EVIDENCE FOR INSHORE SPAWNING OF ATLANTIC COD (GADUS MORHUA) IN TRINITY BAY, NEWFOUNDLAND, FROM 1991 TO 1993

R. KENT SMEDBOL

Evidence for inshore spawning of Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, from 1991 to 1993

by

© R. Kent Smedbol

A thesis submitted to the School of Graduate Studies

in partial fulfillment of the

requirements of the degree of

Master of Science

Department of Biology

Memorial University of Newfoundland

1994

St. John's Newfoundland

ISBN 0-315-96067-1

ABSTRACT

The objective of this thesis was to determine if northern Atlantic cod (*Gadus morhua*) spawn in Trinity Bay, Newfoundland. Prior to this study, only indirect evidence existed for inshore spawning by cod along the northeast coast of Newfoundland. Research reported here confirms that Atlantic cod spawn in Trinity Bay, Newfoundland, during the early summer on an annual basis. This conclusion is supported by evidence from three lines of investigation. These are 1) the observed progressive maturation of inshore cod from spawning to spent condition, 2) direct observation of a spawning aggregation of cod in Trinity Bay, and 3) the presence of recently spawned cod eggs (≤ 10 days old) in the bay. A spawning "window" in Trinity Bay from mid-June to early July is estimated for the period of 1991-1993. This timing of spawning was delayed relative to offshore spawning components of Atlantic cod at similar latitudes. A simple model was proposed to explain this delay based upon the temperature to which inshore cod were exposed during the winter. Predictions of oocyte development times in female Atlantic cod were in phase with observed spawning times. Predictions using cumulative degree-days calculated from monthly seawater temperature profiles were less able to explain the temporal component of the spawning window in Trinity Bay.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Joe Wroblewski, for his guidance and for supplying the necessary push when it was required. I would also like to thank my supervisory committee members, Dr. David Schneider, and Dr. George Rose. Wade Bailey, Bonnie Dean, Susan Marsh, and Martina Hickey provided valuable assistance during the field studies. Further thanks go to the crews of the C.F.V. *Northern Quest*, and the R.V. *Shamook*, for their aid and advice in data collection at sea, and to inshore fisherman Clarence Seward, who suggested the survey of Heart's Ease Ledge for spawning cod. Monetary support was received through a Graduate Studies Fellowship and from the National Sciences and Engineering Research Council of Canada (NSERC)/National Sea Products/Fishery Products International Industrial Research Chair in Fisheries Oceanography. The assistance of Bonnie Dean, Susan Marsh, and Martina Hickey, was supported by the Memorial University Undergraduate Career Experience Program (MUCEP).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Present models of spawning by northern Atlantic cod (*Gadus morhua*) found off the northeast coast of Newfoundland, in North Atlantic Fisheries Organization (NAFO) Divisions 2J3KL, describe the reproductive behaviour of fish which congregate near the offshore banks. Spawning occurs in the spring, predominately over the continental slope off southeastern Labrador (Templeman and May 1965; Serebryakov 1967; Templeman 1979; Fitzpatrick and Miller 1979) at water temperatures usually around 2-3° C (Fitzpatrick and Miller 1979; Rose 1993). Hutchings *et al.* (1993) demonstrated that spawning also occurs on the shelf, and supplied evidence of the presence of cod in spawning condition in inshore regions. There are anecdotal accounts of cod spawning in major Newfoundland bays (Thompson 1943; Graham 1922), but the occurrence has not been scientifically documented. This thesis provides conclusive evidence of spawning in Trinity Bay, and discusses the factors which affect inshore spawning. A model is offered to explain of why inshore spawning (summer) is delayed relative to the offshore spawning period (spring).

Recent sonic tagging and tracking studies have shown that some adult northern cod overwinter inshore in the Random Island area of Trinity Bay (Wroblewski *et al.* 1994a,c), instead of migrating to the offshore banks during the autumn (Templeman and Fleming 1962; Templeman 1974, 1979; Lear 1984). These findings are supported by tag and recapture studies of cod in the Random Island region by the Department of

Fisheries and Oceans (Wroblewski *et al.* 1994c). Also, Goddard *et al.* (in press), demonstrated that some cod use blood antifreeze glycoproteins to overwinter in < 0° C inshore waters.

It is not likely that cod which remain inshore during the winter will travel a hundred kilometres offshore to spawn in the early spring. So where do these cod spawn? In the same inshore waters where they overwinter, perhaps? Graham (1922) cited anecdotal reports of fishermen catching cod extruding eggs in Trinity Bay in the summer months. Thompson (1943) stated that any spawning that occurs in Trinity Bay takes place in May and June, and occasionally as late as August and September, but he did not supply any documentation of a spawning event. Templeman (1979) suggested that there may be some spawning of the northeast Newfoundland stock in May and June on the coastal shelves, during the inshore migration. None of these authors were aware that spawning fish may have overwintered in the bays.

The most recent published evidence of the presence of ripe and spawning stage adult cod in Trinity Bay during the spring is from the years 1967-68 (Hutchings *et al.* 1993). Indirect evidence for inshore spawning comes from a study by Anderson *et al.* (1993), who concluded that it was unlikely that 0-group juvenile cod (mainly larvae) sampled in 1985 in Trinity Bay were advected in from offshore spawning locations. In their study, some of the highest concentrations of cod eggs sampled were from a station in Random Sound, in Trinity Bay (E. Dalley, DFO, St. John's, pers. comm.).

Inshore spawning by cod has been witnessed and reported in other areas of the North Atlantic. McKenzie (1940) provided documentation of autumn spawning in Halifax Harbour, N. S. Cod spawning occurs annually in the fjords of Norway (Trout 1957; Jakobsen, T. 1987). Norwegian coastal cod usually account for approximately 5% of total catches of Arcto-Norwegian cod (Bergstad *et al.* 1987). The size of the stock component of Arcto-Norwegian cod that spawns on the Møre coast of Norway has been estimated at six-eleven million fish (Godø and Sunnanå 1984). It is apparent that inshore spawning is part of the reproductive biology of Atlantic cod. It therefore is expected to occur in Newfoundland inshore waters.

The first step of this investigation was to scientifically document where and when spawning by northern cod, *Gadus morhua*, occurs in the Random Island region of Trinity Bay, Newfoundland. Since cod spawn on the Northeast Newfoundland shelf in waters around 2-3° C (Fitzpatrick and Miller 1979; Rose 1993), I wished to test my hypothesis that inshore spawning occurs in waters > 0° C, specifically where shoal areas intersect the seasonal thermocline (0° C isotherm). Another objective was to test my second hypothesis that the temperature history of cod overwintering inshore delays the initiation of the spawning "window" relative to the temporal peak in offshore spawning for northern cod. The alternative hypotheses are :1) inshore spawning is random in spatial distribution, and 2) the initiation of inshore spawning is independent of temperature effects.

CHAPTER 1

Spawning cod in commercial catches from western Trinity Bay, 1991-1992

An investigation was undertaken to document the presence of spawning cod in Trinity Bay, and to define the timing of spawning. This involved sampling commercial cod landings in the Random Island area of Trinity Bay (Figure 1.1, 1.2a,b). Data was collected during the summer months (May to September) of 1991 and 1992. Complementary data were derived from experimental fishing in the same area during the spring of 1993. My purpose was to observe the progressive maturation of inshore cod to spawning condition.

Methods and Materials

Commercial landings of cod in the Random Island area were sampled during the summers of 1991 (May 29 to September 3) and 1992 (May 20 to August 29). Data collection occurred at dockside. In April, 1993, experimental fishing was undertaken in Northwest and Southwest Arm, near Random Island (Figure 1.2b) (day of year 110-122), aboard the chartered 55′ longliner, C.F.V. *Northern Quest.* A fleet of five gillnets with a total length of 457.5 m (250 fa) was deployed. Each net was 91.5 m (50 fa) in length, 3 m (1.7 fa) in width, with 13.8 cm (5.5 inch) mesh. Variables recorded in both data sets included date of capture, length, weight, sex, and gonadal condition. Length was recorded as forklength measurements (± 1 mm), and weight as whole wet body weight (± 50 g). State of sexual maturity was recorded following the criteria of Morrison (1990) (Appendix A). Fishing locations, sampling dates, and sexual condition of the catch are summarized in Appendices B and C. A maximum likelihood probit analysis was used to calculate the length at 50 % maturity for the commercial catch data sets, employing the PROC PROBIT procedure of SAS statistical software (SAS Institute 1988). The peak and range of probable spawning was estimated from the proportion of catch in spawning condition.

Results and Discussion: Evidence for inshore spawning

A total of 2656 cod were sampled from the commercial catches in 1991 and 1992. Adult cod (defined by length at sexual maturity) underwent a progression in reproductive development during the spring and summer (Figure 1.3, 1.4; see Appendices B and C for full data presentation). In May, most of the daily samples were ripening. As the summer progressed, more fish entered spawning condition. The greatest proportion of ripe fish appeared during the month of June. In August and September most of the adults in the sample were spent (as defined in Appendix A). These spent fish in the late summer reflected the influx (inshore migration) of post-spawning cod from the continental shelf.

The fish caught by experimental fishing in April 1993 were almost all stage 1 or 2 (ripening or in spawning condition) (Figure 1.5). A total of 77 cod were sampled, of which 23 were examined for sexual condition. These fish were caught near shore, in shallow, sub-zero °C seawater. The depth at bottom was approximately 34 m.

The length at 50 % maturity (M_{50}) was calculated from the Random Island commercial catch data. The M_{50} was 41.4 cm (n = 994) in 1991, and 48.3 cm (n = 1662), in 1992. The pooled M_{50} for 1991 and 1992 is 46.1 cm (n = 2656).

This investigation of commercial catches in the Random Island area clearly shows the presence of cod in spawning condition in the late spring. Experimental fishing in the early spring of 1993 in the waters of the Random Island region reveal that most adults are ripening, but not yet ready to spawn (Figure 1.5). This time series documents the development of gonadal tissue in adult cod present in Trinity Bay during the spring of three consecutive years. The data suggest that *Gadus morhua* spawn in the Random Island region of Trinity Bay from late June until mid-July.

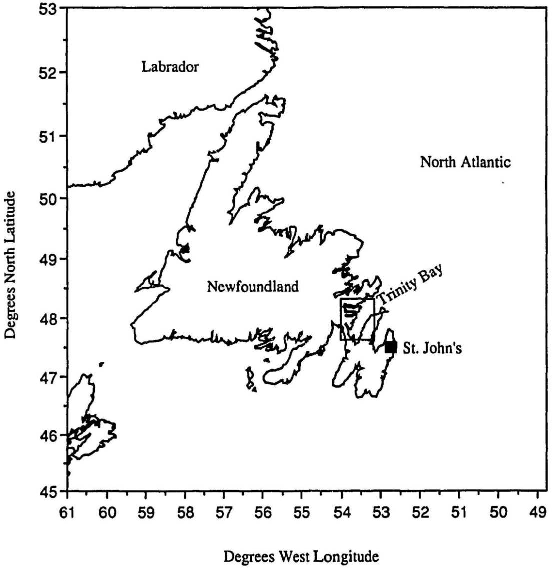

Figure 1.1: The study region is western Trinity Bay, Newfoundland

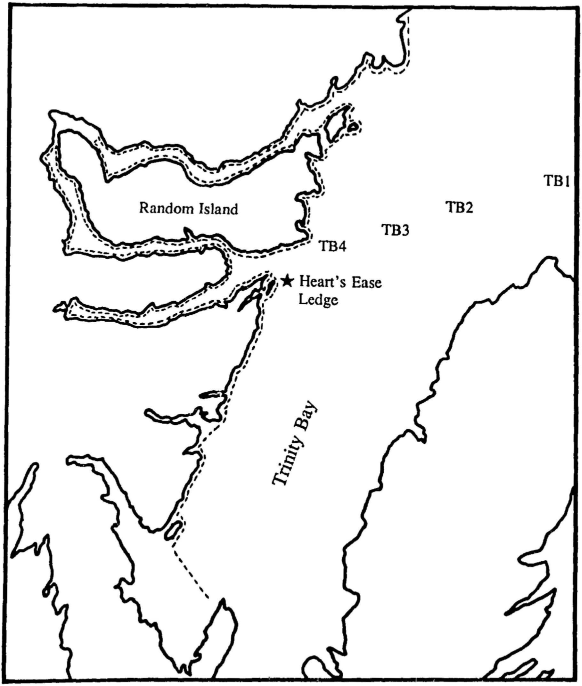

Figure 1.2a: Western Trinity Bay study region. The dashed line represents the path of the hydroacoustic survey in 1993. The position of ichthyoplankton survey stations TB1-TB4 on the transect across Trinity Bay in 1993 are indicated. The star marks the location where spawning cod were found in July 1993.

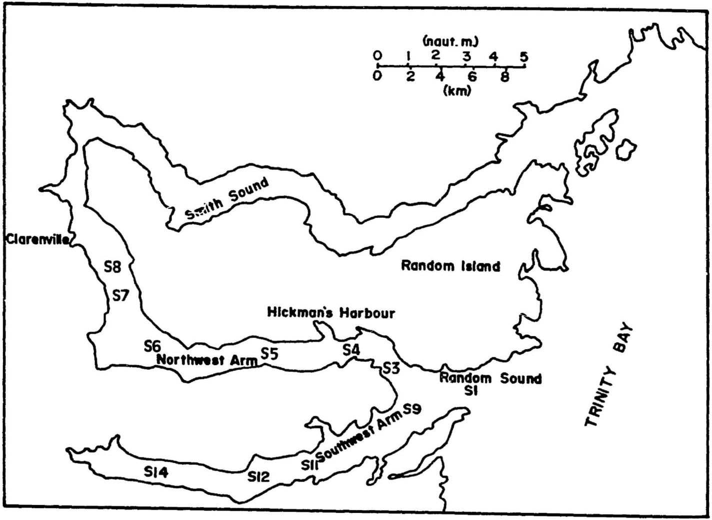

Figure 1.2b: The Random Island region of Trinity Bay, with the locations of the ichthyoplankton survey stations occupied in 1991 and 1993.

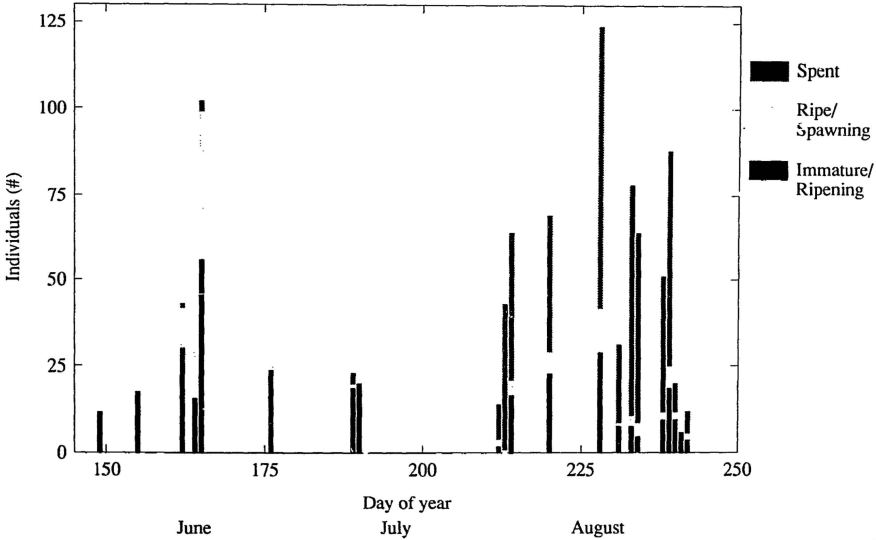

Figure 1.3: Gonadal condition of Atlantic cod (*Gadus morhua*) sampled from commercial catches in the Random Island area of Trinity Bay, NF, during the summer of 1991. n = 960

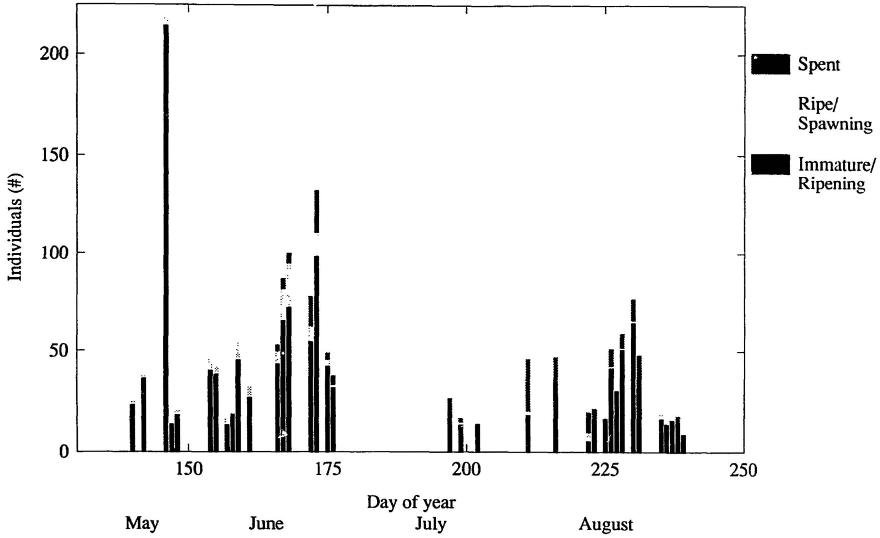

Figure 1.4: Gonadal condition of Atlantic cod (*Gadus morhua*) sampled from commercial catches in the Random Island area of Trinity Bay, NF, during the summer of 1992. n = 1662

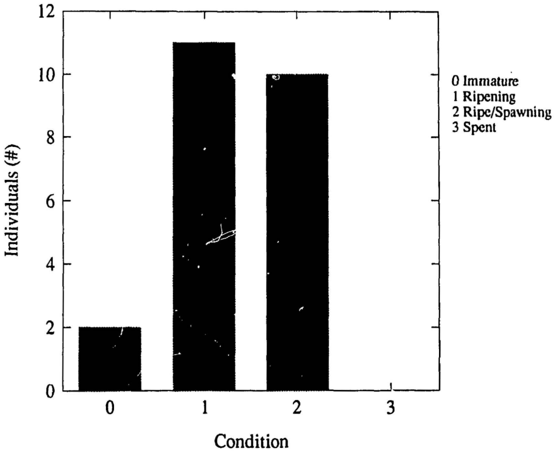

Figure 1.5: Gonadal condition of Atlantic cod (*Gadus morhua*) caught in Southwest Arm, Trinity Bay, NF, on April 22, 1993. n = 23

CHAPTER 2

Hydroacoustic survey for spawning cod in western Trinity Bay, 1993

Following the analysis of commercially caught cod, the next objective was to observe a spawning event by cod in Trinity Bay. The previous study (Chapter 1) was used to set the temporal range of this survey. In both 1991 and 1992, the highest proportion of stage 2 (ripe/spawning) fish was caught in the first half of June. Therefore, the timing of the survey was set for late June and early July.

Possible spawning locations were predicted according to several criteria. Offshore spawning of cod occurs in water temperatures around 3° C (Templeman 1979; Rose 1993). Also, adult cod held in captivity in flow-through seawater tanks at the Ocean Sciences Centre, Memorial University, spawn when water temperatures attain approximately 2° C (L. Crim, OSC, MUN, pers. comm.). Since gonad maturation in teleost fish is temperature dependent (eg. Crim 1982 and references therein), spawning may occur earlier in warmer water. Therefore, the survey focused on inshore areas that were > 0° C for a number of weeks. In summer the thermocline in Trinity Bay does not often extend below 50 m depth (Wroblewski *et al.* 1993). If the distribution of spawning in Trinity Bay is related to hydrography and bathymetry, then cod would spawn over shoals that intersect the thermocline.

Methods and Materials

The survey for spawning aggregations of cod was conducted from June 28 to July 9, 1993, aboard the R. V. *Shamook*. A number of locations that fit the foregoing criteria for the presence of spawning cod were examined using hydroacoustics (Figure 1.1, 1.2a). As a control, the surrounding areas also were examined to search for aggregations of cod at locations other than those posed by the hypothesis. A Biosonics # 105 Portable Sounder with a single beam transducer (120 kHz) was used. Acoustic data were recorded using a Biosonics # 115 Portable Chart Recorder. The ship's sounder, a Simrad EQ100 (38 kHz) was used to investigate depths greater than 100 m. Temperature profiles were recorded at sampling stations to a 0.001° C resolution, using a Sea-bird Electronics CTD, model SBE 19-03. Where spawning aggregations were discovered, cod were caught using the most suitable of several gear types: 1) # 36 Yankee otter trawl with 11.3 cm (4.5 inch) mesh, 2) gillnets with 13.8 cm (5.5 inch) mesh, or 3) Norwegian jiggers. For each individual the length, weight, sex, and gonad condition were recorded in the same manner as in the analysis of commercially caught cod (Chapter 1). In addition, blood samples were collected for the determination of blood plasma antifreeze levels (for methods see Goddard *et al.* 1992). All statistical analyses were performed with SAS statistical software (SAS Institute 1988). The criterion for statistical significance in all tests was set at a level of $\alpha = 0.05$.

Results

A group of spawning cod was discovered 1.8 km off Gooseberry Cove, Trinity Bay, over a shoal named Heart's Ease Ledge (Figure 1.2a). The aggregation was detected with hydroacoustics, and an echogram of the school is provided in Figure 2.1.

Winds were light during sampling, and the survey vessel drifted with the incoming tide. Mean current velocities are usually in the range of 3-5 cms^{-1} (Wroblewski *et al.* 1994b). The fish were aggregated at the peak of the shoal, and the school exhibited a very discrete edge. Some of these cod were actively spawning; individual males had running milt and females were extruding hydrated eggs as they were brought aboard the research vessel. Both mature and immature cod were present. All fish sampled from this assemblage were caught at depths shallower than 45 m. Water column temperature ranged from 8° C at the surface to 2° C at the bottom (Figure 2.2). The spawning concentration was located primarily in the 2-4° C range (Figure 2.2, 2.2).

This school was sampled four times over a six day period, from July 2-7. The proportion of individuals at each sexual stage changed over the four sampling periods (Figure 2.3) (Appendix D). On the first two sampling days the combined proportion of ripe/spawning adults to spent/partially spent adults was 0.38, and changed to 0.16 on the last two sampling days. The change in this ratio over the sampling period was significant when tested using the log likelihood ratio test (G-test: $G = 11.297$, $p = 0.0008$; $G_{adj} = 6.068$, $p = 0.0102$; $n = 53$, d.f. = 1). This statistic was employed because it is sensitive with relatively low sample sizes (Sokal and Rohlf 1981). Length and weight frequency distributions of the samples from this school are provided in Figures 2.4 and 2.5.

Twenty-six fish were captured and taken to Memorial University's Marine Science Research Laboratory (MSRL), Logy Bay. Several individuals spawned in holding tanks several days later. Fertilized eggs were collected and hatched in the laboratory. Blood antifreeze glycoproteins were not detected in these spawning cod (S. Goddard, MSRL, MUN, pers. comm.).

No other concentrations of cod were detected using hydroacoustics in the study area. Most of the western coast of Trinity Bay was surveyed (Figure 1.2a), together with a transect across the bay. However some cod were caught in Smith's Sound (Figure 2.1) using gillnets or jiggers (n = 22), and a capelin trap (n = 28). The scientific fishing licence allowed for the sampling of only 100 fish. Since the majority of these fish were shorter than the length at 50 % maturity (M_{50}) calculated from the Random Island commercial catch data, these cod were released without being sexed.

Two earlier surveys conducted in the region, from April 20-May 2 (day 110-122) aboard the C.F.V. *Northern Quest* (Figure 1.5), and from May 31-June 9, 1993 (day 151-160) aboard the R.V. *Shamook* (C. Taggart, DFO, St. John's, pers. comm.) did not detect spent adult cod. In these surveys, however, only fish that had died during collection were examined for sexual condition.

This discovery of a spawning aggregation over Heart's Ease Ledge near Random Island is the first scientifically documented observation of northern Atlantic cod reproducing in Trinity Bay. This event occurred within the temporal range for inshore spawning estimated from commercial catch data in the region, and at a location and ambient water temperature that were hypothesised as necessary environmental conditions. Prior to this discovery, only the presence of adult cod in spawning condition had been documented, using historical data (Thompson 1943; Hutchings *et al.* 1993). No recent information on the inshore spawning of cod exists, other than the data presented in this study.

Discussion: Spatial distribution of inshore spawning

The hypothesis that inshore spawning occurs in waters ≥ 0° C needs to be tested further. Only one spawning event was discovered in the survey. Nevertheless, this spawning school was discovered at a location (Heart's Ease Ledge) that fit the criteria of the hypothesis. No other aggregations of cod were detected by hydroacoustics in the study region, although areas with similar conditions (≥ 2° C) were surveyed. Further field work is necessary to determine the fine scale spatial distribution of spawning in the Bay.

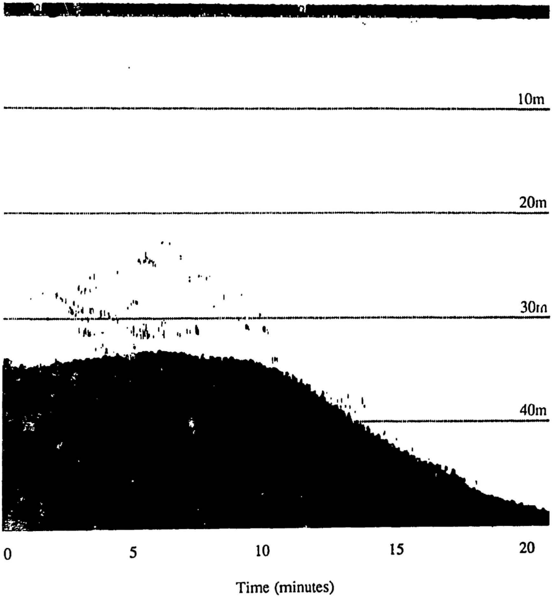

Figure 2.1: Echogram of a spawning aggregation of Atlantic cod (*Gadus morhua*) located over Heart's Ease Ledge, Trinity Bay, NF, on July 2, 1993 at 1645 hrs, NDST. The marks above the bottom represent cod. A Simrad EQ100 (38 kHz) echosounder was used. Depth is recorded in metres. The research vessel was drifting at a speed of approximately 10 cm s^{-1}.

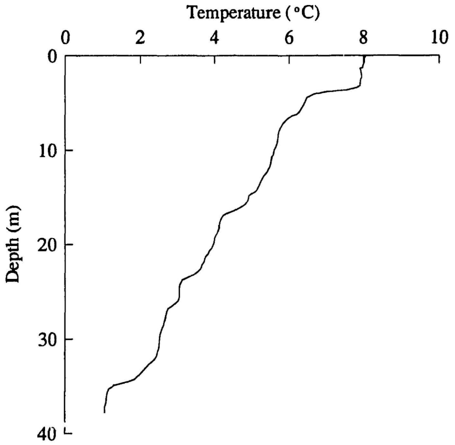

Figure 2.2: Temperature profile near the aggregation of Atlantic cod (*Gadus morhua*) spawning near Heart's Ease Ledge, Trinity Bay, NF, on July 2, 1993.

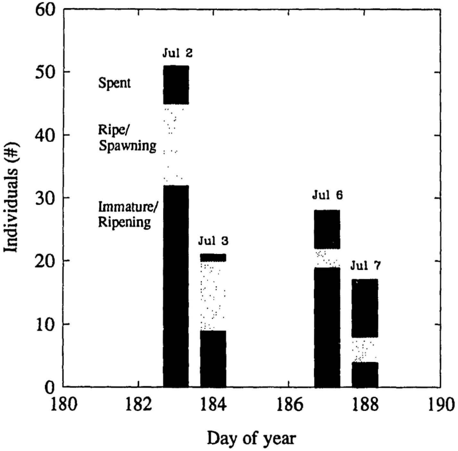

Figure 2.3: Gonadal condition of Atlantic cod (*Gadus morhua*) sampled from a spawning aggregation over Heart's Ease Ledge, Trinity Bay, NF, from July 2-7, 1993. n = 117

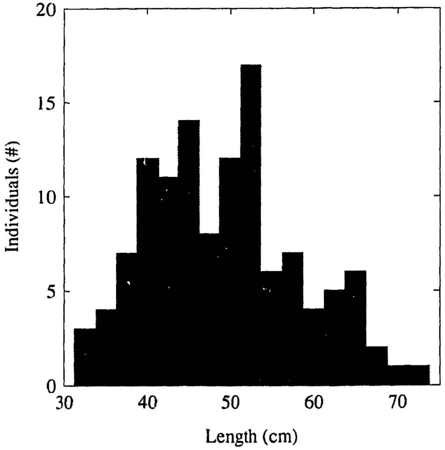

Figure 2.4: Length frequency distribution of Atlantic cod (*Gadus morhua*) sampled using Norwegian jiggers from a spawning aggregation over Heart's Ease Ledge, Trinity Bay, NF, from July 2-7, 1993. n = 121

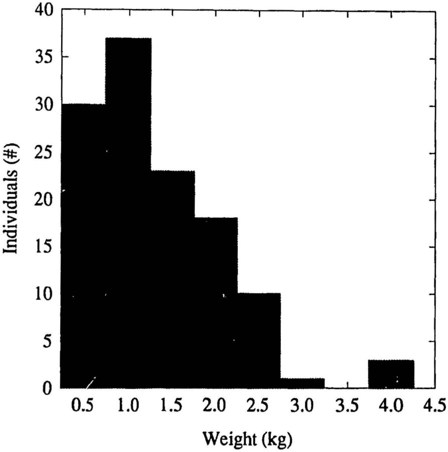

Figure 2.5: Weight frequency distribution of Atlantic cod (*Gadus morhua*) sampled using Norwegian jiggers from a spawning aggregation over Heart's Ease Ledge, Trinity Bay, NF, from July 2-7, 1993. n = 121

CHAPTER 3

Trinity Bay ichthyoplankton surveys, 1991 and 1993

The discovery of cod eggs and early stage larvae in the water column provides further evidence of spawning by Atlantic cod in the Random Island region. A survey of the ichthyoplankton in the Random Island region was carried out in 1991 and 1993. Cod eggs were present in the plankton. Back-calculations to the day of release were performed, and a spatial and temporal window of spawning was generated. This range was compared to the spawning window estimated from the time series of sexual condition in commercially caught adult cod in the Random Island area (Chapter 1). The possibility that cod eggs and larvae from offshore spawning drifted into the Bay was considered.

Materials and Methods

During the summer of 1991 (May to September) ichthyoplankton samples were collected at stations in Northwest and Southwest Arm, Trinity Bay (Figure 1.2b) at roughly monthly intervals. Samples were collected again from these stations June 29-July 6, 1993, together with samples from a transect across Trinity Bay. Ichthyoplankton samples were also obtained near the spawning aggregation of cod on July 2-6, 1993, near Heart's Ease Ledge. Plankton sampling was carried out with a 1 m ring net with 333 µm mesh and a 333 µm cod end. Oblique tows were carried out, with elapsed times that ranged from 7-25 minutes, and a tow velocity of 0.5-1.0 m s^{-1} (1-2 knots), with payout and retrieval rates of approximately 0.5 m s^{-1}. Maximum depth was 45 m. Plankton samples were fixed in a 4 % buffered formalin/seawater solution. Cod eggs were identified to stage of development following the criteria of Page and Frank (1989). Date of spawning of staged cod eggs was back-calculated using the relationship of egg stage duration to incubation temperature reported in Table 9 of Page and Frank (1989),

(1) $$D = a(T + 2)^{b}$$

where: D = egg stage duration (days)

T = incubation temperature (°C)

a, *b* = egg development parameters estimated from regression analysis.

Page and Frank (1989) provided separate equations for each egg stage. The stage-dependent developmental parameters (*a* and *b*) used in the back-calculations were taken from Table 9 of Page and Frank (1989). The reported ages correspond to the oldest eggs in the sample.

Temperature measurements used in the above calculation originated from a time series of temperature profiles for 1991 and 1992 that were recorded at Station 4, located in Northwest Arm, Trinity Bay (48° 05' N, 53° 42' W) (Figure 1.2b; Wroblewski *et al.* 1993). This station was selected as representative of the temperature field to which overwintering cod were exposed. Station 4 was sampled more frequently than the other stations in the study, and there was little variation in the temperature profiles of all stations around Random Island and Random Sound (Figure 1.2a) (see Wroblewski *et al.* 1993).

Early stage cod eggs cannot be discerned from early stage haddock (*Melanogrammus aeglefinus*) and witch flounder (*Glyptocephalus cynoglossus*) eggs (Fahay 1983). Such eggs are termed "chw". Since haddock or witch flounder are very rare in Trinity Bay relative to cod (R. Haedrich, MUN, St. John's, pers. comm.; Anonymous 1994), all chw eggs were considered to be cod eggs. The age reported for each sample was calculated from the oldest eggs collected at the site, and therefore represents a maximum possible age for the eggs from each station. Individual eggs from a sample may be much "younger" (as calculated from temperature-dependent stage duration relationships from Page and Frank 1989).

Results

Cod eggs and unidentifiable cod-haddock-witch eggs were found on all sampling dates, except for September, 1991 (Table 3.1, 3.2). Abundances varied between stations and sampling dates. The highest concentrations were sampled from station 6 in Northwest Arm, on June 29, 1993. Stations 6, 7, and 8 in Northwest Arm usually displayed the greatest abundance of eggs in the later sampling dates (July and August) of both 1991 and 1993. Overall, egg abundances ranged from $< 1 \times 10^{-3}$ to 0.35 $eggs \cdot m^{-3}$. Sampling near the spawning aggregation of cod over Heart's Ease Ledge, July 2-6, 1993 netted early stage eggs in concentrations at the middle of this range (Table 3.2). Samples from the transect across Trinity Bay on July 2, 1993 contained the lowest numbers of eggs recorded in either year, but the eggs were equal in age to eggs sampled in Northwest and Southwest Arm.

The highest proportion of young eggs was collected on the July and August survey dates at stations 6, 7, 8, in Northwest Arm and over the spawning aggregation over Heart's Ease Ledge in 1993 (Table 3.1, 3.2). The oldest eggs at these sites were 10-17 days old. The two months of July and August also provided the youngest eggs (10 days) in the study. This was evident at all stations and both sampling years. Back-calculations place the probable date of spawning of these eggs within the window for inshore spawning estimated in Chapter 2. The calculated time of origin of cod eggs sampled in July and August, 1991 ranges between June 30 and August 4 (calendar day 181-216). The oldest eggs found near the spawning aggregation over Heart's Ease Ledge have an estimated spawning date of June 18-June 26 (day 169-177).

Few cod larvae were collected in the survey. A total of 31 larvae and pelagic juveniles were caught in 1991, and in 1993 only one 22.5 mm pelagic juvenile cod was captured, that being near the spawning aggregation over Heart's Ease Ledge. All but one of the larvae collected in 1991 were less than 14.5 mm in total length. Eighty-one percent of the sample consisted of post-hatch larvae that were ≤ 7.0 mm in length. Most individuals were caught at station 6 in August (n = 9) and September (n = 3). Since larval abundance in the sample was so low, it was excluded from further analysis.

Discussion: Timing of inshore spawning

The spawning period estimated from the age of eggs is supported by independent studies. Methven and Badjik (1994) reported that the timing of the initial arrival and settlement of pelagic juvenile cod in coastal regions of Trinity Bay is relatively consistent (usually during the last 2 weeks of August and first two weeks of September). These authors reported two periods of high abundance of pelagic juvenile cod (August-September and October-November) observed at Bellevue, at the head of Trinity Bay. Back-calculations to the time of spawning of the August-September predicts a June spawning date; coincident with the Trinity Bay spawning period estimated in this study (day 165-195). Anderson *et al.* (1993) estimated spawning times through back-calculations from lengths of larval cod found in Trinity Bay. They computed peaks in cod spawning of May, 1984 (day 130-140), and late May/early June, 1985 (day 140-160). The authors concluded that an offshore source for these larvae was unlikely, and that they probably originated from inshore spawning in the Trinity Bay area. In contrast, Anderson (*et al.* 1993) computed an April peak in offshore spawning for the same years. Historically, Graham (1922) and Thompson (1943) have reported anecdotal evidence of cod spawning in Trinity Bay during the summer months (day 121-181), and Hutchings *et al.* (1993) review reports of the presence of adult cod in spawning condition in May/June, 1967 (day 121-181).

It is improbable that the young eggs found in the Random Island area were advected into the bay from offshore spawning grounds. Lear and Green (1984) proposed that cod eggs and larvae drift southwest from spawning areas on the northeast Newfoundland Shelf into the bays of northeastern Newfoundland. However, due to time of transport, and associated thermal experience, eggs released in these offshore locations would have hatched and become relatively large larvae in Trinity Bay. Also, the above pattern of drift suggested by Lear and Green (1984) is not in agreement with the results of numerical simulations of passively drifting eggs and larvae carried out by Helbig *et al.* (1992), who concluded that the northeast Newfoundland Shelf is a more probable nursery area. The authors stated that favourable storm tracks were required for large numbers of eggs and larvae to be advected into the bays of northeastern Newfoundland. Davidson (1994) used a three-dimensional advection-diffusion model to demonstrate that passively drifting cod eggs spawned near the shelf edge would be carried southward along the shelf by mean current flow, rather than to the coast of eastern Newfoundland. Only spawning locations on the Newfoundland shelf north of Cape Freels (eg 54°-55° longitude) would result in the drift of the majority of eggs into the bays of northeast Newfoundland.

Another possibility is that eggs present in the Trinity Bay survey may have originated from offshore cod spawning during their annual inshore migration. The age of the eggs, together with current velocities in the region makes this alternative less likely than local production. Mean current velocities of 3-5 cms^{-1} have been reported in the Random Island region of Trinity Bay (Yao 1986; Wroblewski *et al.* 1994b). Given the maximum range in age of eggs in the samples (10-17 days), the upper limit of possible drift is 73 km. This distance would place the origin of these eggs beyond the mouth of Trinity Bay. However, some of the lowest egg concentrations of the survey were found at stations TB1 to TB4 across Trinity Bay. If the eggs in question had originated from a patch at the mouth of the Bay, higher egg abundances would be expected in stations upstream along the path of drift.

Table 3.1: Summary of cod egg abundances (10^{-3}eggs·m^{-3}) (upper value) and ages (days) (lower value) from ichthyoplankton surveys in the Random Island area of Trinity Bay during the summers of 1991 and 1993. The egg ages represent the oldest eggs in the sample.

Station	May 1991	June 1991	July 1991	August 1991	September 1991	July 1993
1	0.01	5.70	2.81	17.1	0	28.4
	28	16	10	9	---	10
3	27.3	8.90	4.91	19.2	0	45.1
	28	22	17	15	---	10
5	5.01	5.91	7.51	36.8	0	67.1
	30	16	17	15	---	10
6	---	---	101.2	80.8	0	349.2
	---	---	17	15	---	10
7	0	4.38	---	---	---	75.7
	---	16	---	---	---	12
8	2.69	13.6	91.1	124.0	0	81.6
	28	22	17	15	---	10
9	35.7	91.1	17.4	10.0	0	---
	28	16	17	9	---	---
11	---	---	---	---	---	10.9
	---	---	---	---	---	10
12	12.7	19.9	1.76	5.40	0	1.29
	28	22	10	9	---	10
14	6.70	6.84	5.55	37.8	0	9.02
	28	22	17	11	---	10

Table 3.2: Cod egg abundances and ages from stations near an aggregation of cod spawning over Heart's Ease Ledge, Trinity Bay, July 2-7, 1993. The egg ages represent the oldest eggs in the sample.

Station	Egg abundance ($10^{-3}m^{-3}$)	Age (Days)
Heart's Ease Ledge (July 2)	61.1	10
Heart's Ease Ledge Downwind	69.2	10
Heart's Ease Ledge (July 6)	9.54	10
Trinity Bay 1	29.6	10
Trinity Bay 2	0.64	10
Trinity Bay 3	0.45	10
Trinity Bay 4	0.97	10

CHAPTER 4

A model for inshore spawning of northern cod in Trinity Bay, NF

In the previous chapters, I presented evidence for the occurrence and timing of spawning by cod in Trinity Bay. The proposed inshore spawning period, from mid-June through July, occurs later than spawning over the continental shelf. Templeman (1979) stated that the Labrador-East Newfoundland cod stock spawns from March through May, with spawning occurring later with decreasing latitude. He maintained that most of the spawning is over by June, but can be delayed in years of low temperatures. Cod overwintering in Trinity Bay experience lower water temperatures (< 0° C) (Wroblewski *et al.* 1994a) relative to the temperatures (0-4° C) on the continental shelf during the winter months (Templeman 1979; Rose 1993). I hypothesised that these lower temperatures may delay spawning in cod which spend the winter in Trinity Bay.

To test this hypothesis a model was developed to determine if ambient temperature could explain the timing of cod spawning in the Random Island region of Trinity Bay. Predicted times for inshore spawning were then contrasted with documented offshore spawning times.

Oocyte development in cod overwintering inshore

This model is adapted from relationships derived from laboratory studies reported by Kjesbu (1993). Kjesbu developed a method to predict the initiation of spawning in female Atlantic cod. The technique is based upon diameter measurements of the most mature oocytes as sampled by ovarian catheterization. These observations are then related to the time of first spawning.

Kjesbu used regression analysis to estimate the parameters of his model (a negative power function) in Kjesbu (1993), such that:

(2) $$y = 3.33 \cdot 10^{6}\, x^{-1.817}$$

where: y = time to commencement of spawning (days)

x = most mature oocyte diameter (μm) (300 μm < x < 750 μm)

Kjesbu conducted these experiments 9° C. The time to start of spawning (y) calculated from this equation was then calibrated to lower temperatures using the Q_{10} rule:

(3) $$R_2 = R_1 Q_{10}^{\frac{T_2 - T_1}{10}}$$

where: R_2 = developmental rate ($days^{-1}$) at temperature T_2 (°C)

R_1 = developmental rate ($days^{-1}$) between the time of observation of a certain most mature oocyte diameter and the initiation of spawning at 9° C.

Q_{10} = 2.0 (after Kjesbu 1989)

The temperature quotient (Q_{10}) is defined as the ratio of the rate of a reaction at a given temperature to rate at a temperature 10° C lower (Eckert *et al.* 1988)

The time to commencement of spawning in adult female cod was calculated using equation (2) of Kjesbu (1993), and then calibrated to lower temperatures using the Q_{10} rule (equation 3) (Table 4.1; Figure 4.1). The temperature measurements used to calculate oocyte development times in Trinity Bay originated from a time series of temperature profiles for 1991 and 1992 (see Wroblewski *et al.* 1993) that were recorded at Station 4, located in Northwest Arm, Trinity Bay (48° 05' N, 53° 42' W) (Figure 1.2b). This station was selected as representative of the temperature field to which overwintering cod were exposed. Station 4 was sampled more frequently than the other stations in the study, and there was little variation in the temperature profiles of all stations around Random Island (see Wroblewski *et al.* 1993).

Calculations demonstrate that lower ambient temperatures result in delays in the time of spawning. Not only does the ambient water temperature influence the spawning time, but the length of the exposure period is important as well. For example, at temperatures of 2-3° C, which approximates offshore overwintering thermal conditions (Templeman 1979; Rose 1993), it takes 159-171 days for an oocyte to grow from a diameter of 300 μm in the autumn to the onset of spawning in the following spring (Table 4.2). Atlantic cod initiate vitellogenesis from September to November (Kjesbu 1991). The average temperature in these waters at the thermocline (if present) at Station 4 in Northwest Arm, Trinity Bay, from November 1991 until the middle of June 1992 is 0.54° C. This value was used to calculate a spawning developmental period for inshore cod of 189 days (Table 4.2). This amounts to an estimated delay of 18-30 days when compared to the computed commencement of spawning at 2-3° C on offshore grounds.

These calculations using Kjesbu's laboratory spawning model provide support for the hypothesis of water temperature regulation of inshore spawning by Atlantic cod. Calculations were then performed for field data reported in Chapter 1.

Spawning development times in the Random Island region

With his oocyte development model, Kjesbu (1993) demonstrated that a simple power function provided adequately described his laboratory growth data. However, in the ocean temperature is not constant, but varies with time and depth. This consideration prevented the direct application of the growth parameters in Kjesbu's regression equation to this investigation. Therefore, an additive temperature model was developed because it would approximate the power function of temperature on growth, as evidenced in the oocyte development estimations of Kjesbu (1993).

To investigate in more detail the hypothesis that cold inshore temperatures induce a temporal delay of inshore spawning, data on the water temperatures in the Random Island study area were compiled and summarized for the time period of interest (1991-1993). The number of days in the region with sea temperatures > 0° C during the winter and spring preceding the summer spawning season were compiled as cumulative degree-days. This variable is often used in the literature to measure the length and "quality" of the growing season. For instance, cumulative degree-days have been used to model the temperature regulation of growth in leaves (Stewart and Dwyer 1994), and to predict the generation time in insect pests (Rock *et al.* 1993).

Four assumptions were made in the degree-day calculations. First, I assumed that adult cod always occupied > 0° C water when present. This may not always be true (see Wroblewski *et al.* 1994b). Therefore the calculations of degree-days may overestimate the length of exposure of cod to positive degree seawater. Second, I assumed that the effect of temperature upon time to spawning is additive in nature. Therefore, a cumulative degree-day model was used.

The third assumption was that food was not limiting to gonadal development. Qualitative observations of the 1991 and 1992 commercial catches provide some support for this assumption. Livers of cod were not reduced, nor were stomachs shrunken. Analysis of stomach contents on subsamples in each year revealed that the cod in the region were actively feeding on euphausiids and mysid shrimp, or capelin (see Howse 1993).

The final assumption involved photoperiod effects on spawning times. Trinity Bay lies at a latitude (48° N) that is similar to historical offshore spawning locations (ca 50° N) of the northeast Newfoundland cod stock (eg. Templeman 1979). Therefore, I considered the effect of photoperiod on the timing of spawning by cod to be equivalent in Trinity Bay and offshore spawning locations.

The temperature measurements used in the degree-day calculations are from Station 4, Northwest Arm, Trinity Bay (as in Chapter 3). Again, this station was chosen as representative of the area, and it was determined that the degree of variation between stations in the Random Island area was unimportant in terms of the relatively coarse sensitivity of the model and the infrequent biological sampling.

Temperature profiles were recorded on a monthly basis using a VEMCO Ltd. Sealog-TD temperature depth logger (± 0.1° C resolution), from March 1991, to August 1992. Data from fifteen months were considered. For each profile in the time series the temperature from the surface to the depth of the 0° C isotherm was averaged. If the water column was completely < 0° C, the average temperature for the entire profile was calculated. The monthly mean temperature was then multiplied by the number of days between the sampling day and the previous temperature record. This provides the degree-days over the period between temperature recordings.

(4) $$DD_t = \bar{T}_t \, [t - (t_{-1})]$$

where: DD = degree-days (°C-day) between recording dates

$\bar{T}_t$ = average temperature at time t (°C)

t = sampling date of temperature profile (day of year)

t_{-1} = previous sampling date (day of year)

Maximum and minimum degree-day values were calculated from Equation 4 (Figure 4.2), representing the range of possible spawning development degree-days in 1991 and 1992. These quantities were compared to documented spawning offshore in 1991 and 1992 (G. Rose, DFO, St. John's, pers. comm.; Rose 1993), as well as the historical average spawning times and temperatures reported in the literature (Templeman 1965, 1979; Myers *et al.* 1993) in Table 4.2. The cumulative degree-days calculated for documented offshore spawning (Rose 1993) in 1991 was 2.5 times greater than the maximum value calculated for the Random Island area (413-160° C·day). The ratio of the respective quantities in 1992 was only 1.1:1 (463-420° C·day). Even though there was a large difference in cumulative temperature degree-days between years in Trinity Bay, the timing of the inshore spawning window was the same in 1991 and 1992.

Environmental effects on inshore spawning

It is probable that a cumulative degree-day equation is too coarse a measure of the influence of ambient temperature upon the commencement of spawning in *Gadus morhua*. The incorporation of variation in the temperature field into the model was not an improvement over the oocyte development method. This lack of fit to the data may have been due to the low resolution of the temperature measurements. Small changes in ocean temperature lead to large variations in degree-day levels. The use of only one oceanographic station in the calculations may have inhibited the resolution of fine scale temperature variation. The temperature data may not adequately reflect the thermal experience of the cod. In addition, one of the assumptions of the model states that adult cod overwintering in the bay move to occupy > 0° C seawater as soon as the spring thermocline develops, and thus the model very likely overestimates the magnitude of degree-days that portions of the population actually experience.

Kjesbu's (1993) equations of temperature-dependent oocyte development provide estimates of spawning times that fit the observations much better than the cumulative degree-day method. Templeman (1979) and Myers *et al.* (1993) provide historic spawning times of northern Atlantic cod. The model predicts a delay in the beginning of the spawning period in Trinity Bay of at least 30 days compared to historical spawning offshore. In 1991, adult cod from the Random Island region were beginning their main spawning period on the day when offshore spawning (observed by Rose 1993) was nearly complete; a difference in spawning season of approximately one month. The oocyte model predicts a delay in the beginning of spawning in Trinity Bay in 1992 of approximately 18-30 days compared to similar calculations for offshore spawning (at 2-3° C). The initiation of offshore spawning was not observed in 1992, but the difference in the completion of spawning between inshore and offshore was about 10 days. In both 1991 and 1992, cod spawning in Trinity Bay did not commence until the most southerly components of offshore cod normally complete spawning. Model predictions of a delay in spawning by cod of 30 days are in phase with observed spawning delays of at least 30 days in 1991, and an absolute minimum of 10 days in 1992.

Supporting evidence for spawning delays arising from cooler temperatures is also provided by other field observations. Templeman (1962a) concluded that such a delay had occurred in 1961, because many fish examined from the coastal areas of 3L in July had not spawned. In 1971, spawning in 3L was apparently also delayed, with considerable spawning in June and July (Dias 1972). Recently, Hutchings and Myers (1994) concluded that interannual variation in the spawning time of cod was significantly associated with variation in water temperature prior to spawning in NAFO Divisions 3L and 3Ps. In contrast, Myers *et al.* (1993) found no obvious relationship between spawning or larval emergence time and sea surface temperature in northwest Atlantic cod, and Brander (1994) found no association between mean temperature and mean date of spawning of cod around the British Isles. Unlike cod that overwinter in Trinity Bay, however, cod on the northwest Atlantic shelf and around the British Isles are not exposed to ocean temperatures below 0° C, near *Gadus morhua*'s lower limit of temperature tolerance.

There are several possible reasons why Kjesbu's oocyte development model, with simplified temperature regime, is more effective than the cumulative degree-day method. One possibility is that the influence of degree-days is not additive in nature; a non-linear temperature effect is more probable. An alternative is the existence of a temperature "threshold", where adult cod ripen over the oceanographic winter, but delay spawning until a minimum ambient temperature is reached (eg. 2° C). If this alternative expresses the actual relationship, then a cumulative degree-day model would mask the development of such a threshold and its effects on the beginning of spawning. There are studies involving other species where spawning has been delayed in individual fish that were in spawning condition. The holding of maturity stage has been reported in female herring (*Clupea harengus*) (Ware and Tanasichuk 1990) and in female capelin (*Mallotus villosus*) (Forberg 1983). Wasserman and Smith (1978) state that full-grown oocytes can remain in condition of physiological immaturity for extended periods of time until they resume meiosis in response to the appropriate stimulus. Temperature is one such stimulus that may delay the maturation of oocytes and spermatocytes (eg. De Vlaming 1972; Crim 1982).

The behaviour of individual Atlantic cod overwintering in Trinity Bay may have influenced the fit of the oocyte development model to the observed spawning times. Goddard (*et al.* in press) have shown that individual cod in Trinity Bay experience different temperature regimes. They suggest that, beginning at the end of April, there is a progressive movement of cod out of the sub-zero bottom water and into the warming surface layer. Variations in temperature exposure of cod overwintering in Trinity Bay would lead to a range of oocyte developmental rates. This may shift the interannual peak time of cod spawning, but would have little effect on the time of initiation of spawning. It is also likely that individual fish have the ability to minimize temperature fluctuations by behavioural means.

Estimation of the spawning windows also may have been influenced by fish that had migrated in from offshore grounds and spawned in the bay. This migratory component of the spawning population would have experienced different overwintering conditions than cod in Trinity Bay. Such migratory cod would have had to arrive inshore relatively early in the spring (May) to have influenced the initiation of spawning in Trinity Bay. This is unlikely, as the inshore arrival of migratory cod usually has not been observed until June (Templeman 1979; Lear *et al.* 1986). In 1991, cod trap catches did not show the increase of daily landings, and the proportion of spent adults, indicative of the arrival of offshore cod, until July (Chen 1993; Rose 1993; Figure 2.3, this study).

The spawning of migratory fish may be a factor in Trinity Bay later in the spawning period. For instance, it is possible that the spawning aggregation may have been comprised, at least in part, of recently arrived individuals. If this occurred, it would not affect the initialization of the estimated spawning period, but might serve to lengthen the window into July, and thus shift the estimated time of "peak" spawning.

The effects of behaviour and immigration discussed above would only tend to change the variance in the timing of spawning, in that they would increase the length of the spawning window. They would not, however, affect the initiation of spawning in Trinity Bay, which would be driven by cod that overwintered in inshore regions, and moved up past the thermocline early in the year.

Table 4.1: The length of time until the onset of spawning by female Atlantic cod, *Gadus morhua*, derived from the relationship between oocyte development and water temperature (equations 2 and 3).

Oocyte diameter	Time to spawning (days)						
(μm)	9° C	3° C	2° C	1° C	0° C	-1° C	-1.5° C
300	105.00	159.15	170.57	182.82	195.94	210.00	217.41
350	79.00	119.74	128.34	137.55	147.42	158.00	163.57
400	62.00	93.97	100.72	107.95	115.70	124.00	128.37
450	50.00	75.79	81.23	87.06	93.30	100.00	103.53
500	42.00	63.66	68.23	73.13	78.37	84.00	86.96
550	35.00	53.05	56.86	60.94	65.31	70.00	72.47
600	30.00	45.47	48.74	52.23	55.98	60.00	62.12
650	26.00	39.41	42.24	45.27	48.52	52.00	53.83
700	23.00	34.86	37.36	40.05	42.92	46.00	47.62
750	20.00	30.31	32.49	34.82	37.32	40.00	41.41

Table 4.2: Spawning times and oocyte developmental period of Atlantic cod (*Gadus morhua*) in Trinity Bay and over the northeast Newfoundland shelf in 1991 and 1992.

Location	Spawning Window (day of year)		Average Temperature (°C)		Developmental Period (days)	
	1991	1992	1991	1992	1991	1992
Trinity Bay	165-195	165-195	---	0.54	---	189
NE NF Shelf (G. Rose 1993)	≤165*	≤185*	2.5	2.5	165	165
NE NF Shelf Historical Average (Templeman 1979; Myers *et al.* 1993)	90-164 (main spawning)		3.0	3.0	159	159

* - Dates of spawning for offshore shoals of northeast Newfoundland shelf cod in 1991 and 1992 represent the time at which 90% of the mature females in the sample are spent (G. Rose, DFO, St. John's, pers. comm).

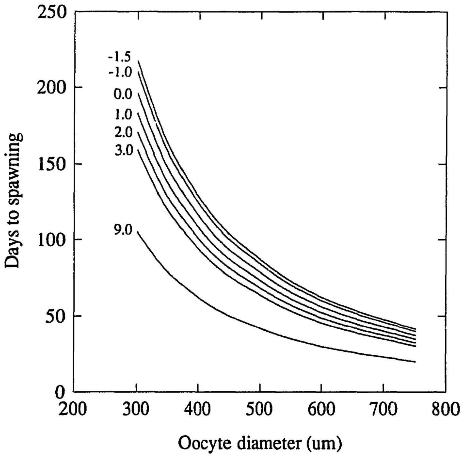

Figure 4.1: A simulation of the effects of water temperature (°C) on the initiation of spawning in individual Atlantic cod (*Gadus morhua*) females in relation to the most mature oocyte diameter, after Kjesbu (1993).

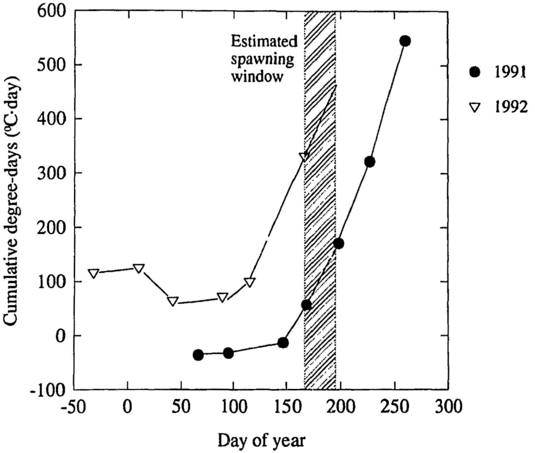

Figure 4.2: Calculated cumulative degree-days experienced by cod (*Gadus morhua*) overwintering in the Random Island area of Trinity Bay, during the years 1991 and 1992.

SUMMARY AND CONCLUSIONS

This study confirms that Atlantic cod spawn in Trinity Bay in the early summer on an annual basis. This confirmation is based on 1) the observed progressive maturation of inshore cod to spawning condition, 2) direct observation of a spawning aggregation of cod in Trinity Bay, and 3) the presence of recently spawned ($\leq$ 10 days) cod eggs in the study region. The hypothesis that the fine scale distribution of spawning is related to hydrographic and bathymetric features needs to be investigated further. Only one spawning aggregation of cod was discovered, but its location and time of spawning support the hypothesis. There is also some evidence to suggest that the temporal distribution of spawning by cod in Trinity Bay is influenced by temperature. The timing of the spawning window can be explained by the oocyte development model. However, the suitability of a cumulative degree-day model as an expression of the influence of ocean temperature on the temporal component of the spawning "window" is rejected.

Future investigations need to address the possibility of a threshold effect of temperature on cod spawning by studying fish in the field to determine when final oocyte maturation is activated. Future studies should monitor the reproductive condition of cod in Trinity Bay on time scales of weeks. Concomitant laboratory experimentation would allow the determination of the actual effect of temperature on the time of spawning, while controlling for other variables. Field surveys would provide a real time comparison of spawning *in situ* with the results of experimental manipulation. This method will increase the accuracy of interpretation of field data. In addition, this comparison may allow us to investigate the influence of other environmental variables, such as photoperiod and food availability, following the allocation of variance due to the effect of temperature.

REFERENCES

Anonymous. 1994. Report on the status of groundfish stocks in the Canadian Northwest Atlantic. DFO Atlantic Fisheries Stocks Status Report 94/4. DFO, Dartmouth, N.S. 61 p.

Anderson, J. T., E. J. Dalley, and J. E. Carscadden. 1993. Distribution and abundance of pelagic 0-group cod in inshore and offshore areas for the northern cod stock (NAFO 2J3KL). NAFO SCR Doc. 93/30.

Bergstad, O. A., T. Jørgensen, and O. Dragesund. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fish. Res. 5: 119-161.

Brander, K. M. 1994. The location and timing of cod spawning around the British Isles. ICES J. Mar. Sci. 51: 71-89.

Carr, S. M., A. J. Snellen, K. A. Howse, and J. S. Wroblewski. Mitochondrial DNA sequence variation and genetic stock structure of Atlantic Cod (*Gadus morhua*) from bay and offshore locations on the Newfoundland continental shelf. Mol. Ecol. in press.

Chen, X. 1993. Spatial and temporal patterns of landing variation in the Newfoundland northern cod inshore fishery. M. Sc. thesis. Memorial Univ. Newfoundland, 111p.

Crim, L. W. 1982. Environmental modulation of annual and daily rhythms associated with reproduction in teleost fishes. Can. J. Fish. Aquat. Sci. 39: 17-21.

De Vlaming, V. L. 1972. Environmental control of teleost reproductive cycles: a brief review. J. Fish Biol. 4: 131-140.

Davidson, F. 1994. Modelling advection of cod eggs and larvae on the Newfoundland shelf. M.Sc. thesis. Dept. of Physics, Memorial University of Newfoundland, St. John's, NF, 146 p.

Dias, M. L. 1972. Portuguese research report, 1971. ICNAF Redbook 1972, Part II: 71-78.

Eckert, R., D. Randall, and G. Augustine. 1988. Animal Physiology: Mechanisms and Adaptations. W. H. Freeman and Company, New York, NY, 683 p.

Fahay, M. P. 1983. Guide to the early stages of marine fishes occurring in the western north Atlantic ocean, Cape Hatteras to the southern Scotian Shelf. J. Northw. Atl. Fish. Sci. 4: 1-423.

Fitzpatrick, C., and R. J. Miller. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905: 14p.

Forberg, K. G. 1983. Maturity classification and growth of capelin, *Mallotus villosus* (M), oocytes. J. Fish Biol. 22: 485-496.

Goddard, S. V., M. H. Kao, and G. L. Fletcher. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 49: 516-522.

Goddard, S. V., J. S. Wroblewski, C. T. Taggart, K. A. Howse, W. L. Bailey, M. H. Kao, and G. L. Fletcher. Overwintering behaviour of adult Northern cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze protein levels. Can. J. Fish. Aquat. Sci. in press.

Godø, O. R., and K. Sunnanå. 1984. Spawning area and distribution of 0-group cod, *Gadus morhua* L., on the Møre coast, p. 519-532. *In*: E. Dahl, D. S. Danielssen, E. Mokness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen rapportser 1.

Graham, M. 1922. Investigations comprising observations on the natural history of the Newfoundland shore cod. Report to the Director of Fishery Investigations, Fisheries Laboratory, Lowestoft, UK.

Helbig, J., G. Mertz, and P. Pepin. 1992. Environmental influences in the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. 1: 39-56.

Howse, K. A. 1993. A modified migration model for Atlantic cod, *Gadus morhua*, off the northeast coast of Newfoundland. M.Sc. thesis. Dept. of Biology, Memorial University of Newfoundland, St. John's, NF. 58 p.

Hutchings, J. A., and R. A. Myers. 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21-31.

Hutchings, J. A., R. A. Myers, and G. R. Lilly. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquatic. Sci. 50: 2457-2467.

Jakobsen, T. 1987. Coastal cod in northern Norway. Fish. Res. 5: 223-234.

Kjesbu, O. S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. 34: 195-206.

Kjesbu, O. S. 1991. A simple method for determining the maturity stages of Northeast Arctic cod (*Gadus morhua* L.) by *in vitro* examination of oocytes. Sarsia 75: 335-338.

Kjesbu, O. S. Time of start of spawning in Atlantic cod (*Gadus morhua* L.) females in relation to fish length, condition, and temperature: experimental and field studies. Presented at the ICES 1993 Symposium on Cod and Climate Change, Reykjavik, Iceland.

Lear, W. H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northw. Atl. Fish. Sci. 5: 143-159.

Lear, W. H., and J. M. Green. 1984. Migration of the "northern" Atlantic cod and the mechanisms involved, p. 309-315. *In*: J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, N. Y.

Lear, W. H., J. W. Baird, J. C. Rice, J. E. Carscadden, and S. A. Akenhead. 1986. An examination of factors affecting catch in the inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1469: iv + 71 p.

McKenzie, R. A. 1940. Nova Scotian autumn cod spawning. J. Fish. Res. Board Can. 5:105-120.

Methven, D. A., and C. Bajdik. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquatic. Sci. 51: 78-90.

Morrison, C. M. 1990. Histology of the Atlantic cod, *Gadus morhua*: an atlas. Part three. Reproductive tract. Can. Spec. Publ. Fish. Aquatic. Sci. 110: 117 p.

Myers, R. A., G. Mertz, and C. A. Bishop. 1993. Cod spawning in relation to physical and biological cycles of the northern North-west Atlantic. Fish. Oceanogr. 2(3): 154-165.

Page, F. H., and K. T. Frank. 1989. Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 68-81.

Rock, G. C., R. E. Stinner, J. E. Bacheler, L. A. Hull, and H. W. Hogmire. 1993. Predicting geographical and within-season variation in male flights of 4 fruit pests. Environ. Ent. 22: 716-725.

Rose, G. A. 1993. Cod spawning on a migration highway in the northwest Atlantic. Nature (Lond.) 366: 458-461.

SAS. 1988. SAS/STAT users guide, release 6.03 edition. SAS Institute, Inc., Cary, N.C. 1028 p.

Serebryakov, V. P. 1967. Cod reproduction in the Northwest Atlantic. Trudy PINRO 20: 205-242. (Transl. from Russian by Fish. Res. Board Can. 1133, 1968).

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York, 859p.

Stewart, D. W., and L. M. Dwyer. 1994. A model of expansion and senescence of individual leaves of field-grown maize (*zea mays* L.). Can. J. Plant Sci. 74: 34-72.

Templeman, W. 1962a. Canandian research report, 1961. A. Subareas 2 and 3. ICNAF Redbook 1962, Part II: 3-20.

Templeman, W. 1974. Migration and intermingling of Atlantic cod, *Gadus morhua*, stocks of the Newfoundland area. J. Fish. Res. Board Can. 31: 1073-1092.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Bull. No. 14: 6-50.

Templeman, W., and A. W. May. 1965. Research vessel catches of cod in the Hamilton Inlet Bank area in relation to depth and temperature. ICNAF Spec. Pub. No. 6: 149-165.

Thompson, H. 1943. A biological and economic study of cod (*Gadus callarius* L.) in the Newfoundland area. Nfld. Dep. Nat. Resour. Res. Bull., No. 14, 160 p.

Trout, G. C. 1957. The Bear Island cod: migration and movements Fish. Invest. Lond. (2), 21(6): 1-51.

Ware, D. M., and R. W. Tanasichuk. 1990. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harrengus pallasi*). Can. J. Fish. Aquat. Sci. 47: 2375-2379.

Wasserman, W. J., and L. D. Smith. 1978. Oocyte maturation in nonmammalian vertebrates. In: *The Vertebrate Ovary*, (R. E. Jones, ed.), Plenum Press, New York, pp. 443-468.

Wroblewski, J. S., W. L. Bailey, and K. A. Howse. 1994a. Overwintering of adult Atlantic cod (*Gadus morhua*) in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 51: 142-150.

Wroblewski, J. S., S. V. Goddard, R. K. Smedbol, and W. L. Bailey. 1994b. Movements of Atlantic cod (*Gadus morhua*) above the spring thermocline in Trinity Bay, Newfoundland. J. Mar. Biol. Assn. U.K. in press.

Wroblewski, J. S., R. K. Smedbol, C. T. Taggart, and S. V. Goddard. 1994c. Behaviour of farmed Atlantic cod (*Gadus morhua*) released in Trinity Bay, Newfoundland. Mar. Biol. submitted.

Wroblewski, J. S., A. Collier, and W. Bailey. 1993. Ocean temperatures in the Random Island region of Trinity Bay, 1991-1992. The NSERC/ Fishery Products International/ National Sea Products Chair in Fisheries Oceanography, Data Report No. 1. Memorial University, St. John's. 48p.

Yao, T. 1986. The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmosphere-Ocean 24(3): 235-252.

Appendix A: Criteria for determining stages of sexual maturity of cod (*Gadus morhua*) (modified from Morrison 1990)

STAGE	FEMALE	MALE
0 - Immature	- Ovary small, translucent in small fish and opaque in larger fish.	- Testis small and translucent, more opaque in larger fish.
1 - Ripening	- Ovary firm, blood vessels visible. Ovary becomes opaque and cream in colour, individual eggs can be seen, blood vessels prominent.	- Testis larger and pink in colour, begin to turn white and translucent distally.
2 - Ripe and Spawning	- Ovary fills most of body cavity, translucent and opaque eggs, eggs easily released from vent.	- Testis white, spermatozoa easily released from vent in later part of stage
3 - Spent	- Ovary shrunken, soft and flabby with whitish cast.	- Proximal testis white and flabby, distal testis develops translucent border as ripe spermatozoa are removed.

Appendix B: Maturity condition of northern Atlantic cod (*Gadus morhua*) sampled from commercial catches in the Random Island area of Trinity Bay, NF, from May to September, 1991.

Date	Location	Sex	n	Condition 0	1	2	3
May 29	Brook Cove	Male	8	1	1	6	0
		Female	9	4	5	0	0
June 4	Canon Cove	Male	10	6	1	3	0
		Female	11	9	2	0	0
June 11	Island	Male	14	2	7	4	1
	Ledge	Female	29	6	14	9	0
June 13	Island	Male	9	1	0	8	0
	Ledge	Female	21	8	7	6	0
June 14	Gull Rock	Male	46	7	6	31	2
	Bight	Female	56	13	30	12	1
June 25	N/A	Male	5	4	0	1	0
		Female	11	8	1	2	0
July 8	Manual's	Male	8	2	2	1	3
	Island	Female	15	13	2	0	0
July 9	Big Island	Male	10	7	2	0	1
		Female	10	2	8	0	0
July 10	N/A	Male	10	6	3	1	0
		Female	17	4	12	1	0
July 31	Burn Point	Male	7	3	0	1	3
		Female	11	0	10	0	1
August 1	N/A	Male	6	1	1	1	3
		Female	8	0	1	0	7
August 2	Big Island	Male	16	0	0	0	16
		Female	27	0	0	1	36
August 8	N/A	Male	28	15	1	1	11
		Female	36	1	2	3	30
August 16	Brook Cove	Male	32	4	4	6	18
		Female	37	0	15	0	22

August 19	Brook Cove	Male	57	8	1	12	36
		Female	67	1	19	1	46
August 21	Brook Cove	Male	8	1	0	1	6
		Female	23	0	7	0	16
August 22	Brook Cove	Male	31	5	0	2	24
		Female	47	0	3	1	43
August 26	Brook Cove	Male	25	1	0	2	22
		Female	39	0	4	2	33
August 27	Brook Cove	Male	19	2	1	2	14
		Female	32	0	6	0	26
August 28	Brook Cove	Male	38	6	0	5	27
		Female	50	0	13	1	36
August 29	N/A	Male	9	4	1	1	3
		Female	11	0	5	1	5
August 30	N/A	Male	2	0	0	0	2
		Female	4	0	2	0	2
September 3	Brook Cove	Male	7	2	1	2	2
		Female	5	0	1	0	4

Appendix C: Maturity condition of northern Atlantic cod (*Gadus morhua*) sampled from commercial catches in the Random Island area of Trinity Bay, NF, from May to September, 1992.

Date	Location	Sex	n	Condition 0	1	2	3
May 20	Cannon Head	Male	15	5	10	0	0
		Female	10	2	8	0	0
May 22	Strong Island	Male	23	0	23	0	0
		Female	15	3	14	1	0
May 26	Strong Island	Male	91	8	82	1	0
		Female	108	37	68	3	0
May 27	N/A	Male	7	2	5	0	0
		Female	7	2	5	0	0
May 28	Gull Rock	Male	14	7	5	2	0
	Bight	Female	7	6	1	0	0
June 3	Cannon Head	Male	20	6	9	5	0
		Female	26	19	7	0	0
June 5	Gull Rock	Male	21	11	6	4	0
	Bight	Female	22	11	11	0	0
June 7	Hungry Cove	Male	8	3	3	2	0
		Female	9	2	6	1	0
June 8	Cannon Head	Male	9	4	5	0	0
		Female	10	5	5	0	0
June 9	Cannon Head	Male	20	4	9	7	0
		Female	34	13	20	1	0
June 11	Strong Island	Male	15	1	9	5	0
		Female	18	11	7	0	0
June 16	Gull Rock	Male	29	5	18	4	2
	Bight	Female	24	5	16	2	1
June 17	Gull Rock	Male	40	4	20	13	3
	Bight	Female	47	17	26	3	2
June 18	Gull Rock	Male	42	18	2	20	2
	Bight	Female	58	30	23	2	3

June 22	Gull Rock Bight	Male	27	7	4	8	8
		Female	51	31	13	0	7
June 23	Hungry Cove	Male	66	39	6	11	10
		Female	66	43	11	1	11
June 25	Gull Rock Bight	Male	19	13	3	1	2
		Female	30	23	4	2	1
June 26	Gull Rock Bight	Male	11	9	0	0	2
		Female	27	20	4	1	2
June 29	Gull Rock Bight	Male	15	7	4	2	2
		Female	10	8	2	0	0
July 16	Passenger's Cove	Male	7	6	0	0	1
		Female	20	15	0	0	5
July 18	Holloway's Rock	Male	3	3	0	0	0
		Female	14	11	0	1	2
July 21	Hungry Cove	Male	3	3	0	0	0
		Female	11	11	0	0	0
July 23	Passenger's Point	Male	4	4	0	0	0
		Female	2	2	0	0	0
July 29	Passenger's Point	Male	2	1	0	0	1
		Female	5	5	0	0	0
July 30	Passenger's Point	Male	21	8	0	1	12
		Female	25	9	2	1	13
August 1	Holloway's Rock	Male	6	5	0	1	0
		Female	3	3	0	0	0
August 4	Passenger's Point	Male	12	9	0	0	3
		Female	35	27	0	0	8
August 5	Holloway's Rock	Male	1	1	0	0	0
		Female	2	2	0	0	0
August 8	Holloway's Rock	Male	2	2	0	0	0
		Female	4	4	0	0	0
August 10	East Random Head	Male	10	3	0	4	3
		Female	10	3	0	0	7

August 11	Holloway's Rock	Male	13	10	0	0	3
		Female	9	5	0	0	2
August 13	Island Ledge	Male	5	5	0	0	0
		Female	12	11	0	0	1
August 14	Red Cliff	Male	26	20	1	1	4
		Female	25	21	0	0	4
August 17	Middle Ledge	Male	10	10	0	0	0
		Female	21	10	0	0	11
August 18	East Random Head	Male	24	19	1	1	3
		Female	35	30	1	0	4
August 20	East Random Head	Male	31	27	0	1	3
		Female	46	34	4	0	8
August 21	East Random Head	Male	18	15	2	0	1
		Female	30	13	3	0	14
August 22	Holloway's Rock	Male	2	2	0	0	0
		Female	5	2	0	0	3
August 25	Passenger's Point	Male	5	3	0	2	0
		Female	14	14	0	0	0
August 26	New Found Out	Male	5	5	0	0	0
		Female	9	9	0	0	0
August 27	Passenger's Point	Male	4	4	0	0	0
		Female	12	10	0	0	2
August 28	Holloway's Rock	Male	8	7	0	0	1
		Female	10	8	0	0	2
August 29	Holloway's Rock	Male	5	3	0	0	2
		Female	4	3	0	0	1

Appendix D: Maturity condition of Atlantic cod (*Gadus morhua*) caught over Heart's Ease Ledge, Trinity Bay, NF, from July 2-7, 1993. n = 117

Date	Numbers at maturity stage			
	0	1	2	3
July 2	23	9	13	6
July 3	9	7	11	1
July 6	13	2	3	6
July 7	6	0	4	9