and then dropping off at sunset (Fig. 1.3). All three experimental days in 1997 showed this pattern, suggesting no effect of tides. The three-way ANOVA indicated that transect timing (day or night) was the sole significant determinant of density ($p < 0.001$); the effects of transect and date were not significant (p's > 0.05; Table 1.1). On each study day, average densities were at least an order of magnitude greater by day than by night (Table 1.2). Averaged across transects and days, the mean 1997 daytime cod density was 0.016 fish

m^{-2} (mean of 119 transects, se = 0.001) while the mean nighttime density was 0.001 fish m^{-2} (n = 64, se = 0.0001).

A visual inspection of nighttime echograms (e.g., Fig. 1.2) indicates that although some of the cod could be detected, most were too close to the bottom to be reliably discriminated from it during echo-integration. In contrast, the majority of fish during the day were found between 0.3 and 4 m from the bottom (Fig. 1.2), and were easily integrated.

Volumetric density estimates were higher during the day than during the night, and showed a major shift in vertical distribution. During daytime, higher cod densities were located at greater heights from the bottom and over a greater range of heights than at night (Fig. 1.4).

Habitat associations and in situ behavioural observations

During both day and night, cod observed on videotape occurred primarily as solitary individuals or in small groups of two to four. Some larger aggregations of up to 50 individuals were also observed. Cod tended to be less active by night, remaining motionless or circling slowly with no sustained directionality. During the day, cod moved much more, often seeming to travel on some particular heading.

In the daytime, cod were found in all habitats and distribution across substrates did not differ significantly from that expected (χ^2 = 2.1, p = 0.351, n = 45 fish observed; Fig. 1.5a). At night, the observed distribution across the three substrates differed significantly from that expected (χ^2 = 26.3, p < 0.001, n = 72; Fig. 1.5b). More fish were found in areas of high cover, and fewer in areas of low cover. During the night, 43.0% (n = 72) of cod observed with the video camera were outside the acoustic lee of any rocks, and no cod were estimated to be more than 1 m off the bottom. By day, 83.3% (n = 66) of observed fish were outside the acoustic lee, and 12.5% were more than 1 m off bottom.

Comparison of acoustic density estimates to submersible video density index

Four full submersible surveys included both video and acoustic transects with positional information. The three daytime acoustic density estimates made from the submersible (0.003, 0.012, and 0.013 fish m^{-2}) fell within the range of daytime estimates made from the surface (Fig. 1.3). The daytime acoustic density measures were positively associated with the video density index (Fig. 1.6). By contrast, the nighttime submersible acoustic transect had a density of nearly zero, while the corresponding video density index was the highest recorded during the study (Fig. 1.6).

1.4 Discussion

Impact of cod behaviour on detectability

This study indicates that behaviourally-mediated variations in detectability caused cod acoustic density estimates to vary by an order of magnitude over the diel cycle, independent of any change in true cod density. Surface acoustic and submersible visual observations indicated that during the day cod moved off the bottom and were not associated with any particular substrate. During daytime, cod were thus detectable to the echosounders and integrated into estimates of density. In contrast, at night fish retired to the bottom and were associated with substrates where they were hidden in the acoustic lee of high rock cover. Hence, I conclude that cod behavioural patterns of vertical movement and habitat associations reduced the detectability of fish to the acoustic survey on a diel basis, generating the observed trend in acoustic densities. This study provides direct evidence of the effects of behaviour on detectability. Previous studies have provided only indirect evidence by documenting changes in acoustic density estimates, and attributing these changes to the target organism's behaviour (Godø and Wespestad 1993; Demer and Hewitt 1995; Michalsen et al. 1996). In the Barents Sea, for example, diurnal and semi-diurnal vertical movements of haddock, redfish, and cod that have been inferred from acoustic data, are thought to have strong impacts on acoustic and bottom trawl surveys (Aglen et al. 1997).

The study of detectability has been hampered by uncertainties as to whether apparent changes in acoustic density arose from variations in detectability or from horizontal dispersion of fish (Shotton and Bazigos 1984). In my study, acoustic measures varied by

an order of magnitude, yet direct visual density measurements made from the submersible indicated no difference in the number of fish observed by day and by night. The low acoustic density measured at night with the submersible was in fact matched with the highest recorded video density index. Moreover, visual inspection of nighttime echograms suggests that fish were present along the acoustic line, but so close to the substrate that their echoes overlapped with those of the bottom and were excluded from echo-integration. Finally, my surface acoustic data demonstrate a vertical shift in density, with higher volumetric density estimates during the day at greater heights off the bottom than at night. All of these lines of evidence suggest a vertical rather than horizontal movement of cod, and that true density did not differ between day and night.

General applicability

A consistent pattern of high acoustic densities during the day and low at night was observed at my study site in two successive years. Nevertheless, it remained uncertain how typical this result was of other regions and times of year. In spring of 1998, an inshore and offshore acoustic cod survey therefore was conducted in the NAFO sub-division 3Ps to confirm the generality of this pattern. This survey included a transect that was run east-west across my study site during the day, and which showed a mean cod density of 0.214 fish m^{-2} (std deviation = 0.130; n = 7 passes). In comparison, three nighttime passes of the same transect gave a mean estimate of 0.004 fish m^{-2} (sd = 0.003). A day-night comparison of density estimates from an offshore transect of this survey

(Fig. 1.1) indicated a mean daytime density of 0.054 fish m^{-2} (n = 2 passes) and < 0.001 fish m^{-2} at night (one pass). Furthermore, bottom trawl catchability in 3Ps has been shown to be higher for cod during the night than during the day (Casey and Myers 1998), which is consistent with my acoustic results because trawl catchability increases with proximity of cod to the bottom (Michalsen et al. 1996). An upwards movement of cod from the bottom during the daytime therefore may be typical of this stock.

In contrast to my results, the general understanding of the vertical migratory behaviour of Atlantic cod is that fish move upwards in the water column at night and return to near bottom during the day. Such behaviour has been observed acoustically or inferred from variation in trawl catches on the Nova Scotian fishing banks (Beamish 1966), in the Gulf of St. Lawrence (Clay and Castonguay 1996), in northern Newfoundland waters (Rose and Porter 1996) as well as in the Northeast Atlantic (Engås and Soldal 1996). However, variation in and deviations from this general pattern have also been reported (e.g., Rose et al. 1995; Casey and Myers 1998). It should be noted that the scales of the vertical movements detected in earlier acoustic studies are typically much greater (tens of metres) than the approximately 1-5 m movements observed in my study. This may relate to the much shallower depths in my study area (40 - 80 m) than in the offshore study sites of previous research (150 - 600 m). This plasticity of cod vertical migratory behaviour underscores the importance of behavioural variability as a key and variable source of bias

in acoustic and trawl surveys, and thereby the importance of understanding the behaviour of fishes subject to such surveys.

Validation of acoustic density estimates

My submersible visual indices of density are thought to be relatively free from bias, and therefore present a reasonable basis for the validation of acoustic density estimates. Bias in visual census arises predominantly from avoidance reactions and an inability to adequately enumerate cryptic species (Dolloff et al. 1996). Within the limits of my field of view, cod seldom avoided the submersible. Studies of juvenile cod in Placentia Bay also using the SDL-1 submersible similarly observed little avoidance behaviour (Gregory and Anderson 1997). Cod colouration relative to substrate appearance, and the large size of cod observed, make it unlikely that any individuals were missed due to crypsis.

A full assessment and calibration of daytime acoustic densities cannot be attempted because my submersible video index data are too few and not absolute. However, bias in daytime acoustic densities might be indicated by non-equivalent increments in acoustic density and the video index, irrespective of scaling. My daytime acoustic density estimates increase with the video index in generally equivalent increments. Furthermore, the ratio of video indices to acoustic density estimates was very close to 2:1 (Fig. 1.6). Though unmeasured, the width of the video camera's field of view was judged to be approximately 2 m. As such, if submersible video and acoustic density estimates are

compared both in units of fish m^{-2}, a ratio of nearly 1:1 is evident. These lines of evidence are consistent with the notion of no bias in the acoustic estimates. I acknowledge that additional data would be required to fully support this conclusion, and that I cannot rule out the possibility that systematic bias might exist in either or both measures despite the fact that they increase in proportion to one another. Although previous studies have attempted to combine submersible with acoustic survey estimates (Zaferman 1981; Starr et al. 1996), the present study represents to the best of my knowledge the first attempt at validating acoustic techniques through the use of submersible visual census.

Acoustic abundance estimates

My results suggest that behaviourally-mediated, systematic variation in detectability can be the major source of bias in acoustic density estimates. In this study, mean detectability was over an order of magnitude (10 dB) lower at night than during the day. It is unlikely that any other source of error would be of that magnitude, be it from target strength, calibration, or species identification. Accordingly, I suggest that a detectability coefficient (D) should be incorporated into the scaling of acoustic backscatter to abundance, following:

$$\text{Abundance} = [(A \times Sa) / \sigma] / D(t)$$

Where A is the survey area, Sa the mean acoustic backscatter per unit cross-sectional area, σ the mean acoustic cross section of one fish, and D(t) gives the detectability coefficient as a function of time

Detectability should be defined as a function of time of day (and thereby of diel behavioural patterns), or of other parameters which affect detectability. In the absence of reliable information explaining systematic variation in detectability, a mean survey detectability coefficient could be employed. Acoustic surveys of Antarctic krill biomass have employed such a time-dependent detectability function to correct for the diel migration of the target species above the acoustic observation window (Demer and Hewitt 1995). Analogous catchability coefficients have also been suggested for trawl survey analyses (Godø 1994).

The central problem in estimating the detectability coefficient is that there is no simple means of assessing true fish density. Comparisons of density estimates from acoustic to other fishery surveys are problematic because the latter suffer from their own biases. Visual censuses from submersibles might provide the least biased estimates possible of true density, and hence of detectability. Unfortunately, submersibles are not commonly available for acoustic surveys. In my case, a lack of sufficient submersible time precluded an absolute estimate of detectability.

Although the quantification of absolute detectability is at present very difficult, every effort should be made to assess detectability on a relative scale. Models of relative detectability may help constrain bias arising from variations within and between surveys. Such models can be based on experimental measurements of cod density made over a

range of factors that may influence detectability. For example, a model could be fit to experimental density estimates plotted by time of day, where the peak of the model curve is defined as the maximum relative detectability, and is set to unity (Fig. 1.7). Subsequent acoustic densities would be scaled by a measure of detectability which would be a function of the time of day at which the estimate was made. In my experiment, nighttime acoustic density estimates were near zero. For such data, a binary step-function of detectability is suitable, where daytime detectability is defined as one and nighttime as approaching zero (Fig. 1.7a). In this study area, acoustic surveys therefore should be performed during daylight hours only, and detectability should be assumed to be unity at this time. In other survey circumstances, however, acoustic densities may not decrease to zero at any time, and a curve might be fit to density data to describe detectability (e.g., Fig. 1.7b). In the hypothetical data of figure 1.7b, low nighttime densities could be corrected by a detectability coefficient extracted from the model curve to remove bias, and 24 hour surveys could be undertaken.

A related method was proposed by Godø and Wespestad (1993) to accommodate variations in detectability (their 'availability') between surveys resulting from interannual changes in stock size and age composition, local density, and vertical and areal distributional dynamics. These authors suggested that all factors that potentially affect detectability be monitored during the actual survey, and incorporated into survey analysis. This approach has the advantage of using data from the survey itself. The use of

survey data to correct for variation in detectability has been successfully employed in the case of Antarctic krill diel migrations into the surface blindzone (Demer and Hewitt 1995). However, the use of survey data does not allow for the separation of the effects of covarying factors which is permitted by the repeated experimental transect approach I advocate. A *post hoc* non-experimental examination of detectability also may result in inefficient use of survey effort that might be expended at times when detectability later proved to have been below working limits.

In conclusion, detectability may be a major source of bias in acoustic surveys for semi-demersal fish. Patterns of variation in detectability may be complex as a result of the plasticity of fish behaviour. It is of note that analogous bias exists in trawl surveys. Incorporation of a relative and time-dependent detectability coefficient into the calculation of acoustic abundance estimates would reduce bias arising from systematic variation in detectability, and thereby enhance the reliability of acoustic estimates within and between surveys. Even then, acoustic estimates must be explicitly recognized as being relative indices, unless survey detectability can be quantified absolutely or shown to approach unity.

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Table 1.1 - Three-way ANOVA results, examining the effects on 1997 cod acoustic density estimates of day and night, survey date (27 Sept., 2 or 7 Oct.), and transect (1 or 2). All two- and three-way interaction effects were non-significant (all p's $\geq$ 0.133).

Effect	Sum of Squares	df	F	significance (p)
Model	2.4×10^{-2}	11	7.7	< 0.001
Day/Night	1.5×10^{-2}	1	50.4	< 0.001
Survey Date	1.6×10^{-3}	2	2.7	0.073
Transect	8.4×10^{-4}	1	2.8	0.096

Table 1.2 - Mean acoustic estimates (standard error in parentheses) of cod density (fish m⁻²), by survey date, transect, and day vs. night. For each date, average densities were calculated separately for day and night from all passes over each transect (n).

Survey Date	Transect 1 Day	Transect 2 Day	Transect 1 Night	Transect 2 Night
September 27	0.024 (0.004) n = 21	0.016 (0.005) n = 15	0.0015 (0.0005) n = 8	0.0019 (0.0006) n = 7
October 2	0.012 (0.001) n = 29	0.009 (0.002) n = 15	0.0002 (0.0001) n = 8	0.0003 (0.0001) n = 10
October 7	0.020 (0.004) n = 25	0.011 (0.004) n = 14	0.0014 (0.0004) n = 20	0.0008 (0.0002) n = 11

Figure 1.1 - NAFO divisions around Newfoundland and Labrador. Placentia Bay indicated by dashed rectangle. Inshore study site represented by plus symbol (✛). Offshore transect represented by star (★).
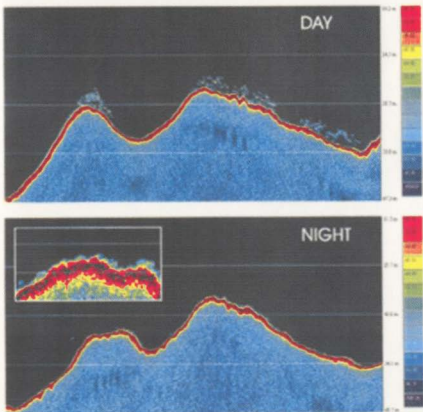
Figure 1.2 - Representative daytime (upper panel) and nighttime (lower panel) echograms from 1997. Signal consists of large single targets. In the day echogram, many cod are well off the bottom, identified by their signal shape and echo intensity. Few cod are evident at night. Inset in the night echogram is an enlargement of the second peak along the transect, from which it is apparent that fish were still present along the line.
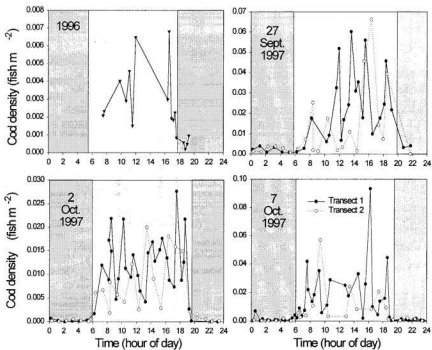
Figure 1.3 - Acoustic cod density estimates (fish m^{-2}) from each surface run of a study transect, by hour of day (Newfoundland Standard Time NST = GMT - 3.5). Separate graphs are given for the 1996 data (27, 28, 31 Oct. and 1 Nov. combined) and each of the 1997 survey days (27 Sept., 2 and 7 Oct.). The 1996 data give density estimates from a number of north-south transects across the study site. The 1997 survey concentrated on repeated passes of transects 1 (closed circles) and 2 (open circles). Nighttime is indicated by gray background, day by white.

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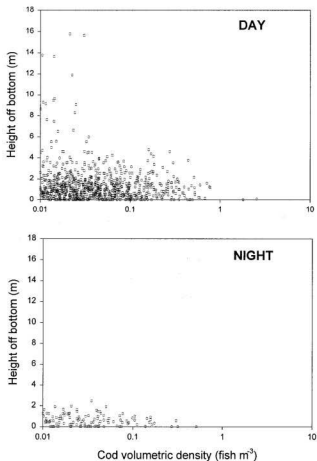
Figure 1.4 - Surface volumetric density estimates of cod (fish m^{-3}) during the day and night, calculated from bins of 1 m depth and 10 m horizontal length, plotted against bin height off the bottom (m) on the y-axis. Note that to make the dataset more manageable, only densities exceeding 0.01 m^{-3} are plotted. Trends of density with height off bottom for densities less than 0.01 fish m^{-3} are similar to those shown, during both day and night.
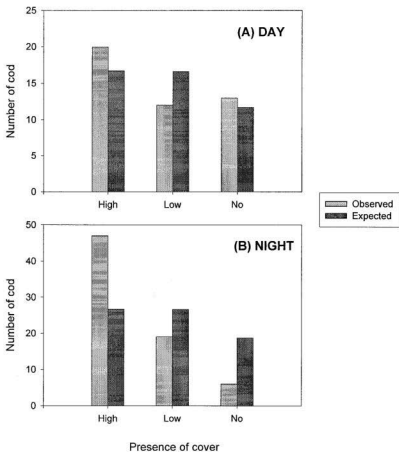
Figure 1.5 - Comparison during the **(A)** day and **(B)** night of the observed number of cod in bottom types of high, low, and no cover, to that expected if the fish were randomly distributed relative to the proportional abundance of each bottom type in the study site. In the day, no difference was evident ($\chi^2 = 2.1$, p = 0.351, n = 45 fish observed). At night, the observed and expected numbers in each bottom type differed significantly ($\chi^2 = 26.3$, p < 0.001, n = 72).
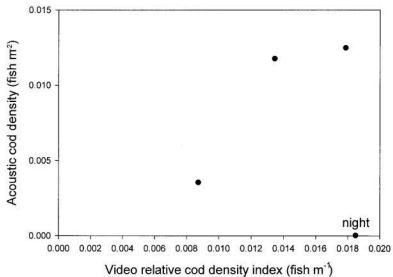
Figure 1.6 - Acoustic density estimates of cod (fish m^{-2}) plotted against corresponding relative density indices (fish m^{-1}) from video censuses. Three submersible surveys were made during the day, and one at night.
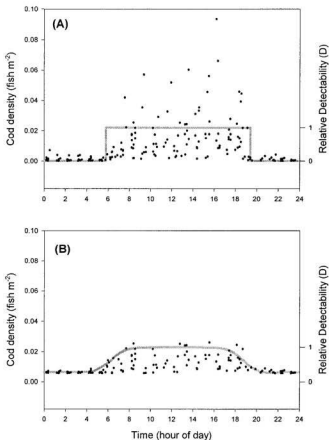
Figure 1.7 - **(A)** Surface acoustic density estimates from all 1997 days and transects, plotted against the time of day at which the estimate was made (NST). A binary step-function of relative detectability is shown in gray, with detectability (D) indicated on the right-hand y-axis. Relative detectability is set to one by day and zero at night. **(B)** Hypothetical acoustic density data in which density changes on a diel basis more gradually, and never decreases to zero. A relative detectability curve has been fit to the data and is plotted by the right hand y-axis. The curve's peak is defined as the maximum relative detectability and is set to unity.

Chapter 2: Variability in cod spawning location, timing, and behaviour in coastal Newfoundland waters

2.1 Introduction

Knowledge of the location and timing of spawning in fishes is fundamental to the study of recruitment and the conservation of spawning stocks. The locations of Atlantic cod (*Gadus morhua* L.) spawning in Newfoundland waters have been controversial (Taggart et al. 1994). Historical records of egg distributions and analyses of commercial fishing catches indicate a concentration of spawning at several seaward locations on the Labrador and northeast Newfoundland Shelves and Grand Banks (Fig. 2.1; Serebryakov 1965, 1967; Fitzpatrick and Miller 1979; Kulka et al. 1995). Rose (1993) observed spawning at the outer part of the northeast Newfoundland shelf and along a well-defined 'migration highway' across the shelf. In contrast, Hutchings et al. (1993) argued that spawning was widespread and common over the continental shelf, and less concentrated near the shelf edge and in northern areas. Coastal spawning has also been documented (Thompson 1943; Hutchings et al. 1993; Smedbol and Wroblewski 1997), and local knowledge of coastal fishers supports the presence of spawning cod in many coastal locales (e.g., Davis et al. 1994). At present, a very large proportion of the extant cod in Newfoundland waters is thought to be concentrated in coastal areas (Rose 1996a). However, the spatial and temporal patterns of coastal spawning are poorly understood, and no direct observations have been made of repeat spawning at particular locations in coastal Newfoundland waters.

Although cod have been reported to spawn at low proportions almost year-round (Pinsent and Methven 1997) and at diffuse densities (Hutchings et al. 1993), the majority of stock egg production probably originates from restricted locations and times (Sund 1935; Rose 1993; Kulka et al. 1995). Locating sites of major egg production requires detailed spatial and temporal knowledge of fish abundance, sex ratio, the proportion of females that are mature and in spawning condition, and fecundity. Several studies have estimated spawning locations and temporal peaks solely from the proportion of mature females (or females and males) in spawning condition (e.g., Powles 1958; J. Jónsson 1961; E. Jónsson 1982; Myers et al. 1993; Hutchings and Myers 1994; Smedbol and Wroblewski 1997). Such an approach could be misleading, because a high proportion of females spawning in low numbers may not contribute significantly to egg production at the population-level.

The major cod stocks of the North Atlantic are believed to use the same spawning grounds year after year, although the intensity of spawning at each ground certainly varies between years (Brander 1994). Spawning locations may be related to temperature preferences and bathymetry, and most importantly to currents and resultant egg dispersion patterns (Harden-Jones 1968). The timing of spawning is strongly influenced by physiological development rates (Kjesbu 1994). Interannual variability in the time of peak spawning may be greater for cod populations in the Northwest Atlantic (Myers et al.

1993) than in the Northeast Atlantic, where spawning timing is relatively invariant (Cushing 1969; Pedersen 1984). Spawning timing of individual cod may be affected by age, size, feeding history, and temperatures experienced while preparing for spawning (Hutchings and Myers 1993; Kjesbu 1994). Individual-level effects, together with gender- and age-specific differences in the timing of spawning migrations, could result in within-season variation in spawning shoal composition. There have been few studies of cod spawning shoal composition and behaviour to test such ideas in the wild. Morgan and Trippel (1996), however, used bottom trawl survey data to demonstrate unequal sex-ratios in cod shoals during the spawning season on the northern Grand Bank, and hypothesized that males arrive on the spawning grounds prior to females (see also McKenzie (1940), Chrzan (1950), Jónsson (1982)). Rose (1993) made acoustic observations of columnar aggregations of cod ('spawning columns') associated with spawning on the northeast Newfoundland shelf.

Several methods have been used to study cod spawning. Bottom trawl data have been used to locate spawning cod (e.g., Hutchings et al. 1993; Morgan and Trippel 1996), but such data typically provide low spatial resolution and may be biased by pelagic or semi-pelagic distributions of spawners (documented by Sund 1935, Rose 1993). Surveys of egg and larval distributions have been used to back-calculate the timing and location of spawning, but this method is biased by drift patterns, differences in mortality rates, variability in temperature-dependent developmental rates, and an inability to distinguish

early stage cod from haddock and witch flounder eggs (Ouellet et al. 1997). Acoustic techniques can detect pelagic or demersal aggregations of spawning cod with less bias, and at enhanced spatial (vertical and horizontal) and temporal resolution (e.g., Sund 1935; Godø and Sunnanå 1984; Rose 1993; Ouellet et al. 1997).

In this paper I employ acoustic methods to examine the location and timing of cod spawning, in Placentia Bay, Newfoundland, in 1997 and 1998. Placentia Bay constitutes the largest coastal component of the NAFO stock sub-division 3Ps (Stansbury et al. 1998), and the contribution of Placentia Bay cod spawners to stock recruitment may be substantial. I also test the hypothesis that males arrive on spawning grounds prior to females, by documenting within-season changes in the composition of spawning shoals. Finally, I examine whether the location and timing of cod spawning can be determined by measuring the proportion of females in spawning condition alone.

2.2 Methods

Location of spawning grounds

Placentia Bay is a large (ca. 115 km x 75 km) bay on the south coast of Newfoundland, in NAFO sub-division 3Ps (centred at 47°15′ N, 54°30′ N; Fig. 2.1). Depths within the bay extend to greater than 400 m, and the bathymetry is characterized by steep slopes and a variety of bottom types.

Acoustic surveys of Placentia Bay were conducted in April, May, and June of 1997 to locate spawning aggregations. A systematic grid of transects was run east-west across the bay at intervals of 4 nmi (7.4 km; Fig. 2.2). The full grid could not be covered on all surveys, because of weather and vessel availability. Surveys employed two BioSonics single beam digital DT4000 echosounders (38 and 120 kHz, 6° half-power beam widths, pulse durations 0.4 ms, 42 kHz digital sampling rates, pulse rates 2 pings s^{-1}). Transducers were mounted on a 'dead weight' body towed at 4 knots (7.4 km h^{-1}) at a depth of 1.5 m alongside either the MV Innovation, MV Mares (Marine Institute of Memorial University of Newfoundland research vessels, < 14 m), or CSS Shamook (Canadian Department of Fisheries and Oceans vessel, 23 m). Calibrations were performed on each vessel *in situ* with a 38 mm tungsten carbide standard target according to standard practice (Foote et al. 1987). Acoustically-located cod were sampled using automatic and manual handlines with feather hooks.

Experiments on the acoustic detection of cod in Placentia Bay have demonstrated that the proportion of the true abundance of cod that is detected by an acoustic survey is maximal and near unity during the day. Detectability is much reduced at night when fish are located near bottom and in the acoustic dead-zone (Lawson and Rose 1999; Chapter 1). All acoustic surveys were therefore conducted during daylight hours.

Spawning grounds were defined as sites where high density cod aggregations (>0.1 cod m^{-3}, averaged over 100 m horizontal bins along transects) were located, with at least 10% of sampled mature females in spawning condition (defined below). Each of the spawning grounds identified by whole-bay surveys in the spring of 1997 were individually surveyed several times during the summer and fall.

In May 1998, Placentia Bay was again surveyed using the same acoustic methods. The outer bay was also surveyed in March and June 1998 with the CSS Teleost (63 m vessel), using a hull-mounted Simrad EK500 split-beam echosounder (38 kHz, 6° half-power beam width, pulse duration 0.8 ms, 7 kHz digital sampling rate, pulse rate 1 pings s^{-1}). Cod were sampled from the CSS Teleost with a Campelen 1800 bottom trawl. Distinct spawning aggregations were less evident in the 1998 surveys than in 1997, and no new spawning grounds were identified. The areas chosen for repeat surveying through the summer of 1998 were therefore the same as in 1997.

In both 1997 and 1998, the deep (> 150 m) trench in the middle of the outer-bay (Fig. 2.2) was allocated much less survey effort than the near-shore slopes. This approach was thought to be appropriate because exploratory surveys in 1996 and the initial April survey in 1997 found few cod at depths greater than 150 m (Fig. 2.2). In June 1998, cod were found in somewhat deeper waters (up to 200 m), but only in close proximity to Oderin Bank (Fig. 2.3). In fall, cod in Placentia Bay have also been shown to be distributed at

depths shallower than 150 m (Rose 1996b), and only in winter have they been observed in numbers greater depth (Chapter 3).

Spawning ground surveys

A fixed acoustic transect was established through the centre of each located spawning ground and run during each ground survey (ranging in length from 5 km at Bar Haven to 15 km at Oderin Bank). Cod were sampled at several locations within each ground using handlines, except during the two surveys from the CSS Teleost which used a bottom trawl. Each gear has biases and unquantified selectivities, but handlines allowed sampling at precise locations and over the entire water column (achieved by varying line length relative to bottom depth). Bottom trawl samples are spatially less precise and do not represent the full water column.

Cod were examined for gender, length, weight, and gonad maturity stage. Otoliths were taken for age analysis. Female gonad stage was used in determining the times and locations of spawning. Females were categorized (*sensu* Templeman et al. 1978; Morrison 1990) as either immature or mature, with mature gonads further divided into three stages. Ripening females had visible opaque eggs. Spawning females had gonads with hydrated eggs present, and possibly some eggs already extruded. Females in the spent stage had completed spawning, and had no or very few hydrated eggs present.

During each survey, several vertical temperature and salinity profiles were measured using a Seabird 19 or 25 Conductivity-Temperature-Depth (CTD) instrument.

Acoustic analysis

The acoustic record generally was comprised of large and often overlapping single targets, with some very dense aggregations at the spawning grounds. Previous acoustic and submersible work in Placentia Bay has suggested that cod form mono-specific aggregations during spring and fall and that there are unlikely to be other species present that might be acoustically mistaken for cod (Lawson and Rose 1998). Fishing sets and acoustic identifications consistently indicated that only cod were present, with the exception of the June 1998 survey of Oderin Bank, during which a large biomass of capelin was present. Acoustic data were manually edited to ensure optimal separation of cod from pelagic backscatter (including the one instance where capelin were present) and from the bottom echo, using FASIT software (Fisheries Assessment and Species Identification Toolkit; LeFeuvre et al. in press), and then integrated along each transect to produce areal backscatter values (Sa), in bins of 100 m horizontal distance. Background and system noise levels experienced during the surveys were less than -100 dB. The 38 kHz acoustic data were analysed in 1997, whereas the 120 kHz data were used in 1998 (the 38 kHz echosounder malfunctioned in 1998).

Whole-bay acoustic survey data used to identify spawning sites were analysed by scaling Sa values per 100m bin to areal density (cod m^{-2}), using a mean target strength calculated for the mean length of cod caught during each survey, from the relationships: $TS_{(dB)} = 20 \log_{10} Length_{(cm)} - 66$ (at 38 kHz) and $TS_{(dB)} = 20 \log_{10} Length_{(cm)} - 65$ (at 120kHz; Rose and Porter, 1996).

Acoustic data from the individual spawning ground surveys were sub-sampled to remove autocorrelation in order to estimate an unbiased mean Sa and confidence intervals for each transect (Rose and Lawson 1999). For all transects, series derived from a random sampling of 25% of the original data were not significantly autocorrelated. Uncertainty was calculated by repeating the random 25% sampling 50 times: the 50 means of 25% samples were then used to calculate mean transect Sa and standard errors. Mean transect Sa, and its uncertainty estimates, were scaled to absolute density using a target strength derived from fishing sets performed during each survey on each spawning ground. This survey target strength was calculated by summing over all length groups (n groups of 4 cm length bins) the product of the proportion of fish in each group (the number of fish caught in length group i, N_i, divided by N_t, the total number of fish caught) and the mean target strength of that group (TS_i):

$$TS_{survey} = \sum\nolimits^n (N_i / N_t) \times TS_i$$

This protocol resulted in a mean cod density estimate with sampling confidence intervals for each survey of each spawning ground. Density of spawning females was calculated by

multiplying total density by the sex ratio, the proportion of females sampled that were mature, and the proportion of mature females that were in spawning condition.

Other analyses

The mean depth inhabited by cod during each survey was calculated by weighting the depth of each 100 m integration bin by the density of cod in that bin. The average of these weighted depths was then divided by mean cod density.

Probit analysis (SPSS 1996) was used to examine the effects of fish age, sample date, and sample year, on female gonad condition, for combined data collected at all spawning grounds. The relationship between these parameters and the probability of a female being in spawning condition was examined by defining all females with maturing gonads as 0, and all spawning females as 1. Cessation of spawning (i.e., the probability of being spent) was studied in a separate analysis by defining ripening and spawning females as 0, and spent females as 1.

2.3 Results

Spawning ground locations

Cod spawning aggregations were located at three sites within Placentia Bay in the spring of 1997 (Bar Haven Island, Cape St. Mary's, and Oderin Bank, see Fig. 2.2). In April 1997, spawning aggregations were present only at the Bar Haven ground. During May

1997, aggregations were found at the Bar Haven and Cape St. Mary's sites, although the southwestern portion of the bay (including the Oderin Bank area) was not surveyed at this time. Reduced densities were observed in June 1997 at Bar Haven and Cape St. Mary's, and high densities of spawning cod were present at the Oderin Bank ground. Concentrations of fish were located at several other sites in the bay but at much lower densities, or were not comprised of spawning cod.

Cod spawning sites were the same in 1998 as in 1997, with no new grounds located. High density aggregations similar to those observed in May 1997 were not detected in 1998, although lower densities of spawning cod were located at Bar Haven and Cape St. Mary's (Fig. 2.3). A very dense spawning aggregation was located in June 1998 at Oderin Bank. As in 1997, other aggregations of cod in the bay were composed of non-spawning fish, or spawners at much lower densities.

The mean depth inhabited by cod at Bar Haven in 1997 decreased from April to May, and then increased over the summer (Fig. 2.4a). A similar pattern was evident in 1998. As a consequence, despite the general warming of near-surface waters over the summer (Fig. 2.4b), spawning cod occupied waters at sub- or near-zero temperatures throughout the spawning season (Fig. 2.4c). The range of inhabited temperatures increased over the summer (delimited by the maximum and minimum depths at which cod were present at

densities >0.001 fish m^{-2}). In the later months of the spawning season, when a thermocline was present, cod were distributed in the colder waters below it.

'Spawning columns' (e.g., Fig 2.5; Rose 1993) were detected at Oderin Bank in June of 1997 and 1998, at Cape St. Mary's in May of 1997 and 1998, and at Bar Haven in April 1997. Spawning columns were never observed at any other time or location in the bay. Column dimensions were characterized by a much greater ratio of vertical to horizontal extension than other observed cod shoals. Areal densities within columns regularly exceeded 1 fish m^{-2}. Although some columns were entirely pelagic, most began at the bottom and extended 10 to 40 m above bottom, ending 15 to 75 m from the surface.

Timing of spawning

Mean cod density in 1997 on the Bar Haven spawning ground was highest in April (0.04 fish m^{-2}), and decreased by two orders of magnitude over the course of spring and summer (Fig. 2.6). The proportion of females in spawning condition, by contrast, increased from 26% in April to a peak of 55% in May, and then decreased in June to remain at background levels (<15%) through late fall. In 1998, cod density at Bar Haven was much lower than in 1997 and peaked in late June at 0.003 fish m^{-2}. The proportion of spawning females in 1998 was highest in late July (Fig. 2.6). In neither year did peak cod density coincide with the peak in the proportion of females spawning. Note that densities were averaged along the entire transect covering the spawning ground. As such, spawning

aggregations could be detected (i.e., internal densities > 0.1 fish m^{-2}), but still result in low mean densities if they were small relative to transect length.

Peak spawning at Bar Haven, measured as spawning female density (as an index of egg production), occurred more than 80 days later in 1998 than 1997 (Fig. 2.7; note that the inferred peak in spawning in 1997 occurred at the first sample period of that year). The within-year peak density of spawning females decreased from 3.5×10^{-3} fish m^{-2} in April of 1997 to 1.1×10^{-3} fish m^{-2} in June of 1998.

The spawning grounds at Oderin Bank and Cape St. Mary's were surveyed less frequently than Bar Haven. The time of peak spawning at these sites is therefore not definitively known. At Cape St. Mary's, spawning was observed only in May of both years (Fig. 2.8a). In May 1997, a higher proportion of fish was already spawning and a lower proportion was still ripening to spawn compared to May 1998. At Oderin Bank in 1997, the percent of females in spawning condition was highest in June (Fig. 2.8b), but cod density was greatest in October. In June 1997 a higher proportion of females were spent and a lower proportion were spawning than in June 1998.

Mean spawning female density at Cape St. Mary's was three orders of magnitude higher in May 1997 (1.6×10^{-2} fish m^{-2}) than in May 1998 (2.4×10^{-5} fish m^{-2}). The density of spawning females at Oderin Bank in June 1998 (9.7×10^{-3} fish m^{-2}) was two orders of

magnitude greater than at any time in 1997 (maximum of 6.7×10^{-5} fish m^{-2}), because only a very minor spawning aggregation was found at Oderin Bank in the latter year. No sampling was done at Oderin Bank in May 1997 when densities were highest at Bar Haven and Cape St. Mary's.

Probit analysis indicated that both age and survey date were positively correlated with the probability of mature females being in spawning condition ($p < 0.01$; Table 2.1). Consequently, at a given time of year, an older female was more likely to have begun spawning than a younger fish, and for a given age of fish, the probability of being in spawning condition increased with time in the sampling period. There were also weakly significant effects of year and the multiplicative interaction between year and date ($p < 0.05$). The proportion of females that were spent was negatively correlated with age, and positively with year ($p < 0.01$). At a given date, an older female was thus less likely to have ceased spawning than a younger one, and for a given fish age and date, a female was more likely to be spent in 1997 than 1998. The interaction between survey date and year also had a significant effect on the proportion of spent females ($p < 0.01$), likely stemming from the dramatic shift in timing of spawning between years (see above).

Shoal composition

In 1997, the sex ratio (females/males) of adult fish at Bar Haven increased from 0.8 in April to 1.2 in May, and then decreased over the summer (Fig. 2.9a). In 1998, the sex

ratio followed the same trend, from a minimum of 0.2 in April to a peak of 1.3 in May, followed by a decrease. Binomial tests determined for each survey whether the observed proportion of females differed significantly from that expected under a 1:1 sex ratio. Sex ratios differed significantly from 1:1 in September and October 1997, and in April 1998 ($p < 0.05$; Table 2.2). The mean length of mature females in the spawning shoal increased somewhat in both years from April and peaked in May of 1997 and June of 1998, before subsequently decreasing (Table 2.2).

The proportion of cod at the Bar Haven spawning ground that were immature followed a similar temporal trend to that of the sex ratio, increasing in both years from April to a peak in May, and then subsequently declining (Fig. 2.9b). At the smaller scale of the fishing sets performed within each spawning ground, a negative relationship was evident between the proportion of mature females that were in spawning condition and the proportion of all fish in the set that were immature (Fig. 2.10).

2.4 Discussion

My data indicate that cod repeatedly spawn at well-defined locations in coastal Newfoundland waters, but that substantial variation exists in spawning intensity and timing between years. Previous reports of Newfoundland coastal spawning have been limited by infrequent or single observations (Thompson 1943; Hutchings et al. 1993), or by a lack of information on the spatial distribution of spawning (Smedbol and

Wroblewski 1997). The present study is the first to address the spatial and temporal patterns of coastal spawning concurrently, and to do so on both an inter- and intra-annual basis.

Three major spawning grounds were located within Placentia Bay. Highest concentrations of cod eggs in 1997 and 1998 were also located only at these sites (Bradbury et al. 1999), suggesting that no additional spawning grounds were present other than those detected by my study. Spawning was more widespread at low densities or low proportions of females in spawning condition. An intriguing question is why cod spawn where they do? Spawning ground locations did not display exceptional temperature (or salinity) regimes or bathymetric characteristics. Although spawning cod inhabited relatively constant temperatures throughout the spawning season, these temperatures were not restricted to the three grounds. Spawning sites were located exclusively in shallow (<100 m) waters, but non-spawning cod also inhabited these depths, and such depths are characteristic of many areas in the bay that were not used for spawning.

The three spawning grounds were used in both 1997 and 1998, but peak densities varied over orders of magnitude between years. The highest spawning intensity (estimated either as total or spawning female density) in 1997 was located at Cape St. Mary's, with lower densities at Bar Haven, and the lowest at Oderin Bank. In contrast, the dominant ground

shifted to Oderin Bank in 1998. These observations are consistent with the notion that persistence of spawning sites with varying interannual spawning intensity is typical of Atlantic cod populations (Brander 1994). My data raise additional questions concerning why spawning intensity varies between years, whether individual cod return to the same spawning ground each year, and whether these grounds represent single or multiple and discrete spawning groups.

My data provide direct evidence that cod spawn in waters at sub-zero temperatures. In offshore Newfoundland waters and in the northern Gulf of St. Lawrence, cod typically spawn in waters warmer than 2°C (Rose 1993; Ouellet et al. 1997). Brander (1994) documented no single spawning temperature preference in a review of 25 North Atlantic cod stocks, although spawning always occurred in waters warmer than 0°C. Sub-zero surface temperatures at spawning locations have been reported (e.g., in the stratified waters off Labrador: Serebryakov 1965), but cod were almost certainly located well below the surface in deeper, warmer waters. Morgan and Trippel (1996) showed a mean temperature of −0.3°C associated with bottom trawl sets made on the Grand Banks off Newfoundland in which sex ratios were skewed towards males, and also hypothesized that such sets represented samples of spawning aggregations. Complimenting this earlier work, my study recorded sub-zero temperatures (which did not rely on averages made over large areas) at the exact depths occupied by known spawning aggregations. My observations are not consistent with the hypothesis that cod spawning in coastal

Newfoundland occurs only after waters warm above 0°C (Smedbol and Wroblewski 1997).

The repeated association of cod columns with sites and times of spawning, coupled with the absence of columns at all other places and times in Placentia Bay, indicate that this form of aggregation is associated with spawning behaviour (Rose 1993). The exact function of spawning columns remains uncertain. However, captive cod have been observed to engage in courtship rituals near the bottom of relatively shallow experimental tanks (Brawn 1961; Hutchings et al. 1999). Brawn (1961) further reports that spawning pairs of cod made a series of vertical circles to the surface and down again, culminating in a 'ventral mount' near the tank surface at which time there occurred extrusion of eggs and sperm. In the wild, coordinated vertical movements of several pairs of fish could result in spawning columns.

Egg production (the product of cod abundance, the sex ratio, and the proportion of females mature and spawning) at Bar Haven peaked 80 days earlier in 1997 than in 1998. I assume that fecundity was constant between years, because mean fish length and condition did not differ from 1997 to 1998 (Marshall et al. 1998). Comparisons of the proportions of females in spawning relative to ripening or spent condition suggests that spawning was also later at Cape St. Mary's and Oderin Bank. A decrease in water temperature of 1°C during the winter period of egg production may delay spawning by 8

to 10 days, as a consequence of the dependence of gonadal development rate on ambient temperature (Kjesbu 1994). However, temperatures were warmer in 1998 than 1997 at all Placentia Bay spawning grounds, and throughout sub-division 3Ps (Colbourne 1999). Earlier spawning in 1997 thus did not appear to coincide with warmer waters, although the actual over-wintering temperatures experienced by the cod are not known. Hutchings and Myers (1994) also reported later spawning in warmer years in shelf waters of this region, and hypothesized that cold waters form a barrier to the spawning migration. Delayed migration could prolong residency in warm slope waters, increase the rate of gonad development, and result in earlier spawning in cold years (Hutchings and Myers 1994). However, the migratory barrier hypothesis does not appear to be pertinent to my data, which indicate that cod density at the Bar Haven spawning ground was lower in the warm spring of 1998 than in the cooler spring of 1997. The hypothesis predicts that spawning migrations, and thereby high densities at spawning grounds, would occur earlier in a warmer year (1998) than in a colder one (1997).

Probit analyses indicate that older females initiate spawning earlier and cease spawning later than younger fish (Jónsson 1961; Pedersen 1984; Ouellet et al. 1997), resulting in a longer spawning season for older fish (Hutchings and Myers 1993). In contrast, Hutchings and Myers (1993) reported that older females in offshore Newfoundland waters started spawning later than younger individuals, and suggested that this phenomenon may be evidence of size-specific assortative mating, or of a requirement for

a longer period of gonad maturation to yield the greater fecundity of older individuals. Kjesbu (1994) suggested that in the wild, older fish may over-winter in warmer waters, counter-acting the increased time requirements of higher fecundity, with the net effect of older cod spawning earlier. Older Arcto-Norwegian cod have been reported to over-winter in warmer waters than younger fish (Nakken and Raknes 1987), and equivalent age-related differences in distribution have been documented in the southern Gulf of St. Lawrence (Swain et al. 1998). Older Placentia Bay cod may likewise over-winter in warmer water than younger individuals, explaining my observation of older females spawning earlier.

Spawning shoals on the Bar Haven ground in both 1997 and 1998 were dominated by males early in the spawning season. The gender composition then shifted over the season to a peak dominated by females, followed by a subsequent decrease in the proportion of females as spawning subsided. Small sample sizes, however, led to ambivalent statistical results, and as such these trends must be approached with a certain degree of caution. Morgan and Trippel (1996) detected skewed sex ratios in trawl samples over a widespread area in the Newfoundland offshore region, with higher proportions of spawning males and females in sets dominated by males. My data add support to the hypothesis of Morgan and Trippel (1996) that male cod arrive first on the spawning grounds (advanced earlier by McKenzie (1940) and Chrzan (1950)). Females appear to arrive at the spawning grounds later, and they also move off grounds earlier than males

once they have spawned. In contrast, reports of cod sex ratios in Iceland (Jónsson 1982) and the Barents Sea (summarized in Bergstad et al. 1987) have suggested a predominance of females early in the spawning season. Unfortunately, it is not possible to determine from these studies whether a higher proportion of males may have been present prior to the observation period, nor to what extent their measurements of sex ratio were biased by gear selectivity. It is noteworthy that previous studies have measured sex ratio over large spatial scales and often from a single survey within each year, rather than from surveys repeated over the spawning season at the scale of an individual spawning ground, as reported here.

In summary, my data indicate that the sequence of behaviours associated with cod spawning is complex and variable. Spawning in coastal Newfoundland occurs primarily at well-defined and persistent locations, where densities and proportions of females spawning are very high relative to surrounding areas: densities on spawning grounds exceeded 1 fish m^{-2}, and the percent of females spawning reached 76%. Cod on spawning grounds form the peculiar columnar aggregations observed in other areas of the northwest Atlantic (Rose 1993), and frequently spawn at sub-zero temperatures. Males appear to arrive on the grounds earlier than females. The similarity of seasonal trends in the sex ratio and proportion of fish that were immature suggests that females may be accompanied in their movements onto spawning grounds by juveniles. Juveniles also tend to be distributed within the spawning ground in areas of low spawning activity. Larger

females begin spawning earlier than smaller individuals, but likely stay on the grounds longer due to their greater number of egg batches and longer spawning duration (Kjesbu et al. 1996). As smaller females complete spawning and leave the grounds, mean length increases somewhat as overall densities decline. Since initial densities are high, peak egg production may occur before the peak in proportion of females spawning. As the spawning season progresses, the densities, proportion of females spawning, and mean length, all decline. On average, females remain on the grounds for a shorter duration than males, skewing the sex ratio back towards males later in the season.

Quantifying where and when cod spawn

Several studies have attempted to identify the location and timing of spawning in cod populations by examining the proportion of fish in spawning condition (e.g., Powles 1958; J. Jónsson 1961; E. Jónsson 1982; Hutchings et al. 1993; Hutchings and Myers 1994; Smedbol and Wroblewski 1997). However, the most important consideration in terms of recruitment to the population is potential egg production (Serebryakov 1990; Marshall et al. 1998). Egg production is a function not only of the percent of mature females spawning, but also of abundance, sex ratio, and fecundity. In my study, peak abundance and peak spawning female density did not coincide with peak proportion of females spawning in either year studied. Hence, documentation of the proportion of females in spawning condition alone would not have been diagnostic of the timing of egg production, nor of its location because of the existence of areas of high percent spawning

but low density. Scaling the proportions of females spawning by bottom trawl catch per unit effort as an index of abundance is preferable (e.g., Hutchings et al. 1993), but likely introduces bias as a consequence of pelagic spawning (Sund 1935; Rose 1993), uncertainty in the areal extent of inferred densities, and low spatial resolution. My data suggest that at the densities recorded on Placentia Bay spawning grounds during times of major egg production, a bottom trawl set over a distance comparable to my acoustic transects (0.5 h set at 3 knots with a 17 m swept area) would encounter 50 - 750 spawning females. In close agreement, a single bottom trawl through a high density spawning aggregation at Oderin Bank in June 1998 caught 580 spawning females in a 0.25 hour set. I believe that these high densities are typical of Newfoundland cod during the spawning period (Rose 1993; Kulka et al. 1995; Morgan et al. 1997), and that such sites are likely to be the dominant source of egg production; indeed, egg surveys of the study area confirm that the majority of eggs originated from the identified grounds (Bradbury et al. 1999). I believe that differences in methodology may have contributed to the disparity in historical accounts of where cod spawn in Newfoundland waters.

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Table 2.1 - Probit analysis coefficients for the effects of female age, survey date, survey year, and the year x date interaction on the proportions of females in spawning vs. ripening state, and females in spent vs. spawning or ripening condition. SE are given in parentheses. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Effect	Spawning vs. ripening	Spent vs. non
Female Age	0.299***	-0.384***
	(0.073)	(0.109)
Survey Date	0.020**	0.004
	(0.006)	(0.004)
Survey Year	-0.966*	1.813**
	(0.485)	(0.661)
Year x Date Interaction	-0.014*	0.023**
	(0.007)	(0.007)

Table 2.2 – Sex ratio (females: males) and mean length (cm) of mature females sampled at the Bar Haven spawning ground for each survey period of 1997 and 1998. Two asterisks (**) indicates that observed sex ratios differed from 1:1 binomial distributions at p<0.05, and one asterisk (*) indicates a difference at p<0.25. Length SE given in parentheses. Bonferroni multiple comparisons following a one-way ANOVA indicated that in 1997, mean length in May differed from April, August, and September (p<0.05). Mean lengths in 1998 differed only in April from June. A t-test comparing the lengths of all mature females sampled at Bar Haven in 1997 to those captured in 1998 found no difference (p>0.05).

Survey month	1997 Sex ratio	1997 Length	1998 Sex ratio	1998 Length
April	0.8*	61.0 (1.5)	0.2**	60.8 (1.3)
May	1.2*	66.8 (1.4)	1.4	67.8 (2.3)
June	1.0	60.0 (3.6)	1.2	70.2 (2.2)
July/August	0.8*	61.2 (1.3)	0.7	62.3 (2.1)
September	0.6**	55.2 (1.2)	0.7*	62.4 (3.2)
November	0.4**			
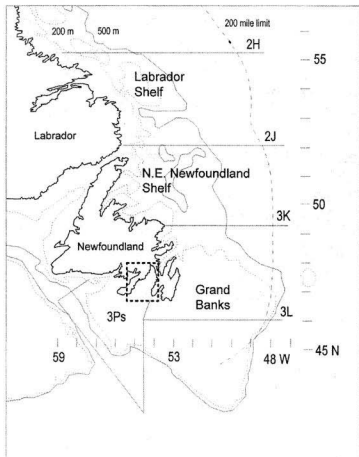
Figure 2.1 - Map of Newfoundland and NAFO stock divisions, with Placentia Bay indicated by rectangle. The shelf break occurs near the 500 m depth contour, where depths drop sharply from 300 to >1000m.
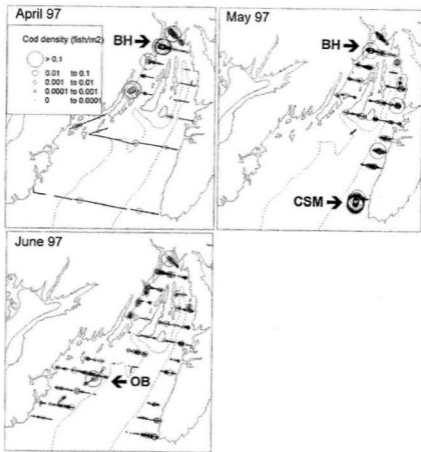
Figure 2.2 - Bay-scale acoustic surveys performed to locate cod spawning aggregations in April - May 1997. Dotted line indicates 160 m depth contour. Expanding circles represent increasing cod density (fish m^{-2}). Arrows indicate sites where cod density was at least 0.1 fish m^{-2}, and more than 10% of sampled mature females were in spawning condition (i.e., fulfilled the criteria of a spawning ground). BH indicates the spawning ground at Bar Haven Island, OB the Oderin Bank ground, and CSM the ground at Cape St. Mary's.
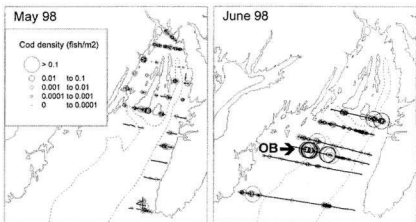
Figure 2.3 - Bay-scale acoustic surveys performed to locate cod spawning aggregations in May and June 1998. The June 1998 survey was conducted from the CSS Teleost. Expanding circles represent increasing cod density (fish m^{-2}). Arrow indicates the only site where more than 10% of sampled mature females were in spawning condition, and cod density was at least 0.1 fish m^{-2}.
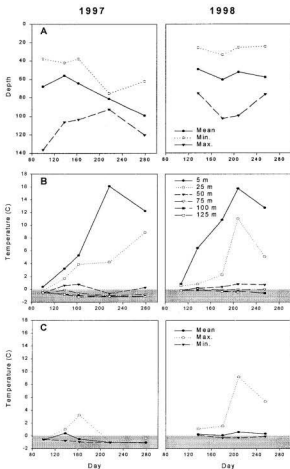
Figure 2.4 - **(A)** Depth inhabited by cod during each survey at the Bar Haven spawning ground in 1997 and 1998, vs. Julian survey day. Mean depth inhabited was calculated from mean depths of acoustic integration bins, weighted by bin cod density. Maximum and minimum depths are the depth limits at which cod were present in densities greater than 0.001 fish m^{-2}. **(B)** Bar Haven temperature (°C) profiles (values at 5, 25, 50, 75, 100, and 125 m) for each survey of 1997 and 1998, vs. Julian survey day. Gray background indicates sub-zero water. **(C)** Temperature (°C) at the mean, maximum, and minimum depths (defined above) inhabited by cod at Bar Haven during each survey.
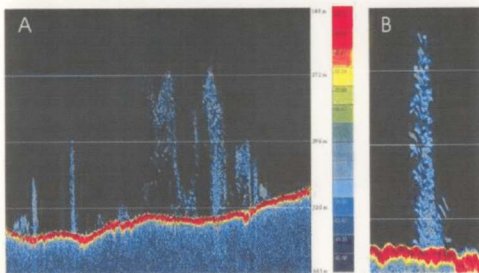
Figure 2.5 - **(A)** Echogram showing examples of spawning columns at Cape St. Mary's in May 1997. Horizontal axis represents linear distance along the transect (ca. 2.5 km), and the vertical axis shows depth. Intensity of echoes indicated by colour scale, in decibels. Black represents the water column (i.e., no echoes), while the yellow/black trace is the bottom. Cod echoes are the blue traces above the bottom, identifiable by their signature echo intensity and shape. **(B)** Enlarged view of the second column from the left on the transect, allowing the identification of individual cod within the spawning column.

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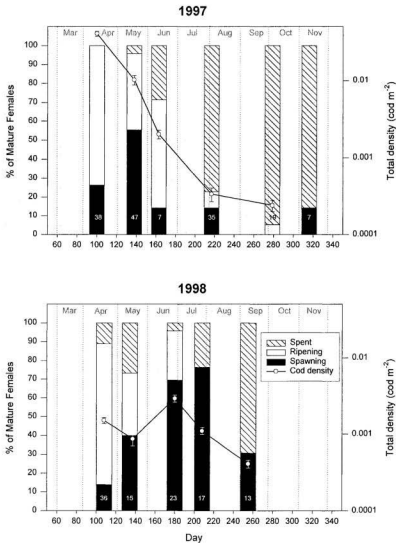
Figure 2.6 - Spawning at Bar Haven in 1997 and 1998. Bar plot shows the percent of sampled mature females that were in spawning, ripening, and spent condition (left axis), plotted by the Julian date of sampling. Number of mature females sampled indicated on each set of bars. Line graph shows acoustic estimates of cod density (right axis, log scale), with error bars showing 95% sampling confidence intervals.
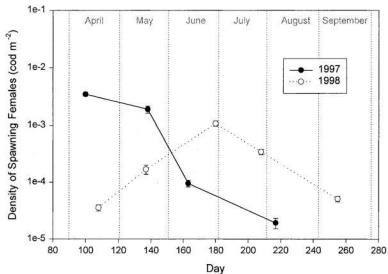
Figure 2.7 - Estimates of spawning female density at Bar Haven in 1997 (closed circles) and 1998 (open circles) on a log scale, by Julian survey date. Error bars show 95% sampling C.I. Density of spawning females calculated by multiplying total density by the sex ratio, the proportion of females sampled that were mature, and the proportion of mature females that were in spawning condition.
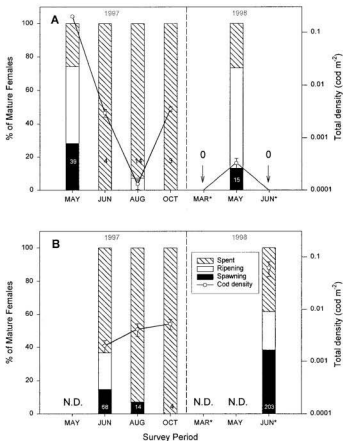
Figure 2.8 - Spawning at **(A)** Cape St. Mary's and **(B)** Oderin Bank. Bar plot shows the percent of sampled mature females that were in spawning, ripening, and spent condition (left axis), plotted by survey month. Number of mature females sampled indicated on each set of bars. Line graph shows acoustic estimates of cod density (right axis, log scale), with 95% C.I. Sample periods indicated with an asterisk were sampled from the large research vessel (CSS Teleost), and ran slightly different transects than at other times. N.D. indicates no data from that survey period, 0 indicates that no fish were present on the ground.
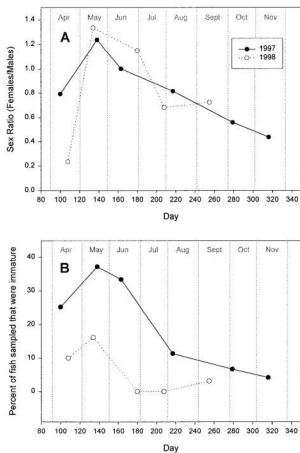
Figure 2.9 - **(A)** Sex ratio (females/males) of cod sampled during each spawning ground survey at Bar Haven in 1997 (closed circles) and 1998 (open circles), plotted by Julian survey date. **(B)** Percent of cod sampled at Bar Haven that were immature in each year, by survey date.
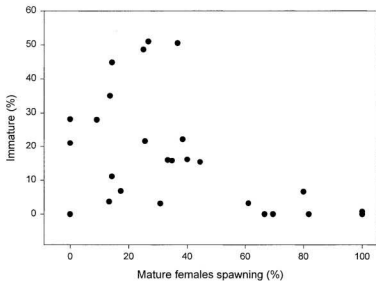
Figure 2.10 - Individual set data, for all grounds and years. Percent of cod sampled in each set that were immature is plotted vs. percent of sampled mature females that were in spawning condition.

Chapter 3: Seasonal distribution and movement patterns of Atlantic cod (*Gadus morhua* L.) in coastal Newfoundland waters

3.1 Introduction

Much of the extant Atlantic cod (*Gadus morhua* L.) biomass in Newfoundland waters in the 1990s is believed to be located in coastal areas (Rose 1996). There is increasing evidence to suggest that these coastal cod are discrete from populations that spawn on the adjacent continental shelves (Ruzzante et al. 1996). Cod have been shown to over-winter (Goddard et al. 1994; Wroblewski et al. 1994) and spawn (Hutchings et al. 1993; Smedbol and Wroblewski 1997; Lawson and Rose 1999a; Chapter 2) in coastal Newfoundland waters. However, little is known of the seasonal distribution and movement patterns of coastal cod.

Placentia Bay constitutes a large coastal component of NAFO sub-division 3Ps off the south coast of Newfoundland (hereafter 3Ps; Fig. 3.1), and holds the largest known coastal spawning population in Newfoundland waters (Rose and Lawson 1998). Limited evidence suggests that the cod of Placentia Bay belong to the Avalon stock complex (Templeman 1979, termed 'Avalon-Burin' by Templeman 1974): a group of stocks thought to spawn in Placentia and St. Mary's Bays, on St. Pierre Bank, in offshore 3Ps, and on the western slope of the Grand Bank, and to intermingle during the summer feeding period in coastal areas from the Avalon to Burin Peninsulas (Fig. 3.1b). No detailed surveys have previously examined the seasonal distribution of Placentia Bay cod,

and only four mark-recapture experiments have been conducted in the bay in the past five decades (Taggart et al. 1995). Furthermore, none of these experiments were performed during the spawning period, despite Templeman's (1983) recommendation that studies aimed at determining stock structure be carried out at this point in the fish's life history.

The habitat associations of commercial fish species may affect availability to assessment surveys (Godø and Wespestad 1993; Smith and Page 1996), catchability (Godø 1994), and the interpretation of large-scale shifts in distribution (Rose et al. 1994). Atlantic cod are thought to inhabit a specific range of depths and temperatures (Jean 1964; Scott 1982; Rose and Leggett 1988; Ottersen et al. 1998) ultimately related to physiological optima (Fry 1971). Variations in depth and temperature-related distribution may arise from age- and density-dependent effects (Swain 1993; Swain and Kramer 1995) and the location and abundance of prey (Rose and Leggett 1989). Given that temperature, food availability, and other conditions often vary widely over seasons, the distribution of cod is likely to shift accordingly. However, the majority of previous work has addressed annual trends in cod habitat associations, and not seasonal patterns in distribution (exceptions include Murawski and Finn 1988; Perry and Smith 1994; Swain et al. 1998; Castonguay et al. 1999). Furthermore, although many aspects of the distribution of juvenile cod have been investigated in nearshore waters of Newfoundland (e.g., Gregory and Anderson 1997; Grant and Brown 1998; Methven and Schneider 1998), adult cod habitat associations have not been studied in coastal Newfoundland.

In this paper, I describe seasonal patterns in the movements and distribution of cod in Placentia Bay in 1997, based on sequential acoustic surveys and mark-recapture experiments performed on spawning aggregations. The migrations of Atlantic cod have been suggested to be size-dependent (Templeman 1974, 1979; Nordeide and Salvanes 1988; Rose 1993). I therefore hypothesized that larger coastal cod would migrate longer distances than smaller individuals, with the possible exception of very large fish whose range might be more restricted (as suggested by Templeman 1974). I also examine seasonal changes in the habitat associations of Placentia Bay cod, with the expectation that the association of cod with depth and temperature might change from spring to fall, as cod shifted from the spawning to feeding components of their annual cycle.

3.2 Methods

Acoustic surveys

Placentia Bay is a large (ca. 115 km x 75 km) bay on the south coast of Newfoundland, in NAFO sub-division 3Ps (Fig. 3.1a). A systematic series of transects was established running east-west across the study region at intervals of 4 nmi (7.4 km; Fig. 3.1b). Acoustic surveys were conducted along these transects in April, May, June, August, and October of 1997 from the MV Innovation, MV Mares (Marine Institute of Memorial University of Newfoundland research vessels, < 14 m), or CSS Shamook (Canadian Department of Fisheries and Oceans vessel, 23 m). The full grid could not be covered in

all surveys, because of limitations posed by weather and boat availability, but the six northernmost transects were run in all five surveys (Fig. 3.1b). The deep (> 150 m) trench in the middle of the outer-bay was allocated much less survey effort than the near-shore slopes, because exploratory surveys in 1996 and the initial April survey in 1997 found few cod at depths greater than 150 m (Fig. 3.2). Additional transects were run over areas where cod were expected to aggregate (based on previous surveys and discussions with fishers). Less comprehensive acoustic surveying also was performed in January of 1997 and 1998, from the CSS Teleost (63 m vessel). Transect design in these latter surveys differed from those conducted in April-October because this larger vessel could not navigate the shallow inner bay transects.

Small vessel surveys employed two BioSonics single beam digital DT4000 echosounders (38 and 120 kHz, 6° half-power beam widths, pulse durations 0.4 ms, 42 kHz digital sampling rates, pulse rates 2 pings s^{-1}). Transducers were mounted on a 'dead weight' body towed at 4 knots (7.4 km h^{-1}) at a depth of 1.5 m alongside the vessel. Surveys from the Teleost used a hull-mounted Simrad EK500 split-beam echosounder (38 kHz, 6° half-power beam width, pulse duration 0.8 ms, 7 kHz digital sampling rate, pulse rate 1 ping s^{-1}). Calibrations on each vessel were performed *in situ* with a 38 mm tungsten carbide standard target according to standard practices (Foote et al. 1987). All acoustic surveys, other than those from the Teleost, were conducted during daylight hours, at which time

detectability was expected to be unbiased and near unity (Lawson and Rose 1999b; Chapter 1).

Acoustically-located cod were sampled using handlines with feather-hooks from the small vessels, and using a Campelen 1800 bottom trawl from the Teleost. Cod were sampled for length and stomachs were frozen. Cod stomach contents were quantified as percent occurrence (the percent of all stomachs sampled in which a given prey type was present), and employing a mean partial fullness index (PFI; Fahrig et al. 1993) for each prey type, calculated as:

$$PFI_x = 1/n \left(\sum^n W_{xi}/L_i^3 \times 10^4 \right),$$

where n is the number of fish sampled, W_{xi} is the weight (g) of prey type x in the stomach of cod i, and L_i is the length (cm) of cod i.

During each spring-fall survey, temperature and salinity profiles were measured by vertical casts of a Seabird 19 or 25 Conductivity-Temperature-Depth (CTD) instrument at stations spaced at intervals of 4 nmi along every second acoustic transect (i.e., transects 2, 4, 6, etc.; Fig. 3.1b).

Acoustic analysis

The acoustic record was comprised for the most part of large and often overlapping single targets, with some very dense aggregations. Previous acoustic work in Placentia Bay has

suggested that no species are normally present that might be acoustically mistaken for cod (Lawson and Rose 1998). Fishing sets in this study caught only cod, although acoustic observations occasionally indicated the presence of pelagic scatterers (likely capelin, herring, or zooplankton). Separation of cod from pelagic backscatter in the acoustic analysis followed the methods of LeFeuvre et al. (in press). Background and system noise levels during surveys were less than -100 dB. Acoustic data were manually edited to ensure optimal separation of cod from bottom, using FASIT software (Fisheries Assessment and Species Identification Toolkit; LeFeuvre et al., in press). Data were then integrated with FASIT to produce areal backscatter values (Sa), in bins of 100 m horizontal distance along each transect. Only data from the 38 kHz echosounders were used in this study.

Acoustic data from each survey in each of four quadrants in Placentia Bay (Fig. 3.1b) were analysed by scaling Sa values per 100 m bin to areal density (cod m^{-2}), using a mean quadrant target strength (from $TS_{(dB)} = 20 \log_{10} Length_{(cm)} - 66$ (Rose and Porter 1996)). Mean quadrant target strengths were calculated from length distributions of captured cod by summing over all length groups (n groups of 4 cm length bins) the product of the proportion of fish in each group (the number of fish caught in the quadrant in length group i, N_i, divided by N_t, the total number of fish caught) and the mean target strength of that group (TS_i):

$$TS_{quadrant} = \sum{}^n [(N_i / N_t) \times TS_i]$$

Density data from each of the six transects repeated in every survey (with transects 3-6 divided into east and west components, and transect 6W excluded from analysis since it was not surveyed in April) were sub-sampled to remove autocorrelation in order to then estimate an unbiased mean density for each transect during each survey, with confidence intervals (Rose and Lawson 1999). For all transects, datasets derived from a random sampling of 25% of the original data were not significantly autocorrelated. Uncertainty was calculated by repeating the random 25% sampling 50 times: the 50 means of 25% samples were then used to calculate mean transect density and standard errors. The total abundance of cod in the inner bay during each survey was calculated by extrapolating transect density means over blocks defined in a north-south direction by the midpoint between adjacent lines and in an east-west direction by land.

Tagging protocol

Spawning grounds (Lawson and Rose 1999a; Chapter 2) were chosen as the primary sites for mark-recapture experiments (Bar Haven Island, Cape St. Mary's, and Oderin Bank; Table 3.1). Additional experiments were conducted on a juvenile-dominated aggregation in the inner bay at Clattice Harbour, and on an aggregation of cod at Rowland's Rock thought to be migrating into the bay in late fall (based on consultations with fishers). All but the latter experiment were initiated in the spring or early summer of 1997. In total, 5235 cod were tagged (Table 3.1). Cod were captured with handlines, and placed in a

large tank filled with running sea-water for at least ten minutes to ensure that they had not been injured by the capture process. Only cod judged to be in excellent condition were tagged. The length of each fish was recorded, and one or two 2.5 cm spaghetti t-bar tags were inserted at the base of the first dorsal fin. The tagging program, its reward scheme, and the logistics for reporting recaptures were widely publicized among those involved with the fishery. Only recaptures reported by December 31, 1998, where exact coordinates of recapture were available, are considered here.

The distance moved by each recaptured fish was calculated as the shortest distance by sea between the site of marking and the site of recapture. Distance moved was examined only for fish recaptured within five months of tagging to reduce complication in the distance-length relationship arising from fish growing larger with increasing time since tagging, and to reduce the number of fish that may have been on the return portion of any migration.

Analysis of distribution relative to environmental parameters

The mean depth of each 100 m integration bin was measured and the relationship between cod density and depth was examined for each survey, using only data from acoustic transects repeated during every survey.

The temperature of each integration bin was estimated from bin depth and temperature profiles, under the assumption that all cod were distributed on the bottom. CTD profiles were reduced to bins of 10 m in depth, using the temperature at the midpoint of each 10 m depth bin to represent the entire bin. Each CTD profile was assumed to be representative of a horizontal distance along the transect delimited either by land or by the midpoint between adjacent CTD stations. Integration bins located within this horizontal distance were assigned a temperature based on the depth bin within which they fell. Analysis of cod density relative to temperature could only be carried out for those transects where acoustic and temperature data coincided for every survey (i.e., transects 2, 4, and 6E). A second analysis was also performed where temperature profiles were assumed to be representative of integration bins over only a 1 km horizontal radius.

The habitat associations of cod were first examined graphically by plotting the cumulative distribution functions of available habitat (temperature and depth) and cod density relative to habitat (Perry and Smith 1994), from:

Available: $f(t) = 1/n \left(\sum^n I(x_i) \right)$, where $I(x_i) = 1$ if $x_i \leq t$, and $= 0$ otherwise.

$I(x_i)$ is calculated for each integration bin's depth or temperature (x_i) and summed over all n integration bins from the survey to give $f(t)$, for values of t ranging from the lowest to the highest recorded values of habitat (increasing at intervals of 1 m or 0.25°C).

Inhabited: $g(t) = 1/n \left(\sum^n y_i/\bar{y} \, I(x_i) \right)$,

where $I(x_i)$ is defined as above, and $y_i/\bar{y}$ is the ratio of bin density (y_i) to the mean cod density of all bins ($\bar{y}$).

The mean depths and temperatures available and inhabited (i.e., mean of habitat values weighted by density) were also calculated, as:

$$\text{Mean available} = 1/n \left(\Sigma^n \, x_i \right)$$

$$\text{Mean inhabited} = 1/n \left(\Sigma^n \, (y_i/\bar{y}) x_i \right)$$

The statistical significance of the difference between the observed distribution of cod density relative to depth during each survey and that expected if cod were distributed randomly relative to the proportional abundance of depths surveyed was examined via chi-square analysis. The number of cod in each integration bin was calculated by multiplying density by bin area (500 m^2, assuming a bin width of 5 m). The observed number of cod was then calculated in depth categories of 10 m (i.e., no. of cod at 0-10m, 11-20m, etc.). The proportion of all integration bins in each 10 m depth range was multiplied by total cod abundance (the sum of abundances in all bins) to give expected cod abundance per depth category. Similar analyses were performed for temperature in categories of 1°C.

3.3 Results

Acoustic surveys of cod distribution

In January 1997, very few cod were observed. A small aggregation (peak density of 0.07 cod m^{-2}) was located at the edge of deep water areas of the eastern channel in the northern end of the bay (Fig. 3.2). In January 1998, fish were found at low densities along several acoustic transects of the inner bay. Almost no fish were located in the outer bay at this time, with the exception of a dense aggregation (max. 0.11 cod m^{-2}) found in the deep waters immediately south of the inner bay's western channel. Mean depths weighted by cod density in January 1997 and 1998 were 90.5 and 169.4 m, respectively.

In April 1997, cod were highly concentrated in the northwestern reaches of the bay, particularly at the Bar Haven spawning ground (see Lawson and Rose (1999a) and Chapter 2 for definition of and evidence for spawning ground locations), and few cod were detected elsewhere (Fig. 3.2). Total abundance in the inner bay in April was the highest recorded during the study, and 99% of cod occupied 11.5% of the area sampled (Fig. 3.3). In May, cod were more spread out, and dense aggregations were located all along the eastern side of the bay (Figs. 3.2 and 3.3). Very high densities were also present at the Bar Haven and Cape St. Mary's spawning grounds (Chapter 2; Fig. 3.2). Inner bay abundance decreased substantially from April to a level which remained relatively constant over the remainder of the summer and early fall (Fig. 3.3). By June, densities were more dispersed over the entire surveyed area (99% of inner bay abundance located in 17.4% of the surveyed area; Fig. 3.3), with high density aggregations detected only at the Bar Haven and Oderin Bank spawning grounds (Fig. 3.2). In August and October, cod

were again more concentrated (Fig. 3.3), and many sites of high density were observed (Fig. 3.2).

No cod stomach samples were available from April and May, and very few in June, due to freezer malfunctions. A limited sample of cod stomachs in June (19 stomachs) showed the highest partial fullness index of all prey types for capelin, followed by hyperiid amphipods (Table 3.2). Percent occurrence was maximal for hyperiids, ignoring unidentified stomach contents. In August, no capelin were present in the cod stomachs (although some unidentified fish were recorded), and both percent occurrence and PFI were highest for hyperiids. Other prey, notably echinoderms and euphasiids, had increased in percent occurrence, but showed relatively low PFI. By October, hyperiids had reached a peak PFI, and were again the most frequently observed prey type. The contribution to diet of echinoderms (PFI and percent occurrence) had also increased.

Mark-recapture experiments

The results of mark-recapture experiments are highly dependent on the spatial and temporal distribution of fishing effort (Templeman 1983). In both 1997 and 1998, the fishery for cod in sub-division 3Ps caught very few fish during winter and early spring (Kulka and Inkpen 1998; Kulka et al. 1999). Catches were highest in mid-summer, and were greater in Placentia Bay than in Fortune Bay or coastal areas farther west. Only low catches were made in offshore areas of 3Ps. Catches in the adjacent NAFO division 3L in

1997-98 were very low and restricted to small scale 'sentinel', test, and recreational fisheries, and bycatch (Anon. 1998, 1999).

Tagging experiments conducted in April and May 1997 on spawning aggregations at the Bar Haven spawning ground and an aggregation comprised largely of immature fish in Clattice Harbour revealed a post-spawning outward movement in summertime of cod along both the east and west sides of the bay (Fig. 3.4). Trends in recapture locations made from each of these three experiments were very similar to one another. Relatively few tagged fish were recaptured from the west side of the bay farther south than 43 ° 47.2 N (approximately half-way out the bay) or farther west in Fortune Bay. In both 1997 and 1998, the majority of recaptures were made within the bay (94%; Fig. 3.4; Table 3.1). Many recaptures in both years were made at the mouth of the bay near Cape St. Mary's, and from regions further east and north around the Avalon Peninsula, with thirteen recaptures (4% of all cod recaptured) made in coastal areas of NAFO Division 3L. One recapture was made in 3O, and two in shelf regions of 3Ps.

The majority of first-year recaptures from the May 1997 tagging of the spawning aggregation at Cape St. Mary's occurred close to the tagging site, with one recapture in Conception Bay in summer (3L), and four from the northern portions of Placentia Bay in the fall (Fig. 3.5). Only one cod was recaptured inside the bay during the summer of

1997. By 1998, a few recaptures were made in Fortune Bay, and one offshore. Again in 1998, the majority of recaptures within the bay were made in fall and not summer.

The tagging experiment on the spawning aggregation at Oderin Bank in June 1997 generated only 10 recaptures in 1997 (Fig. 3.6), two of which were from the tip of the Burin Peninsula, three from inner Fortune Bay, and the remainder from near the tagging site. During 1998, however, fish were recaptured all along the south coast, and well up the Avalon Peninsula (11% in 3L; Table 3.1). Recaptures were concentrated on the western side of Placentia Bay. Three recaptures were made in offshore 3Ps, and one further west in sub-division 3Pn (adjacent to and west of 3Ps).

Cod tagged in November of 1997 at Rowland's Rock were recaptured in spring, summer, and fall of 1998 within Placentia Bay and around the Avalon Peninsula (22% in coastal 3L; Fig. 3.7).

Within the first five months after tagging, intermediate-sized fish (55 - 75 cm) were recaptured at longer distances (> 100 km) from tagging locations than smaller (< 55 cm) or larger (> 75 cm) fish (Fig. 3.8), which were recaptured close (< 100 km) to sites of tagging. Small fish were caught primarily by cod traps. Intermediate-sized and large cod were recaptured by a mixture of gear types (Fig. 3.8). Of the 5235 cod initially tagged, 31.9% were small, 59.6% intermediate-sized, and 8.5% large.

Quantitative analysis of distribution

In all five spring-fall surveys, the observed distribution of cod density over depth differed significantly from that expected if cod were distributed randomly relative to the proportions of depths surveyed (Fig. 3.9). Cod were always located at depths significantly shallower than was available to them in the surveyed areas: the majority of cod (87.5th-99.3rd percentiles of density) were located at depths shallower than 100 m. Examining mean and median inhabited depths shows that cod were located in increasingly shallow depths over the course of spring and summer, with much shallower depths inhabited in August and October (Fig. 3.10). The range of cod distribution (bounded by the 10th and 90th percentiles of inhabited depths; Figs. 3.9 and 3.10) likewise became shallower over the time period studied, and decreased substantially in magnitude. By August and October, cod inhabited a very narrow range of depths (Figs. 3.9 and 3.10).

Cumulative distribution functions for temperature profile data interpolated over the full length of acoustic transects, and over 1 km radii relative to profile location, were similar (1 km data not shown). All results presented are therefore based on full transects. Cod density most closely paralleled available temperatures in April, although more cod were located in sub-zero water than was expected (Fig. 3.11). Increasingly strong differences between observed and expected distributions were observed in June through August, with cod generally occupying significantly warmer waters than expected (Figure 3.11). Many

cod were still located at sub-zero temperatures (37th, 18th, and 20th percentiles of density in June, August, and October, respectively). Median temperature occupied by cod increased from April to October (-0.5 to 2.75°C; Fig. 3.12). Both mean inhabited temperature and the range of inhabited temperatures showed stronger seasonal trends than the median, increasing to a peak in August then subsequently decreasing by October, corresponding to a similar trend in available temperatures (Fig. 3.12).

3.4 Discussion

This study suggests that a large proportion of Placentia Bay cod spend much of the year within the bay. In keeping with this conclusion, moderate acoustic densities of cod were found in the bay in spring, summer, and fall. Nonetheless, the present results also demonstrate that the distribution and habitat associations of cod in Placentia Bay vary seasonally, and that extensive migrations of this population occur both within and outside Placentia Bay. The movements patterns observed are generally consistent with historical descriptions of the putative Avalon stock complex (Templeman 1974, 1979).

Within Placentia Bay, there exist major seasonal changes in distribution. Some cod over-winter in deep waters, but many more fish spawn within the bay in April and May, at which time they are highly concentrated at spawning grounds. After spawning, cod disperse from the grounds. An April-June emigration of cod from the inner bay outwards and to the east is evident in recapture locations of marked fish, in the acoustic estimates

of high cod density along the eastern side of the bay in May, and in the decrease in abundance in the inner bay from April to June. Only limited movement towards the west was observed. The number of cod recaptured in 3L (Fig. 3.13; Table 3.1) despite very low fishing pressure in this stock division, indicates that a substantial proportion of the cod that spawn in northern and eastern sites in Placentia Bay migrates around Cape St. Mary's and along the coast of the Avalon Peninsula, as far as the Northeast Newfoundland coast. It must be noted in considering the results of the present mark-recapture experiments that the 1997 and 1998 fisheries were highly concentrated in both space and time, and therefore the inferred patterns may be biased towards sites and times of high fishing pressure. This is particularly the case in comparing the present results to historical tagging experiments performed at times when the fishery was more evenly spread out over the year and throughout the stock area (e.g., Templeman 1979).

My data suggest that intermediate-sized cod (55 - 75 cm) migrate further after spawning in spring than smaller or larger individuals. All but one of the fish recaptured at distances greater than 100 km were in this intermediate size range. Rose (1993) suggested that large-scale migrations in northern cod begin at age 4 and are fully developed by age 5, and Anderson and Gregory (in press) similarly argue for an ontogenetic development of migratory tendencies in juvenile Northern cod. Cod in Placentia Bay at ages five and six were on average 51.5 and 55.1 cm in length, respectively. The present observations therefore are consistent with an ontogenetic threshold to cod migratory behaviour, which

perhaps occurs at age 6 in Placentia Bay cod. Larger Norwegian coastal cod also are believed to migrate longer distances than smaller individuals (Nordeide and Salvanes 1988). Templeman (1974) reported that larger cod (90-129 cm) moved shorter distances than smaller fish (defined as 50-89 cm), similar to the present findings.

In interpreting my results, the effects of gear-selectivity and the spatial distribution of fishing effort must be acknowledged. Traps caught almost all of the smaller fish, and were closer to the sites of tagging. Furthermore, the gillnets most commonly used in this fishery (5.5 - 6" mesh) are less likely to catch small or large cod than intermediate-sized fish (Myers and Hoenig 1997). Despite these limitations, recaptures from each gear type are consistent with the interpretation that intermediate-sized cod migrate further (Fig. 3.8). Traps did capture intermediate-sized and larger fish (Fig. 3.8), and some traps were located at long distances from tagging sites (Fig. 3.13). In addition, larger mesh gillnets capable of catching fish in the large size range were also used in this fishery (FRCC 1999), but did not capture any large cod at long distances. Handlines and linetrawls are capable of catching fish over the entire range of lengths tagged (Myers and Hoenig 1997), and were frequently used at long distances from the sites of tagging (Fig. 3.13). However, they did not capture any small fish at long distances. Thus, the present results are consistent with the hypothesis that smaller and larger cod in Placentia Bay may migrate shorter distances than intermediate-sized fish, which venture further from the bay after spawning.

Many cod that migrate from Placentia Bay in spring return to Placentia Bay in fall. The majority of cod tagged at Bar Haven, Clattice Harbour, Cape St. Mary's, and Rowland's Rock were recaptured in late fall and early winter within inner Placentia Bay. Historical mark-recapture studies of cod tagged in late fall at and around Cape St. Mary's (Templeman 1974, 1979) generated a majority of recaptures in winter and early spring within Placentia Bay, and the local knowledge of coastal fishers in this area also suggests a return movement (Davis et al. 1994). It is not known if all migrants return to the bay to spawn again, or whether some stray to other grounds.

While some cod leave Placentia Bay in summer, others appear to arrive from the west, based on the large number of cod tagged at Oderin Bank and subsequently recaptured in Fortune Bay during the late fall and winter, and in Placentia Bay during the next summer. Intense spawning occurred on Oderin Bank in both 1997 and 1998 (Lawson and Rose 1999a; Chapter 2), and large schools of capelin have been observed on Oderin Bank in June 1996-1998 (O'Driscoll and Rose 1999). This migration from Fortune Bay therefore may be related to feeding, to spawning, or to both. Templeman (1974, 1979) documented summer movements of cod that spawn on both St. Pierre and Burgeo Banks to coastal areas, and notably to the western side of Placentia Bay. The single recaptures on St. Pierre Bank and in 3Pn from the Oderin Bank experiment suggest that some of these Oderin Bank fish may be migrants from offshore regions.

Habitat associations varied substantially from spring to fall. Mean and median depths inhabited by cod decreased dramatically (by 20 m) over this time period. In contrast, once water temperatures above zero were available to cod (i.e., by June), the median temperature inhabited was relatively constant (ranging from 1.5 to 2.8°C). Furthermore, while the range of inhabited depths decreased from spring to fall (i.e., cod became more selective), the mean and range of temperatures inhabited increased as temperatures available became warmer. Cod typically occupy a wide range of temperatures, varying from -0.5 to 10°C (Jean 1964; Scott 1982; Rose and Leggett 1988; Ottersen et al. 1998). After April, the majority of temperatures available to cod were within this range. I therefore conclude that the shifts in cod habitat associations were likely more related to depth than temperature.

Evidence from stomach content analysis suggests that seasonal changes in the association of cod with depth may be related to food availability. Cod cease feeding during the pre-spawning and spawning periods (Fordham and Trippel 1999). In the present study, cod in the inner bay were located in relatively deep waters during the time of peak spawning (i.e., April and May; see also Chapter 2), and a related study (Chapter 2) documented that depths inhabited by spawning cod became deeper from April to October at the Bar Haven ground. Analysis of stomach contents suggests that in June, cod were feeding primarily on capelin. Capelin are abundant in Placentia Bay in June at depths to 250 m, and are

thought to leave the bay in late summer (R. O'Driscoll pers. comm.). In late summer and early fall when cod were located at shallower depths, their diet was dominated by hyperiid amphipods. Although the depth range of such prey in Placentia Bay has not been documented, hyperiids are a pelagic zooplanktoner (Bowman and Gruner 1973), and likely to be located above the pycnocline at relatively shallow depths. Hence, cod may be found at increasingly shallow depths over the course of the spring-fall period as a result of feeding behaviour. The deep distribution of the few fish still spawning (and presumably not feeding) at later times in the summer and fall, also supports the contention that the shallower association with depth later in the year stems from the majority of cod progressing from the spawning to the feeding period of their yearly cycle.

Comparisons of winter and summer surveys have suggested that cod in the Gulf of St. Lawrence modify their associations with depth and temperature between seasons (Swain et al. 1998; Castonguay et al. 1999). The present study examined sequential surveys to demonstrate gradual changes in depth- and temperature-related associations of cod over the short time scale of the spring spawning to fall feeding period. Cod habitat associations likely continue to shift over the course of the entire year, as cod progress from the over-wintering to spawning to feeding phases of their yearly cycle.

3.5 References

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Table 3.1 - Locations, dates of sampling, and number of cod tagged during each mark-recapture experiment. Recaptures are presented by area, as percents of total recaptures reported with position. See figures 3.4-3.7 for tagging site and recapture locations.

Location	Dates	No. cod tagged	No. recaptures with position	Recaptures Placentia Bay (%)	Recaptures coastal 3L (%)	Recaptures Fortune Bay (%)	Recaptures offshore 3Ps (%)	Recaptures other areas (%)
Bar Haven Is.	9 - 12 April	996	98	88.8	8.2	2.0	1.0	0
Clattice Harbour	10 April	966	98	93.9	4.1	1.0	0	1.0 (Div. 3O)
Bar Haven	17 - 18 May	817	105	98.1	1.0	0	1.0	0
Cape St. Mary's	25 - 28 May	709	54	88.9	1.9	7.4	1.9	0
Oderin Bank	24 -26 June	963	56	58.9	10.7	23.2	5.4	1.8 (Div. 3Pn)
Rowland's Rock	6 - 8 Nov.	784	27	66.7	22.2	3.7	3.7	3.7 (Div. 3O)
All Experiments		5235	438	87.0	5.9	4.8	1.6	0.7

Table 3.2 - Cod stomach contents, for June, August, and October surveys. The percent occurrence and partial fullness index (PFI) are given for each major prey type. See text for calculations. 'Other' prey types included bivalves, sea urchins, sponges, squid, sea anemones, sea cucumbers, and bryozoans.

| Prey Type	JUNE (n=19)		AUGUST (n=205)		OCTOBER (n=91)	
	% Occurrence	PFI	% Occurrence	PFI	% Occurrence	PFI
Capelin	21.1	0.94	0	-	1.1	0.004
Unidentified fish	10.5	0.03	27.8	0.07	11.0	0.03
Hyperiid amphipods	36.8	0.21	58.5	0.16	67.0	0.38
Gammarid amphipods	5.3	0.0004	1.0	0.0001	0	-
Echinoderms	0	-	14.6	0.04	33.0	0.15
Crabs	0	-	9.8	0.03	11.0	0.03
Euphausiids	0	-	9.3	0.004	5.5	0.0005
Shrimp	21.1	-	21.0	0.01	11.0	0.009
Plant matter	0	0.003	13.2	0.003	18.7	0.002
Unidentified matter	73.7	-	28.3	0.03	28.6	0.07
Other	15.8	0.15	2.9	0.01	6.6	0.07
Empty	0	0.01	7.8	-	7.7	-
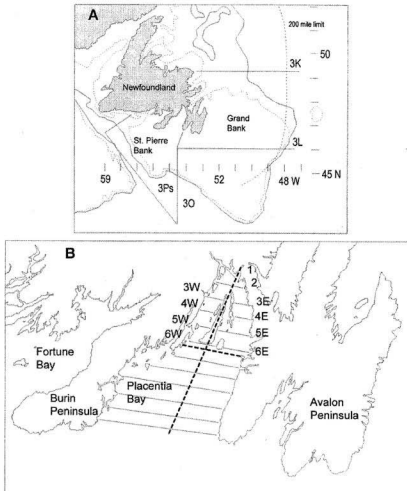
Figure 3.1 - **(A)** Map of Newfoundland and Labrador, showing NAFO stock divisions, and locations of Grand Bank and St. Pierre Bank. **(B)** Coastal waters of NAFO sub-division 3Ps. Transects in Placentia Bay for acoustic surveys and temperature profiles are indicated, and numbered for the six northern transects repeated in all five surveys. Hatched lines divide the bay into quadrants used in scaling acoustic backscatter to cod density. The area north of the hatched line running east-west is referred to in this paper as the 'inner' bay.
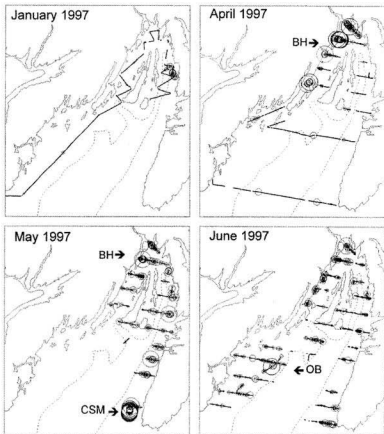
Figure 3.2 - Acoustic survey results in January, April, May, June, August, and October 1997, and January 1998. Circles represent increasing cod density (fish m⁻²). Dotted line indicates 160 m depth contour. Spawning ground (Lawson and Rose 1999a; Manuscript 2) locations are indicated as BH=Bar Haven, CSM=Cape St. Mary's, and OB=Oderin Bank.
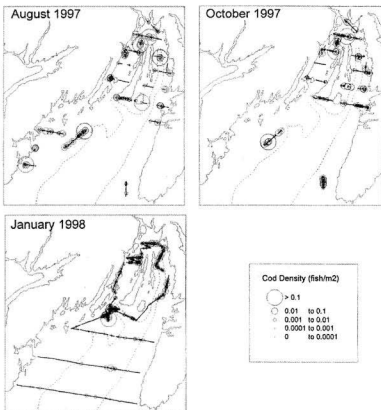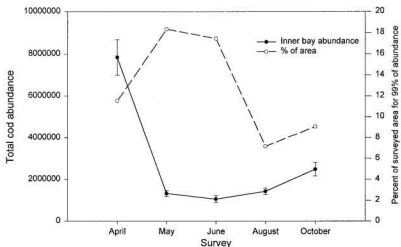
August 1997

October 1997

January 1998

Cod Density (fish/m2)

> 0.1
0.01   to 0.1
0.001   to 0.01
0.0001 to 0.001
0   to 0.0001

Figure 3.2 (continued)

Figure 3.3 - Total cod abundance in the inner bay for the five survey periods (see text for calculations), plotted on the left axis. Error bars show 1 SE. The percent of the total surveyed area in the inner bay that accounted for 99% of the measured cod abundance is plotted by survey month on the right axis.
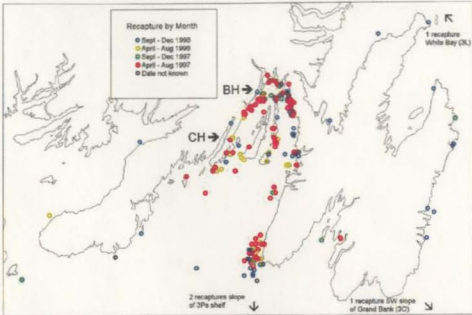
Figure 3.4 - Recapture locations of cod marked at Bar Haven (BH) and Clattice Harbour (CH) in April and May 1997 (see Table 3.1 for details of experiments), plotted by season of recapture. Three tagging experiments have been combined as the results were very similar for all three.
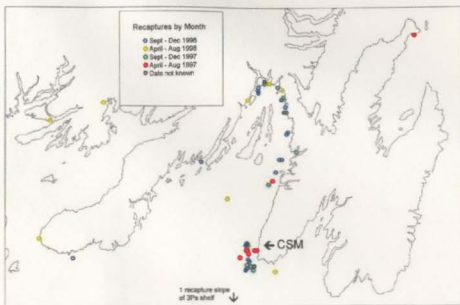
Figure 3.5 - Recapture locations of cod marked at Cape St. Mary's (CSM) in May 1997 (see Table 3.1 for details of experiment).
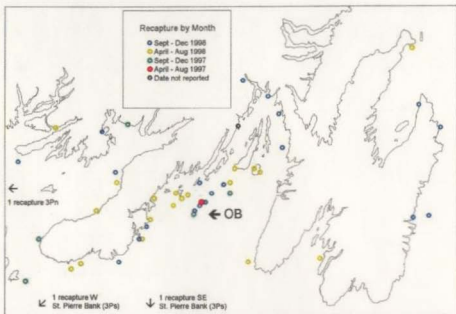
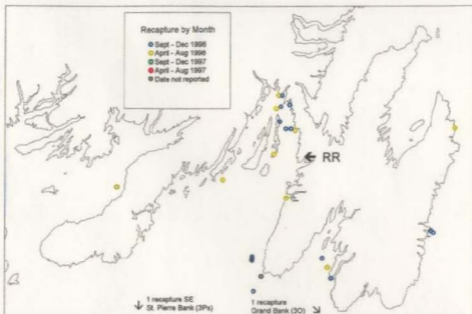Figure 3.6 - Recapture locations of cod marked at Oderin Bank (OB) in June 1997 (see Table 3.1).

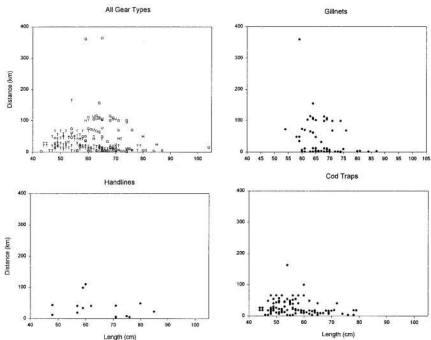Figure 3.7 - Recapture locations of cod marked at Rowland's Rock (RR) in November 1997 (see Table 3.1).

Figure 3.8 - Distance (km) moved between sites of marking and recapture relative to fish length (cm). In the first panel, datapoints are plotted by gear type used in recapture: T = cod trap, G = gillnet, H = handline (linetrawls included in this category since their selectivities are similar (Myers and Hoenig 1997)), O = other (includes lumpfish and herring nets, and lobster pots), U = unknown. The three other panels show recaptures for gillnets, traps, and handlines individually.
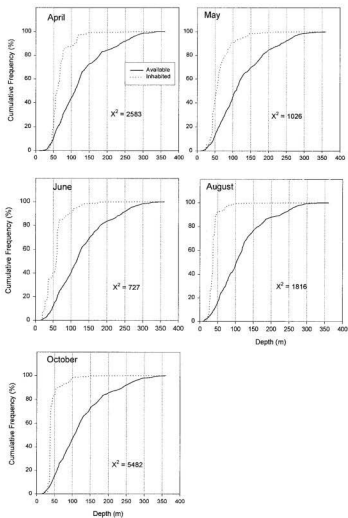
Figure 3.9 - Cumulative distribution functions for available depths (i.e. depths surveyed), and cod density relative to depth, for each survey. Chi-square analysis results of observed compared to expected cod distribution relative to depth are indicated. df = 13 for all tests, all p < 0.001.
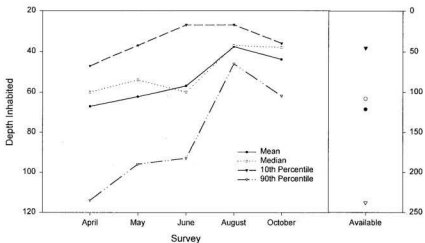
Figure 3.10 - Depths of the mean, median, 10th, and 90th percentiles of cod density distribution in each survey. Available depths (averaged over all surveys since differences between surveys were small) are indicated on a separate depth scale.
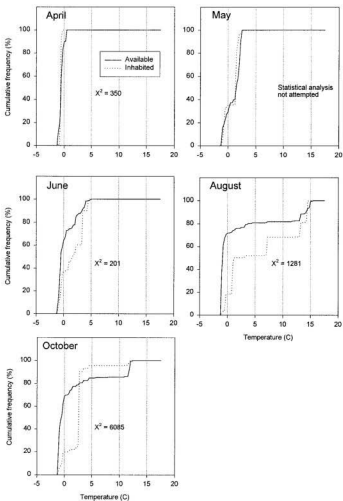
Figure 3.11 - Cumulative distribution functions for available temperatures (see text for estimation of temperatures) and cod density relative to temperature, for each survey. Chi-square results indicated. df=6 for all analyses other than April, when df=2. All p < 0.001.

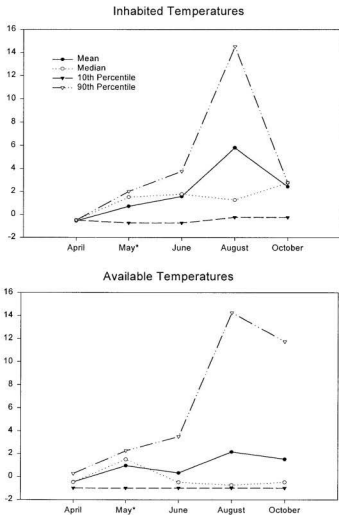Figure 3.12 - **(A)** Temperatures of the mean, median, 10th, and 90th percentiles of cod density distribution, by survey. Note that temperature profiles in the May survey were very few, and are not necessarily accurate representations of temperatures inhabited or available. **(B)** Temperatures available, by survey.
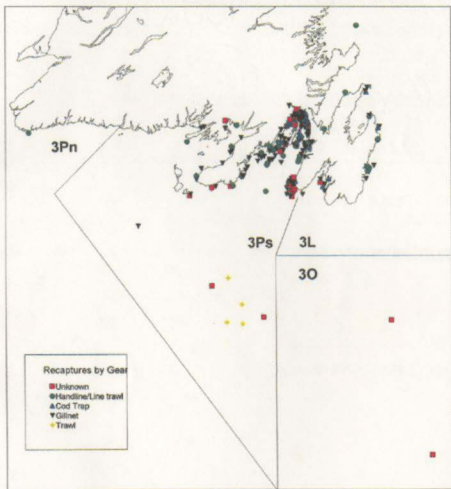
Figure 3.13 - Mark-recapture results for all experiments combined.

Summary and Conclusions

I have demonstrated that acoustics can provide a powerful and accurate tool for the study of cod distribution and behaviour in the coastal environment of Newfoundland, provided that measures are taken to account for systematic bias stemming from behaviourally-mediated variation in detectability. My work is the first to use sequential acoustic surveys in establishing the location and timing of cod spawning in coastal Newfoundland waters, and specifically to document substantial and repeated spawning at grounds within Placentia Bay. More directed studies may be useful in confirming some of the spawning behaviours hypothesized from the present results. Cod in Placentia Bay exhibit marked seasonal movement and distribution patterns, as well as seasonal shifts in habitat associations thought to relate to fish progressing from the spawning to feeding phases of their life history. Further work is required to determine to what extent the movements documented here represent return migrations and to what extent cod stray from Placentia Bay. As a whole, I believe that this study represents one of the most detailed and intensive investigations of coastal Newfoundland cod yet undertaken.

Templeman (1979, 1983) defines a stock as a group of fish whose spawning is spatially or temporally isolated from other stocks, and which shows particular distributional and migratory patterns. Templeman (1974, 1979) thus hypothesized the existence of a Placentia Bay stock, based on the recapture during the spring spawning period of many cod in Placentia Bay that were marked at and around Cape St. Mary's. Prior to my study,

the locations and timing of cod spawning in Placentia Bay were not known, although the presence of spawning cod in the bay had been documented (Thompson 1943; Hutchings et al. 1993; Davis et al. 1994). The repeated presence of cod spawning at particular locations in the bay supports the existence of a Placentia Bay cod stock. The existence of a Placentia Bay stock is further supported by the conclusions that cod migrating from Placentia Bay spawning grounds in spring return to the bay in fall, and that some cod remain resident within the bay year-round.

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