FECUNDITY AND REPRODUCTIVE BEHAVIOUR OF ATLANTIC COD (GADUS MORHUA) USING ACTIVE AND PASSIVE ACOUSTICS

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FECUNDITY AND REPRODUCTIVE BEHAVIOUR OF ATLANTIC COD (*GADUS MORHUA*) USING ACTIVE AND PASSIVE ACOUSTICS

By

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1. What interests you about this particular position?

2. Would you outline any experience in your former position(s) that prepares you for this position?
   Follow-up: In which areas of the position would you feel most competent?

3. What experience have you had working with community-based volunteer organizations, particularly in the cultural sector?
   Follow-up: Tell us about your background in the performing arts (if no formal background, ask about interests or experiences in the performing arts)?

4. What additional training do you feel that you would require to manage the fine art collection responsibilities of this position and how would you go about getting it?
   Follow-up: Are there other areas of the position that you feel you would need some assistance or training?

5. What experience have you had in dealing with donors and potential donors?

6. Would you outline your experience in appraisal for retention of archival materials?

7. Information technology is pervasive in the library and archives world. Can you tell us about specific ways that you have used IT to do archival work?
   Follow-up: Are there ways in which you would like to bring IT to bear on your work which your previous employment history has not allowed you to explore?

8. What experience have you had in carrying out financial appraisal of archival materials?

9. Have you ever created exhibits: if so, tell us about them?
   Follow-up: If not, how would you go about planning one?

10. Have you ever provided library or archival instruction?
    Follow-up: Do you have teaching experience outside the archival setting – in the community?

11. What experience do you have in being responsible for a project or service?

12. What do you identify as major trends, challenges or problems in archives?
    Follow-up: What do you see as particular challenges of this position?

13. If you could create the ideal job in an archive for yourself, what would it be?
    Follow-up: What would be a pleasant day for you?
    Follow-up: What is your ideal work environment?

14. What makes a successful reference interview in your experience?

15. Have you ever performed a liaison function in any of your previous jobs?
    Follow-up: What makes for a successful liaison?

Extra questions, if needed

1. How did you prepare for this interview?

2. How do you describe your style of working with other people? How do you see the function of committees, task forces and similar groups?

3. You are staffing the archives desk at a time when no other archivists are available and someone asks a question you can't answer. What do you do?

4. A patron comes in and looks angry. She complains that she was given a wrong source of information several days ago. That piece of information wasn't given by you but by one of your co-workers. How would you handle the complaints? And how would you talk ~~with~~ to your co-worker about this issue?

Abstract

Fecundity-size-age relationships in Atlantic cod (*Gadus morhua*) for the late 1990s and early 2000s off Newfoundland and Labrador were compared with historical data and with similar relationships from cod stocks in Icelandic and Norwegian waters and in the, Baltic and the North Seas. For southern Newfoundland stocks that have fared relatively well in the 1990s and early 2000s, fecundity-size relationships did not differ from historical norms, although age at maturity was lower. In the highly stressed northern stock off Labrador, however, age at maturity was much lower than historical norms or in southern stocks, and fecundity much higher in small and young fish. Mortality rates were higher in the northern fish. These changes are explored in the context of changed life histories and the potential for rebuilding in stressed gadoid stocks.

For the behavioural component of the study, passive and active acoustic properties of an Atlantic cod spawning aggregation were observed at depths of 40-50 m at the Bar Haven grounds in Placentia Bay, Newfoundland in April 2003. Sounds recorded by hydrophone were identical to those recorded from captive spawning cod of the same stock, but heard less often. From a surface-mounted transducer (EK500; 38kHz), cod were observed to undertake relatively rapid periodic vertical migrations approximately half way to the surface (20-25 m) which resulted in the formation of cod columns. This work is the first to demonstrate the simultaneous incidence of cod sounding and vertical behaviours resulting in column formations during spawning.

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INTRODUCTION AND OVERVIEW

The Atlantic cod (*Gadus morhua)* is a large dominant predatory fish species which occurs throughout the continental shelf regions of the North Atlantic, forming many identifiable stocks with various behaviours (e.g., Robichaud and Rose 2004). In Newfoundland waters, cod is found from the coast to the continental shelf edge and at times to deeper waters beyond the shelf break in water temperatures ranging from approximately -0.5^{0}C to 8.5^{0}C. The Northern cod off Newfoundland and Labrador have historically been one of the largest stocks, supporting a commercial fishery for nearly 500 years (Scott and Scott 1988; Rose 2007). Until the 1960s before the industrialization of the fisheries, annual catches reached up to 400 000 tonnes. Since the mid-1960s onward, with the coming of heavily industrialized fleets which had catches up to 800 000 tonnes, this stock experienced catastrophic declines (Rose 2004). A general moratorium on the northern cod fishery was announced in 1992, however, the stock continued to decline and since the 1990s has been in a collapsed state (only a few percent of its historical biomass). Despite the low biomass and general lack of recovery of the northern cod to date, there have been limited commercial and recreational fisheries on the northeast coast in recent years.

Not all cod stocks experienced such severe declines or lack of response to fishery closures in the early 1990s. For example, the more southern population of cod from NAFO subdivision 3Ps did not experience as serious a collapse as the northern stocks. Cod from the southern waters generally have higher growth rates, greater reproductive potential, and overall better condition compared to cod from more northern areas (DFO 2008).

The spawning season for cod typically occurs in the spring but varies and is influenced by environmental factors, such as temperature (Scott and Scott 1988). Spawning begins in the north as early as February and ends in the south as late as December. Cod spawn at specific sites across their range, sites vary in location from offshore banks at depths to 500 m and to less than 50 m in coastal areas (Rose 1993). Cod are broadcast spawners and typically spawn in large aggregations (Robichaud and Rose 2002). Before spawning a female cod gonad contains three sizes of eggs; large translucent eggs approximately 1.5mm in diameter that are ready for release; middle-sized yolky eggs that will be released within weeks; and small whitish eggs (May 1967). In general, fecundity is defined as the reproductive output of an individual or number of offspring produced (Thain and Hickman 1994). There are three types of fish fecundity: *Relative fecundity* is the number of oocytes per unit body weight; *realized fecundity* is the total number of eggs spawned per season; and *potential fecundity* is the number of developing oocytes per female fish prior to spawning and is a measure of reproductive potential (Murua et al. 2003; Kraus et al. 2000). The eggs and sperm are broadcast by the adult, and the number of eggs produced is thought to increase with the size of the female (Scott and Scott 1988). Historically a 51 cm female would produce approximately 200 000 eggs per spawning period, while a female at 140 cm may have produced 12 million eggs (Powles 1958; May 1967). A relationship between gamete production and fish size was recognized in the 1800s and has been repeatedly documented (Earll 1880; Fulton 1890). May (1967) found strong correlations between fecundity and length, weight and age in cod sampled off

Newfoundland and Labrador as did Postolakii (1967) in what he called the Labrador cod stock (NAFO division 2J). North Atlantic studies by Postalakii (1967), McIntyre and Hutchings (2003) and Pinhorn (1984), have all demonstrated spatial differences in fecundity-growth relationships.

Despite hundreds of years of fisheries, still little is known about cod spawning behaviour. Differences in spawning behaviours among substocks and among ages and sexes have been reported (Robichaud and Rose 2002). Fisheries acoustics technology has had a major influence on commercial fishing and fisheries science. The use of active acoustics has lead to several observations of different spawning aggregation structures in cod stocks (Sund 1935; Rose 1993; Rose 2007). One of the largest spawning components of Atlantic cod in Newfoundland waters has been studied using active acoustics for several years, Placentia Bay, located on the south coast of Newfoundland (NAFO division 3Ps). Annual acoustic surveys using SIMRAD EK500 echo sounders have provided insights into stock migrations and spawning behaviours. Sonar tagging studies have been conducted to investigate the homing ability of Atlantic cod to specific spawning grounds. Robichaud and Rose (2002) found that approximately 50% of tagged cod returned to the same spawning ground in subsequent years and 25% of the tagged cod returned 3 years in a row. This study provided some of the first direct evidence that cod undertaking long-distance feeding migrations may home to a specific spawning location in consecutive years.

We have learned a great deal about cod spawning aggregations and migratory behaviour using active acoustics in surveys and sonar tagging studies. Cod are also known to have specific social behaviours related to spawning. Fish are known to produce low frequency sounds, especially members of the families Sciaenidae, Gadidae, Ictaluridae, Cyprinidae, Batrachoididae, Haemulidae, Lutjanidae, and Serranide (Luczkovich et al. 2008). The drumming muscle surrounding the swimbladder produces the sounds, and drumming muscle mass is thought to be correlated with sound production in cod (Rowe and Hutchings 2006). Passive acoustics studies have provided important insight into specific reproductive tactics. Laboratory studies have shown that cod have elaborate courtship behaviours (Brawn 1961a; Rowe and Hutchings 2006). Brawn (1961a) observed distinct courtship behaviours performed by males towards females, as well as territorial aggressive behaviour of males towards males. Both sexes can produce sound, although it is the males whose sound production is thought to play an important role in spawning, such as attracting females and holding territories (Brawn 1961b). As spawning is the first step towards recruitment and rebuilding cod stocks, there is a continuing interest in the specific behaviour of spawning.

The sampling sites for this study were areas that have been intensively studied since the mid 1990s. There were two offshore sampling sites for the fecundity work: Hawke Channel and the Bonavista Corridor. Hawke Channel lies within NAFO subdivision 2J between Hamilton Bank and Belle Isle Banks, and holds one of the largest known concentrations of cod in the northern range. Acoustic trawl surveys and fisheries oceanographic research has been conducted in the area since 1994. The Bonavista Corridor (3KL) straddles the boundary between NAFO subdivisions 3L and 3K and is the most southern migration route of northern cod. The Corridor held the last large offshore spawning aggregation of northern cod in the early 1990s (Rose 1993). Two inshore sites were utilized: Smith Sound, Trinity Bay and Bar Haven, Placentia Bay. Smith Sound is a fjord and currently holds the largest known spawning concentration of coastal northern cod. Bar Haven currently holds the most consistently used spawning ground in Placentia Bay (e.g., Lawson and Rose 2000; Windle and Rose 2005) and was the *in situ* site for the behavioral work as well as a site for fecundity estimation.

My thesis has several objectives, firstly to quantify the potential fecundity of Atlantic cod and its relationship with growth parameters in three major management areas, and then to compare results with historical data from the same stocks as well as other cod stocks from across the North Atlantic. Secondly, to investigate the theory of life history co-variation of traits within these specific stocks. For the behavioural component of the study, the aim was to investigate the natural movements and behaviour of cod spawning as well as to investigate the natural movements and behaviour of cod spawning in the lab and in the wild.

Thesis Overview

In this thesis I investigated two approaches to studying cod reproduction. In the first component I investigated the relationships in cod stock fecundity off Newfoundland and Labrador and used historical modeled data of fecundity-size relationships to compare the life histories of Newfoundland cod stocks with stocks from Iceland, Norway, Baltic and the North Sea. The temporal changes observed in the Newfoundland stocks are discussed in the context of changed life-histories and rebuilding in stressed gadoid populations. The second component of the thesis focussed on spawning behaviour of cod. I used passive and active technologies to investigate movement behaviour associated with spawning as well as sound production *in situ* in the wild and in the lab in *ex situ* studies. I discuss the patterns of the behavioural results, how they support previous work as well as provide new information for spawning behaviour in wild cod.

CO-AUTHORSHIP STATEMENT

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.

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Chapter 3 (Fudge and Rose) is in press for the ICES Journal of Marine Science Special Issue based on the Proceedings of the Symposium on the Ecosystem Approach with Fisheries Acoustics and Complementary Technologies (Bergen, Norway, June 2008).

1 CHAPTER 1: CHANGES IN FECUNDITY IN A STRESSED POPULATION: NORTERN COD (*GADUS MORHUA*) OFF NEWFOUNDLAND

1.1 Abstract

Recently determined relationships in stock fecundity off Newfoundland are compared with historical data from Newfoundland, Iceland, Norway, Baltic and the North Sea and are used to establish baseline relationships between fecundity and size at age in Atlantic cod (*Gadus morhua*). A total of 200 prespawning female cod were sampled in 1999 and 2003 in three Northwest Atlantic management areas. For southern Newfoundland stocks that have fared relatively well in the 1990s and early 2000s, fecundity-size relationships did not differ from historical norms, although age at maturity was lower. In the highly stressed northern stock off Labrador, however, age at maturity was much lower than historical norms or in southern stocks, and fecundity much higher in small and young fish. Mortality rates were higher in the northern fish. I discuss these changes in the context of changed life histories and rebuilding in stressed gadoid stocks.

1.2 Introduction

Fecundity is a fundamental property of reproductive potential. Despite this importance, and the long history of Atlantic cod (*Gadus morhua*) fisheries in the North Atlantic, there have been relatively few fecundity studies on this species. The first studies were done by Earll (1880) and Fulton (1890), and later in the 20th century by Powles (1958). In the northwest Atlantic, May (1967), Postolakii (1967) and Pinhorn (1984) provided estimates of fecundity for several stocks. More recently, many stocks off Newfoundland and Labrador have experienced exceptional declines in biomass and remain at all time low levels (e.g., Lilly et al. 2005). Despite evidence of change in life history characteristics such as depressed age at maturity (Olsen et al 2004), growth (Dutil et al. 1999) and lower condition (Rose and O'Driscoll 2002) there has been no reassessment of historical fecundity information for these stocks.

In general, fecundity is the reproductive output of an individual, or number of offspring produced (Thain and Hickman 1994). There are three main types of fish fecundity described in Murua and Saborido-Rey (2003) and Kraus *et al.*(2000): *Relative fecundity* is the number of oocytes per unit body weight; r*ealized fecundity* is the total number of eggs spawned per season. And *potential fecundity* is the number of developing oocytes per female fish prior to spawning.

The objective was to quantify the potential fecundity of Atlantic cod and its relationship with growth parameters in three major management areas. I then compare the results with historical data from the same stocks and from other cod stock areas across the North Atlantic.

1.3 Materials and Methods

Study areas

Cod fecundity was investigated within three populations in NAFO (Northwest Atlantic Fisheries Organization), sub-divisions 2J, 3KL and 3Ps (Figure 1.1). Hawke Channel in sub-division 2J is located between Hamilton and Belle Isle Banks, and was the northernmost sampling site. Acoustic trawl surveys and fisheries research have been conducted in this area since 1994 (e.g., Anderson and Rose 2001). Samples from 3KL were taken from two areas; the offshore site, Bonavista Corridor, straddles the southeast limit of 3K and the northeast boundary of 3L. The Bonavista Corridor is the most southern migration route of northern cod and held the last large spawning aggregations in the early 1990's (Rose 1993). The inshore site, Smith Sound, Trinity Bay (Figure 1.1A) is a fjord within sub-division 3L and currently holds the largest known concentration of over-wintering northern cod, estimated at 26, 000 tons in 2001. The cod that migrate along the Bonavista Corridor cross the 3K and 3L sub-division boundary lines, hence these areas were combined into 3KL for analysis. The third and final sampling area was Placentia Bay (Figure 1.1B), which forms part of the inshore component of the sub-division 3Ps stock. Of all the cod stocks in the Northwest Atlantic, 3Ps rebounded the quickest after rapid decline in the late 1980s. This stock has had a small commercial fishery (average TAC of 15, 000 tonnes per year) since 1997. Placentia Bay cod have been under intensive study since 1996 (e.g. Lawson and Rose 2000, Mello and Rose 2005, Rose et al. 2008).

Collections and preparation

Before egg release, a female cod gonad contains three sizes of eggs: large translucent eggs approximately 1.5 mm in diameter which are ready for release; middle-sized yolked eggs which will be released within weeks; and lastly small whitish eggs (May 1967). The large and middle-sized eggs are first generation eggs and will be released in the current spawning season. The small whitish eggs are second-generation eggs, which will not be released until succeeding spawning years. Release of the large translucent eggs begins soon after oocytes become hydrated, therefore in order to measure fecundity gonads must be sampled before any hydrated eggs are visible (Raitt 1932). Female cod were sampled prior to and during the spawning seasons of 1999 and 2003. In 2J and 3KL, fish were sampled with a research otter trawl (Campelen 1800), whereas samples were caught using handlines in 3Ps. Standard lengths, and whole, gutted, liver and gonad weights were recorded, with otoliths taken for aging. Fish sizes varied between areas (Table 1.1). In all analyses, gutted weight was used as opposed to whole weight to reduce bias resulting from seasonal changes and variations due to feeding. Extracted ovaries were cut down the middle and placed in a labelled jar, Gilson's fluid (Simpson 1951) was then added to cover the ovary, to aid in the breakdown of connective tissues and the separation of eggs from each other and the ovarian wall. Samples were topped up with fluid and agitated once a week to help speed the breakdown process, then were left for an average of three months before processing. When separation was complete, each sample was passed through a series of interlocking sieves of differing mesh sizes (1.4 μm, 1.0μm, 500μm, 300μm, 180μm, 125μm respectively). Remnant ovarian wall tissue and second-generation eggs were discarded then eggs were stored in jars with 90% ethanol until processed.

Subsampling and counting

Most methods used to measure fecundity involve taking a subsample of the total volume of eggs in an ovary. The motoda splitter (Motoda 1959) is primarily used for plankton subsampling, but has been used in fecundity studies (Allian 1999) and was used in the present study. The splitter produces subsamples by successive fractionations. Counts were done manually using a stereomicroscope and handheld counter: two subsamples from each gonad were counted three times. All samples met the required < 5% variation. The combined total 6 counts were averaged and used in the estimation for the total number of eggs in that sampled ovary. The potential fecundity per fish was determined by the following equation:

$$N_{eggs} = N_{eggs\ in\ subsample} \times \text{subsample split fraction} \quad (1)$$

For comparison, 6 egg samples of random sizes were subsampled a second time using the whirling vessel. Average difference of potential fecundity estimates between the Motoda Splitter and the Whirling vessel was 10%. Using a paired t –test, no significance difference was found in the determined fecundities between the two methods ($p>0.05$, $\alpha = 0.05$).

Fecundity analyses

Initially all data were pooled and a series of regressions were performed to determine the presence or absence of general relationships between fecundity and specific measured growth variables. Fecundity was investigated in relation to fish length , age, gutted weight, and liver and gonad indices. Liver index (LI) and gonad index (GI) are defined as:

$$LI = \text{liver weight} / \text{total weight} \quad (2)$$

$$GI = \text{gonad weight} / \text{total weight} \quad (3)$$

Fecundity was also investigated in relation to condition (Fulton's K). Fulton's Condition examines the relation between length and weight and is used to quantify the state of well-being of a fish (Wooton 1990), and is measured as:

$$K = \text{total weight (kg)}/\ \text{length}^3\ \text{(cm)} \qquad (4)$$

Significant relations were further explored through a series of 3-factor ANCOVAs, after which the data were categorized by study area. Results include samples from 1999 and 2003 except for the offshore area of Bonavista Corridor within 3KL (Figure 1.1). Data were transformed into base 10 logarithms to standardize variance and facilitate historical comparisons (eg. Pinhorn 1984).

A comparison of linear regressions of fecundity-weight relations of cod from different geographical regions of the North Atlantic was also performed. Available data and original equations were gathered from 11 published studies, representing Labrador, North Sea, Norway, Baltic and Iceland (Table 1.2).

1.4 Results

The overall range of lengths, weights and ages of cod sampled was 40-94 cm, 0.355-4.61 kg, and 4-14 years, respectively (Table 1.1). On average, mature female cod sampled from 2J were of lesser length, weight and age than those at the other sites in both sampled years (Table 1.1, Figures 1.2, 1.3, 1.4); mature 2J cod were all less than 7 years of age (Figure 1.3).

Regression analyses indicated the strongest predictors of fecundity were weight, length and age respectively (Table 1.3). The regressions of fecundity on these variables were significant in all regions, with the amount of explained variation ranging from 31 to 72 %. Fecundity was also associated with Fulton's K in all regions ($p < 0.05$). No overall association was evident between fecundity and liver (LI) or gonad index (GI), however, fecundity was significantly correlated with liver index in 2J, and to gonad index in 3Ps. Month was factored into a GLM model to control for seasonality. It was found that the relation of fecundity to gonad index did not change across months sampled in 2J, 3KL or 3Ps.

Fecundities differed significantly between the two years of sampling (1999 and 2003) by a factor of 2 to 4. In a 3–way ANOVA using year, region and gutted weight as factors, year and region were significant effects but did not interact ($p=0.08$). Hence for all subsequent analyses data were pooled by year.

Analysis of covariance indicated that the slopes of the regression lines of fecundity on length, age, and weight differed significantly between 2J, 3KL and 3Ps (p`*s*<0.01). Among the years the relationships were strongest in 3Ps cod (Table 1.3). Cod in 2J had much higher fecundities at small sizes and younger ages than did cod from other regions. In 2J and adjacent 3KL, fecundities differed greatly from those reported by May (1967) and Postolakii (1967). At age 5 cod had fecundities similar to those at age 12 historically (Figure 1.5), and with cod six times their size (Figure 1.6).

Additional fecundity and weight data for 5 North Atlantic cod populations were examined (Labrador area, NAFO subdivisions 2J-3K, Baltic (east and west), North Sea, Iceland, and Norway (Barents Sea)) (Table 1.2, Figure 1.7). Where more than a single fecundity relationship was available for an area (except Norway), weighted averages were used to produce a representative regression. Due to large variance between the samples from Norway, these data sets are separated, but both indicate some of the highest weights and fecundities overall. Historical data from 863 female cod from 2J-3K (Postolakii 1967 and May 1967) have the lowest fecundities (and smallest weights) of all the stocks examined, but in the present study cod from this area had much higher fecundities at the same weights.

1.5 Discussion

Results of the present study indicate that potential fecundity of Atlantic cod is moderately correlated with weight, length, and age and less so with somatic and liver condition. A relationship between gamete production and fish size was recognized in the 1800's and has been continuously documented (Earll 1880; Fulton 1891). May (1967) found strong correlations between fecundity and length, weight and age in cod sampled off Newfoundland and Labrador as did Postolakii (1967) in what he called the Labrador cod stock (2J).

Spatial variations in cod fecundity were evident in all three management area locations, as well as between offshore (Bonavista Corridor) and inshore (Smith Sound) cod groups. These differences parallel others in group states and life histories. Cod in the northern offshore regions are not seen beyond age 7 and occur at relatively low densities, while inshore cod that overwinter in Smith Sound from the same stock (3KL) consist of a wide size range (35-120 cm) and ages reaching 15-20 years and occur at very high densities

(Rose et al. 2000b; DFO 2004a). North Atlantic studies by Postolakii (1967), McIntyre and Hutchings (2003) as well as studies for Newfoundland cod stocks by May (1967) and Pinhorn (1984) have all demonstrated differences in fecundity–growth correlations between areas. Temporal variation in fecundities between 1999 and 2003 in Smith Sound cod may be related to reproduction suppression or atresia (Rideout et al. 2000). Rideout and Rose (2006) found that for cod sampled from Smith Sound during 1999-2004, the 1999 sample had the highest rate of skipped spawning. This event was positively correlated with population age structure and diet.

The strongest fecundity to size, age and condition relationships were evident in cod from Placentia Bay, where stock rebuilding following a fishing moratorium in 1993 enabled reopening of a modest commercial fishery in 1997 (average harvest about 15, 000t/yr). In most respects the 3Ps cod stock, is the northwest Atlantic stock in the best condition. (Lawson and Rose 2000; DFO 2004b). This stock has the biomass, migrations, growth rates, reproductive potential, and condition closer to historical norms than in the formerly larger cod stocks on the Grand Banks and to the north (Sherwood and Rose 2005). In terms of fecundity our results differ little from those of Pinhorn (1984) for this area.

In comparison, cod life histories in the northern offshore areas (Hawke Channel and Bonavista Corridor) bear little resemblance to historical norms. Cod here historically matured at earlier ages and smaller sizes than cod inhabiting southern waters (Fleming 1960, May 1967, Lilly et al. 2005). However, lengths-at-age and weights-at-age declined in the 1980's and early 1990's, with the greatest declines occurring in the northernmost extents of the stock. The age composition of this population has become extremely truncated and since the early 1990's very few cod older than 6 years have been found

(Lilly et al. 2005). Furthermore, an increasing proportion of these fish are maturing at even younger ages. In the early 1960's, 15% of females were mature at 6 years of age: this increased to 50% in the 1970's to 80's and to 80% in the 1990's (Fleming 1960; Lilly et al. 2005). Currently, the average age at maturity for cod in 2J is 4-5 years whereas historically it was 6-7 years (this paper; Lilly et al. 2000). Cod sampled by May in the mid-1960's from offshore 2J-3K in similar areas to the present study were of greater age and size ranges (5 - 15 yrs; 3 - 9 kg, respectively) than were cod found in this study (4 – 6 yrs of age and 0.5 – 2 kg in weight).

This study also looked at a comparison of the fecundity - weight relation across North Atlantic cod stocks. May (1967) noted that the relatively high fecundity from the western Baltic and Norwegian coast might result from the low age and small size at maturation, and was not necessarily representative of the northeast Atlantic as a whole. Oothuizen and Daan (1974) presented that North Sea cod fecundities are among the highest of all stocks North Atlantic stocks, and that Newfoundland-Labrador cod fecundities were significantly lower. This has changed, the data show that not only are cod from 2J maturing at earlier ages but are producing a higher number of eggs at equivalent sizes and ages than in any other reported study for any cod stock.

There are several hypotheses for these changes in life history, and although the present work does not allow me to resolve these, a few comments are appropriate. Drinkwater (2002) provides evidence that severe climate conditions (cold temperatures) played a role in the slower growth rates and reduced size at age evident in the 1990s. Pörtner et al. (2001) showed a significant relation between temperature fluctuations and recruitment and found that a cold-induced shift in energy budget occurs which is unfavorable for growth performance and fecundity. In addition, capelin (*Mallotus villosus*) all but disappeared in the northern areas surrounding Newfoundland and Labrador after 1990 and shifted their range southward, followed by a southward shift in cod (Narayanan et al. 1995, Carscadden et al. 1997, Rose et al. 2000b). Historically capelin has been the most important food of northern cod (Carscadden et al. 2001, Lilly 1994), and a primary energy source for the development of eggs (Henderson et al. 1984), but in the 1990's few offshore cod could locate them (Rose and O'Driscoll 2002). Meanwhile an increase in shrimp (a lower energy prey compared to capelin) occurred (Sherwood et al. 2007). A poor capelin diet may be contributing to the lack of survivorship past age 6, and may be related to an earlier investment of energy reserves into maturation and high fecundity in the offshore areas (2J-3K). Growth and reproduction at some level compete for the limited resources of available energy. If food availability is sufficient and maintenance energy costs are taken care of, the surplus energy will bolster energy reserves and production of eggs (Wooton 1990). The results suggest that northern cod are investing a large amount of relatively scarce energy reserves into reproduction and in doing so may be subject to an increased risk of mortality (Lambert and Dutil 2000). Changed life history parameters could also be a survival tactic in response to the present low state of the population, the lowest recorded in history (Waiwood 1982; deYoung and Rose 1993; Sinclair and Murawski 1997). Another hypothesis is that life history changes are genetic and induced by fishing. Olsen et al. (2004) suggested that the pressures of size selective exploitation could change the life-history of cod, and that early maturation may be a genetic response to increased mortality. However there is still no quantitative evidence linking fecundity and genetic change.

This study provides contemporary data on cod fecundity in the northwest Atlantic. Southern cod groups have fecundity schedules similar to historical norms, but the formerly dominant northern fish are maturing at earlier ages and smaller sizes, and dying young. Early maturation, early mortality and high fecundity are likely to be linked life history responses to either environmental, population or genetic changes. Further investigation of these changes is needed for fisheries management.

1.6 References

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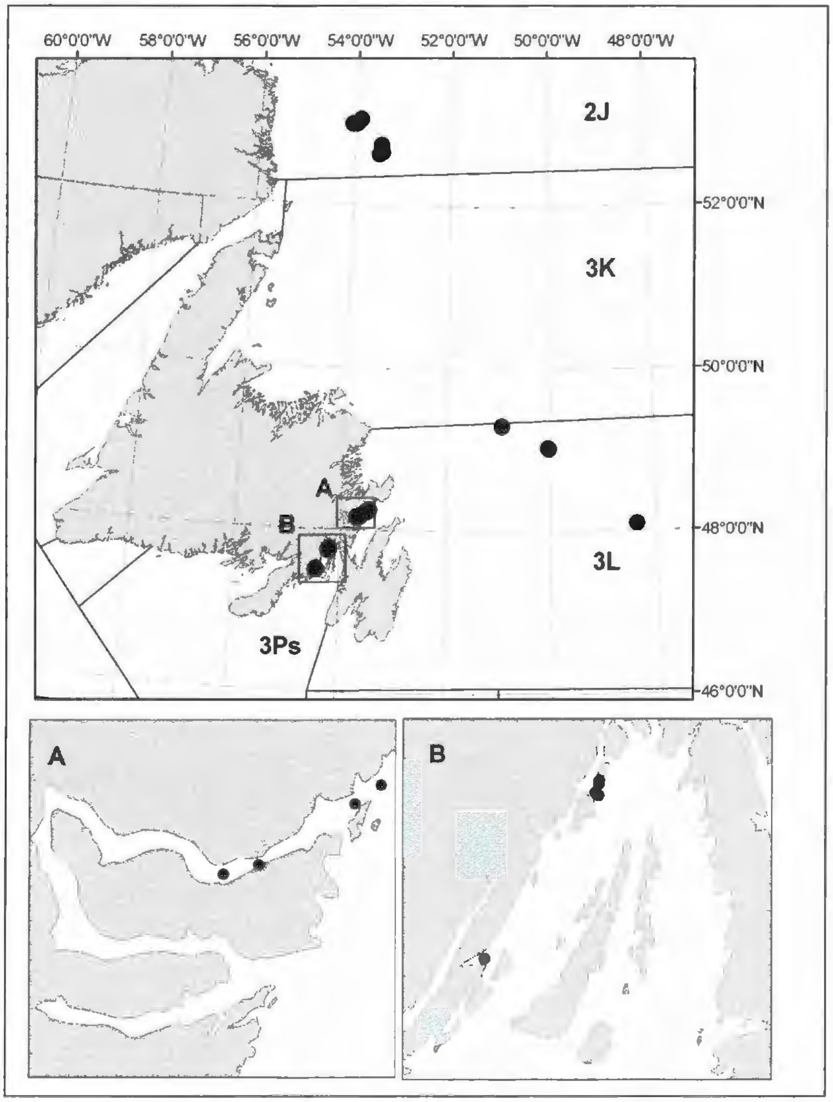

Figure 1.1 Sampling sites (•) and NAFO subdivisions for 1999 and 2003. Inserts represent coastal sampling sites, Placentia Bay (A) and Smith Sound (B).

Table 1.1 Summary of female cod sampled during 1999 and 2003 within three NAFO sub-divisions 2J, 3KL, and 3Ps. Information includes number of fish sampled, size (lengths and gutted weights), ranges and standard deviations.

Area	Year	Sample Size	Standard Length (cm)		Gutted Weight (kg)	
			Range	Average ± St. Dev.	Range	Average ± St. Dev
2J	1999	31	40-60	48.6 ± 4.7	0.465-1.81	0.918 ± 0.270
	2003	12	42-61	49.3 ± 7.0	0.540-1.63	0.927 ± 0.396
3KL	1999	27	35-82	62.0 ± 10.5	0.355-3.95	2.02 ± 0.962
	2003	60	40-94	56.5 ± 12.0	0.472-6.60	1.53 ± 1.27
3Ps	1999	18	56-84	68.3 ± 9.3	1.21-4.61	2.57 ± 1.12
	2003	52	45-72	59.0 ± 5.2	0.653-2.61	1.61 ± 0.85
Total	-	200	-	-	-	-

Table: 1.2 Comparison of original fecundity-weight relations in cod of different geographic regions of the North Atlantic.

Population / Area	Original Function	Weight units	n	Source
NAFO 2J	$F = 2.09W+6.04$ [a]	Kg	43	This study
2J-3K	$F = 0.48W + 0.01$ [a]	Kg	8	May, 1967
Labrador	$F = 0.2118W + 0.041$ [b]	g	65	Postolakii, 1967
North sea	$F = 569W-807000$	g	92	Oothuizen and Daan, 1974
	$F = 526W - 548000$	g	47	Schopka, 1971
Norway	$F = 790W - 41600$	g	49	Botros, 1962
	$F = 0.334W^{1.126}$	Kg	240	Kjesbu et al., 1998 (weighted average)
Baltic	$F = 633W + 88791$	g	807	Kraus et al., 2000 (weighted average)
	$F = 860W - 297000$	g	71	Botros, 1962
	$F = 746W + 95000$	g	84	Schopka, 1971
Iceland	$F = 519W$	g	42	Joakimsson, 1969
	$F = 584W - 832000$	g	49	Schopka, 1971

[a] log-log regression

[b] fecundity in thousands of eggs

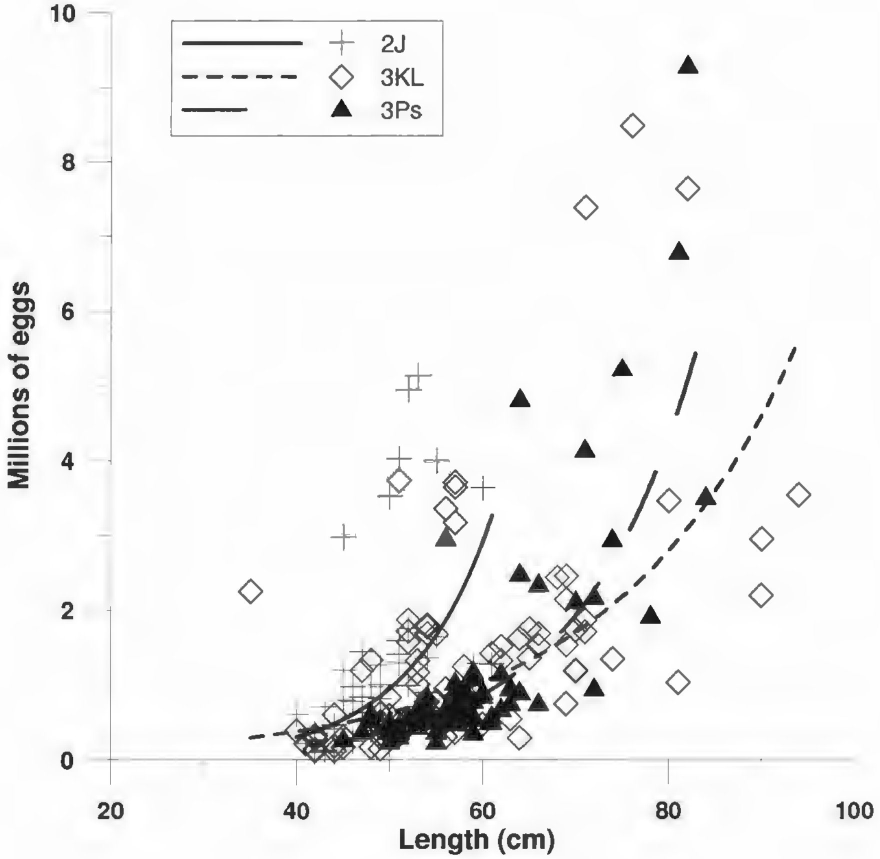

Figure 1.2 Scatter diagram of fecundity against length for three NAFO areas sampled, 2J, 3KL and 3Ps

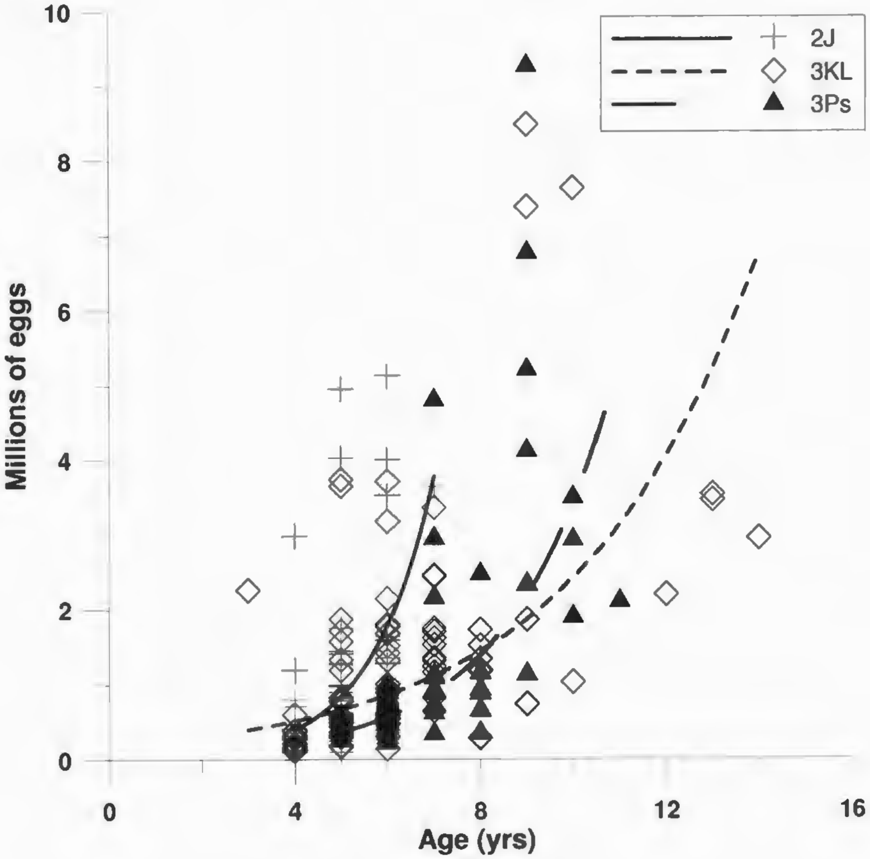

Figure 1.3 Scatter diagram of fecundity against age for the three NAFO areas sampled 2J, 3KL, 3Ps.

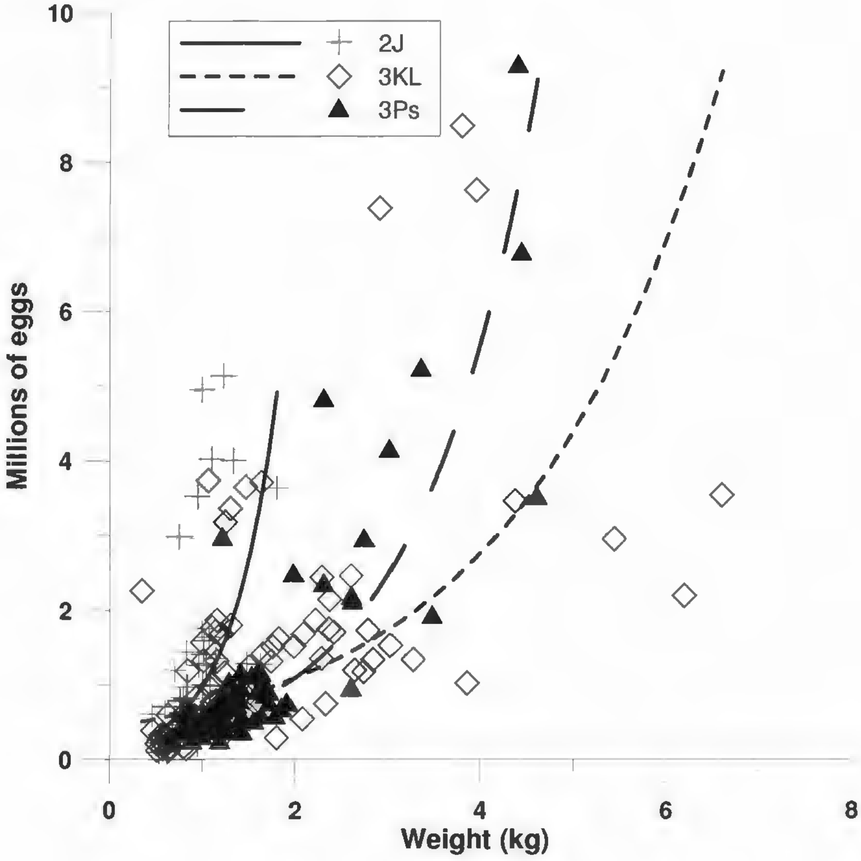

Figure 1.4 Scatter diagram of fecundity against weight fot the three NAFO areas sampled 2J, 3KL and 3Ps.

Table: 1.3 Log_{10} regression parameters and significance results for relations of cod fecundity and growth variables in various NAFO regions. Fecundity is number of eggs, K represents Fulton's condition factor, GI is gonad index and LI is liver index. Results rounded to the nearest 0.01.

Relation and Area		Log_{10} Regression parameters					
		slope	intercept	R^2	p	F	n
Fecundity-Length	2J	5.70	-3.70	0.36	< 0.01	23.56	43
	3KL	3.01	0.69	0.38	< 0.01	53.08	87
	3Ps	4.96	-2.85	0.68	< 0.01	145.43	70
	All	3.15	0.44	0.36	< 0.01	111.02	200
Fecundity-Age	2J	3.73	3.34	0.31	< 0.01	18.58	43
	3KL	1.87	4.52	0.32	< 0.01	40.36	87
	3Ps	3.28	3.21	0.56	< 0.01	87.71	70
	All	1.91	4.46	0.28	< 0.01	77.65	200
Fecundity-Weight	2J	2.09	6.04	0.42	< 0.01	30.15	43
	3KL	1.04	5.84	0.43	< 0.01	64.95	87
	3Ps	1.63	5.64	0.72	< 0.01	178.40	70
	All	1.11	5.82	0.41	< 0.01	138.27	200
Fecundity – K	2J	6.09	4.92	0.10	0.03	4.80	43
	3KL	3.74	6.22	0.15	< 0.01	15.15	87
	3Ps	2.84	6.08	0.06	0.04	4.31	64
	All	3.24	15.9	0.09	< 0.01	20.35	194
Fecundity – GI	2J	0.47	6.58	0.07	0.07	3.40	43
	3KL	0.23	6.35	0.02	0.21	1.58	87
	3Ps	-0.53	5.13	0.07	0.04	4.55	64
	All	0.08	6.07	0.00	0.49	0.49	194
Fecundity – LI	2J	2.32	8.96	0.23	< 0.01	12.53	43
	3KL	0.36	6.46	0.01	0.33	0.96	87
	3Ps	-0.23	5.59	0.01	0.59	0.29	64
	All	0.47	6.58	0.01	0.07	3.40	194

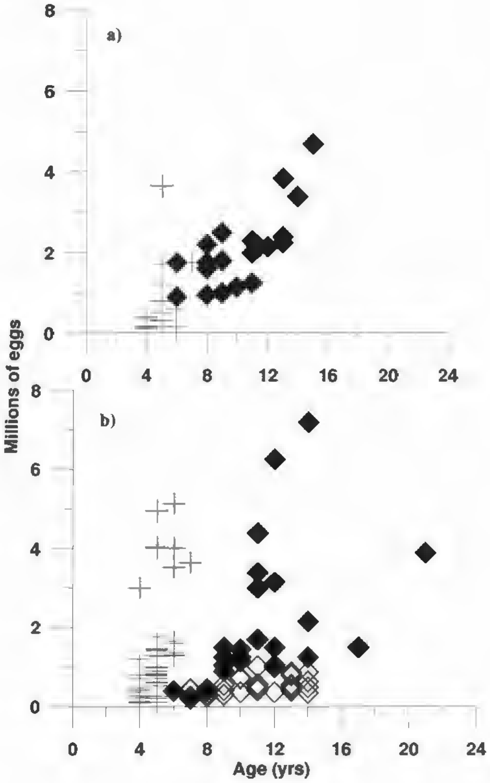

Figure 1.5 Fecundity at age for this study (+) and historical data from May, 1967 (♦) and Postolakii, 1968 (◊). Data from NAFO sub-divisions 3L **(a)** and 2J-3K **(b)**.

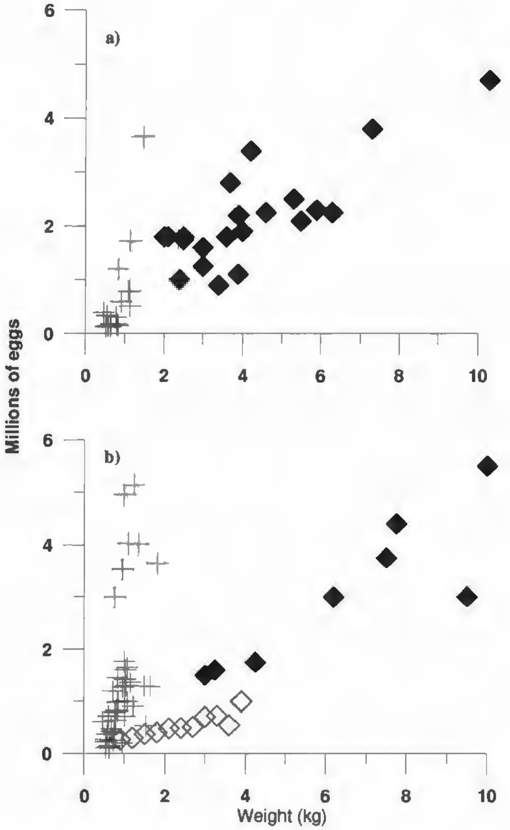

Figure 1.6 Fecundity at weight for this study (+) and historical data from May, 1967 (♦) and Postolakii, 1968 (◊). Data from NAFO sub-divisions 3L (**a**) and 2J-3K (**b**). Weight is gutted except for Postolakii, 1968 data for which only whole weights were available.

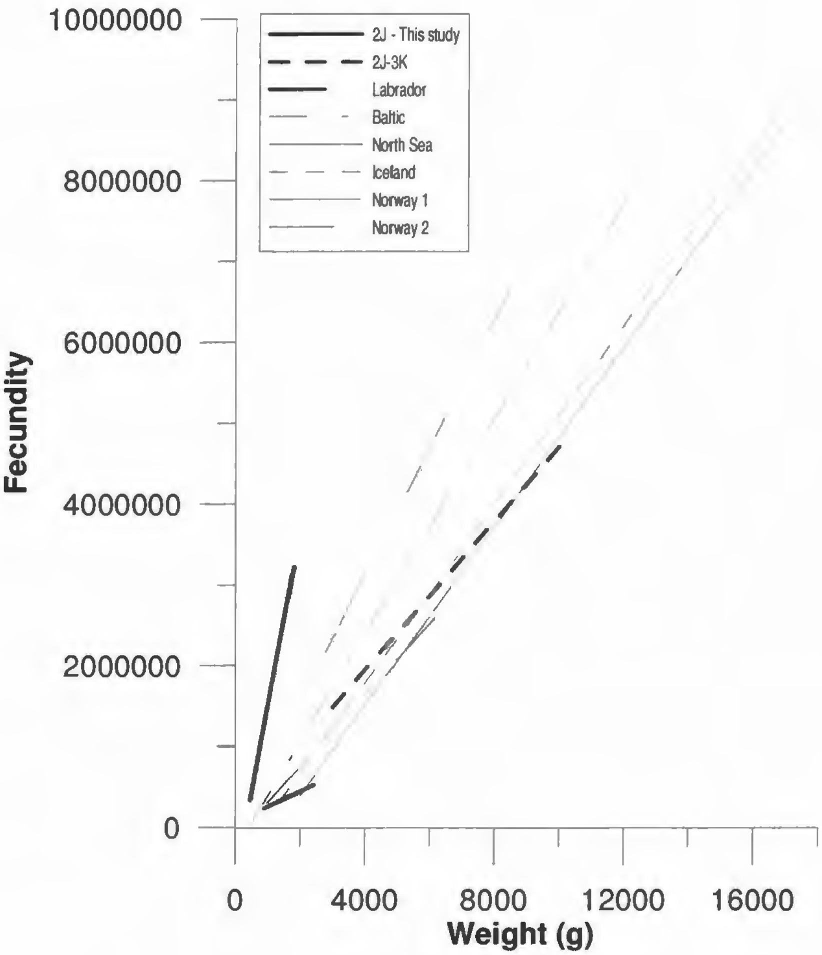

Figure 1.7 Comparison of linear regressions of fecundity–weight relations in cod of different geographical regions of the North Atlantic. Data were combined by weighted averages for Baltic, North Sea and Iceland (Table 1.3). Norway 1 represents data from Botros, 1962; Norway 2 data were weighted averaged data from Kjesbu et al., 1998. Weights are whole weights except for cod sampled from Labrador for which only gutted weights were available.

2 CHAPTER 2: LIFE HISTORY CO-VARIATION IN A FISHERY DEPLETED ATLANTIC COD STOCK

2.1 Abstract

The northern stock of Atlantic cod (*Gadus morhua*) once supported one of the world's largest fisheries, but since the early 1990s has been in a collapsed and post-industrial state. Extreme life history trait changes have occurred in this stock, most evident in early maturation and increased fecundity and mortality. Using historical data from the early 1960s (pre-industrial) and previously unpublished data from 1999 and 2003 (post-industrial), I show co-variation of these traits. Few fish in the later period reached 6 years of age or > 60cm (formerly many reached >12 years and > 80cm), but fecundity at size in the early maturing fish was higher than ever recorded in any cod stock. Post-industrial cod at 4 years had a potential fecundity of about 0.5 million eggs, which did not occur until age 6 in pre-industrial times. Coincidentally, mortality was low ($Z = 0.42$) during the pre-industrial period but above any previously reported in the post-industrial period. Using an egg-per-recruit model, fit to age structure data from the two periods, I also show how reduced survivorship, earlier age at maturity and increased fecundity resulted in a compensated fecundity per recruit that was >75% of pre-industrial levels. The cause of these changes, whether they represent traits selected for by the fishery, responses to reduced densities, or a combination of these factors is discussed, but remains uncertain.

2.2 Introduction

Atlantic cod (*Gadus morhua*) of the Newfoundland northern stock (NAFO subdivisions 2K3KL) historically numbered in the millions of tonnes and was comprised of slow growing and long-lived (to 20+ years) fish that matured at 5-8 years of age (Fleming 1960). Until the 1960s the fishery can be said to have been in a pre-industrial state, with annual catches of up to 400,000 t (most years much lower), but since the mid-1960s, the coming of heavily industrialized fisheries (with the increase in factory freezer trawlers) and catches of up to 800,000 t per year led to catastrophic stock declines (Rose 2004). A general moratorium on the northern cod fishery was instituted in 1992, however, the cod stocks continued to decline and since the late 1990's has been in a post-industrial and collapsed state.

Changes in life history traits are unlikely to occur in isolation from other traits (Roff 2002). Overfishing or selective fishing may force changes in life histories of fishes (Rochet 1998). Changes in some life history features from what are thought to be historical norms, in particular age and size at maturation, and elevated mortality, have been reported and modelled for northern cod since the moratorium (Lilly and Murphy 2004; Olsen et al. 2004; Hutchings 2005; Stares et al. 2007). However, the importance of fecundity has generally been overlooked, or where addressed based on pre-industrial data (e.g. May 1967; Stares et al. 2007). Stares et al. (2007) used data from 1988-1990, when stock biomass was still in the range of 0.5-1.5 million tonnes); these data do not represent current conditions in this stock (Fudge and Rose 2008). I hypothesize that early maturation and higher mortality rates (lower survivorship) were components of covarying life history traits that would include higher individual and population fecundity. I also hypothesize that increases in growth as a consequence of density-dependent food availability would explain the early maturation, with cod maturing at similar size but not age.

The goal of this paper was to examine the co-variation and growth hypotheses by comparing life history traits (age and size at maturity, mortality rates and fecundity) for the northern cod stock in the pre- and post-industrial eras, and to compare total potential fecundity for these periods using an egg-per-recruit model.

2.3 Materials and Methods

Age structure, age at maturity, fecundity and length data from the early 1960s (Fleming 1960; ICNAF 1961; May 1966; May 1967) were used to represent the stock in the pre-industrial state. These data were compared with original data collected from similar range within 2J3KL (Figure 2.1) of the northern cod stock in the post-industrial fishery period (1999 - 2003). A total of 8723 cod were sampled during January and June of 1999 - 2003 in the offshore areas of the northern cod using a Campelen 1800 research trawl (small mesh) aboard the *CCGS Teleost*. Each fish was measured for length, weight and maturity (according to Morrison, 1990) and otoliths from 8090 fish were subsequently read to determine age. During January 1999 and 2003, prior to the spawning season, 62 randomly selected female cod were sampled for fecundity analyses. May (1967) reported a comparable gonad sample size (n = 48) for northern cod for years 1964 and 1965. Female gonad sampling followed the protocol of May (1967); for detailed sampling procedure see Fudge and Rose (2008). Fecundity-size relations are given in Table 2.1. Table 2.2 gives a summary of data used and sources. These were the only data available to describe these two eras.

To test the effects of era (pre versus post-industrial) on fecundity and percent maturity at age and length, several ANCOVAS (Type III SS) were preformed using routines in SYSTAT software. A logistic model of maturity state could not be used because no individual data (only averages) were available from the pre-industrial period. We used an egg production-per-recruit (EPR) model, a derivation of a yield-per-recruit model, to compare the reproduction performance and mortality rates between the pre- and post-industrial periods. Terms were included for fishing mortality (F), natural mortality (M) and an age-dependent spawning mortality event (Msp) that only applied to the estimated proportion of the fish that were spawning. The central equations of this model for age were:

$$\mathrm{EPR} = \sum_{t=3}^{t=15} P_t \, g_{m_t} \, F_t$$

$$\mathrm{P_t = Ps_{t-1} - Ps_{t-1}\,(1 - e^{-(F+M)})}$$

$$\mathrm{Ps_{t-1} = P_{t-1} - S_{t-1} * Msp}$$

Where:

Ps_{t-1} = proportion of fish surviving at age t

P_t = proportion of fish at age t (fish after M)

S_{t-1} = spawners at age

g_m = percent mature

F_t = number of eggs

The equations for length-based models were similar except length was substituted for age and other terms modified accordingly. Models were fitted to the normalized age or length structure data from the two periods in an iterative minimal error least squares approach in which F, M and Msp were estimated so as to provide the best fit of modeled age structure to the age structure data. Estimates of survivorship, and potential fecundity at age (eggs per recruit) over the life of an average recruited female were the main outputs of the model.

2.4 Results

I first compared the data between pre- and post-industrial periods. The population age structure differed significantly, with older fish in the pre-industrial period; in the earlier period many cod lived to age 12 or older, in the later period almost all cod were 6 years of age or younger (χ^2 test; $p < 0.05$) (Figure 2.2a). Similarly population length structure differed between eras with larger fish in the pre-industrial period reaching 100cm but most fish < 60cm in the post-industrial period (χ^2 test; $p < 0.05$) (Figure 2.2d). There was a highly significant difference between fecundities of the two eras (ANCOVA; $p < 0.01$);

percent maturities also differed but not as much as with fecundity (ANCOVA; $p < 0.05$). In the pre-industrial period, female cod matured at 6-8, but in post-industrial times at ages 3-5 (50% maturity at about age 4, approximately 90% at age 5). With respect to length cod reached 50% maturity at 55 cm in the pre-industrial period and 45cm in the post-industrial period. (Figures 2.2b and 2.2e). Interestingly, percent maturities did not differ significantly between eras controlling for length (ANCOVA; significant at $p = 0.1$ level only), demonstrating that the length effect is not as strong as the age effect on maturity. Younger, smaller fish are producing more eggs but younger fish are growing faster at present than they did historically (Figures 2.2c and 2.2f). Early maturing females produced many more eggs at an increased rate as compared to pre-industrial fish of the same age. Post-industrial cod at 4 years of age had a potential fecundity of about 0.5 million eggs, which in pre-industrial times did not occur until age 6.

Controlling for age and then length, model outputs for survivorship and eggs per recruit differed between eras (ANCOVA; $p < 0.05$ in both cases). For the pre-industrial period controlling for age, the best fit model indicated a relatively modest total mortality ($Z = F+M$) of 0.34 with $Msp = 0$. This result compares favourably to previous estimates of relatively modest levels of pre-industrial fishing mortality (e.g. Rose 2004). For the post-industrial period, the best fit model indicated a remarkable increase in mortality, and an increase in spawning mortality ($Msp = 0.24$)

The total calculated mortality rate controlling for age approached 1 ($Z = 0.64$) is comparable to that determined from assessment survey data by Lilly and Murphy (2004) where $Z = 0.75$, and Shelton et al. (2006) where $Z = 0.8$. For the pre-industrial period, controlling for length, the best fit model indicated a total mortality of 0.34 with null spawning mortality. For the post-industrial period, total mortality again increased, as was the case when controlling for age. The total mortality, controlling for length in the post-industrial era was 0.55.

The post-industrial survivorship curve was steeper than in pre-industrial times ($p < 0.05$) (Figures 2.3a and 2.3d). In the pre-industrial era, egg production per recruit peaked between ages 7 and 10, with considerable egg production continuing to age 15, while in the post-industrial era egg production peaked at age 4, and then declined rapidly as a result of high mortality (Figure 2.3b). Egg production peaked at lengths of 60 – 70cm in pre-industrial times, while in post-industrial times it peaked at 45cm and declined rapidly thereafter (Figure 2.3e). Cumulative egg production approached approximately 600,000 per recruit in the pre-industrial era, in comparison to approximately 400,000 per recruit in the post-industrial era (post-industrial egg production is a remarkably high 75% of historical egg production per surviving female given the smaller body size and much higher mortality rates) (Figures 2.3c and 2.3f). I could not assess the quality of post-versus pre-industrial period eggs. The relatively large egg potential per recruit in post-industrial northern cod may not translate into higher egg survival, as small first time spawners produce lower quality eggs (smaller and decreased hatching success) (Kjesbu, 1996; Trippel, 1998).

2.5 Discussion

Were changes in growth the cause of the changed age at maturation, such that fish of similar size were maturing early because of density-dependent growth responses at reduced population sizes? Female cod in the post-industrial era had greater length than pre-industrial fish up to age 4, but age five and older fish showed no consistent difference (Figure 2.4). Nevertheless, post-industrial cod were maturing at much smaller sizes (< 40cm) than in pre-industrial times (> 50cm), suggesting that while increased growth of young cod was occurring in the post-industrial period, increased growth alone cannot account for the changes in this trait. Moreover, the large disparity in length of mature and immature pre-industrial fish at age 5 is much less in post-industrial fish, which suggests that there was a much greater size influence on maturation in pre-industrial than post-industrial times. Any early advantage in growth in post-industrial fish appears to disappear after age 5, when most fish were spawning. It is of interest that these fish traditionally relied heavily on a diet rich in capelin (*Mallotus villosus*) beginning at approximately age 4, but have had to rely on shrimp (*Pandalus spp.*) since the decline of capelin in their range around 1990 (Rose and O'Driscoll 2002). Shrimp is a traditional food for young cod, and their increase in growth in the post-industrial period is consistent with a density-dependent response. However, a switch to capelin feeding at age 4-5 cannot take place at present, and any density-dependence appears to be overshadowed by a lack of high quality food. Wroblewski et al. (1999) fed wild-captured farm cod to satiation over several seasons which resulted in greatly increased fecundities compared to free-living cod, demonstrating that higher fecundity relates to nutrition. Stearns and Crandall (1984) suggested that when fishing effort increases, part of the response to reduced population density is a decrease in intraspecific food competition, leading to increased growth and fecundity. In a freshwater species, Baccante and Reid (1998) found a lagged increase in fecundity of two walleye populations with an increase in exploitation, which correlated with an increase in food availability. In contrast, poor feeding conditions should lead to substantial energy losses and result in a decrease in fecundity in fish of small sizes (Rijnsdorp 1993). I suggest that an increased availability of food for young northern cod (shrimp) has contributed to increased growth, earlier maturity and higher fecundity, but that this effect is fleeting and by age 5 the lack of a richer food supply reverses this situation (Sherwood et al. 2007).

The extreme changes in life history observed here could relate to the intensive fishery that was prosecuted on this stock from 1960 to 1992 (Ernande et al. 2004). Several studies have documented an increase in fecundity with a decrease in population size in various fish species (Kipling and Frost 1969; Bowen et al. 1991). Koslow et al. (1995) found a 20 % increase in fecundity in a 50% reduced population of orange roughy off Tasmania. Like northern cod, North Sea haddock spawning stock biomass declined to very low levels in the 1990s, and an increase in fecundity at earlier ages and smaller sizes was reported (Wright 2005).

A recent study by Stares et al. (2007) did not find an inverse relationship between population size and fecundity in northern cod comparing data from the 1960s with data from 1988-1990, prior to the final major decline of this stock. The northern cod biomass was > 1 million tonnes in 1988 and did not reach its lowest levels of perhaps 1-2% of historical levels and 10% of those of the late 1980s until the mid to late 1990s (DFO 2007). Hence, the conclusions of Stares et al. (2007) are thought to provide a time line of sorts for comparison with the present results.

Although the timing of the changes in northern cod life history traits cannot be determined exactly, the likely decline in age and length at maturity began at least as early as the mid-1980s (Olsen et al. 2004), and likely preceded the other changes. Stares et al. (2007) reported higher fecundity in 1990 than in 1988, suggesting the beginning of the elevated fecundity began during this period of rapid stock decline and followed the earlier decline in age at maturity. Higher mortality rates may have been precipitated by the combination of early maturation and high levels of energy required to generate the increase of spawning products (Lambert and Dutil 2000).

The causes of the changes in life history remain uncertain. There are two ways in which the fishery could have induced early maturation. First, disproportionate removals of larger spawning fish by the fishery could lead to genotypic selection for early reproduction. Increases in mortality translate into decreased spawnings for late-maturing individuals, hence selection will favour early-maturing phenotypes, even if these have lower age-specific fertility (Heino et al. 2002). Second, changed life history parameters could be a response to the present collapsed state of the population or to the environment, or a combination of these factors. For example, with increased growth stemming from reduced intraspecific competition for available prey, fish reach the size at maturity earlier, a possible phenotypic response (Trippel 1995; Heino et al. 2002). It is also possible that low population size directly influences reproductive physiology, although little is known of this possibility. In any case, the early maturation and higher fecundities have partially compensated for the reduced size at maturation and increased mortality rates. Environmental changes which have resulted in a narrower prey base for maturing cod may be interacting with early maturation, leading to lower energy reserves and elevated mortality (Lambert and Dutil 2000). Present data do not enable me to distinguish between these hypotheses, and the need for further research in this area is compelling.

In conclusion, co-variation in life history traits of Atlantic cod in the post-industrial fishery period since 1992 has resulted in fecundities and mortalities seldom if ever observed in any Atlantic cod stock (Brander 2005; Fudge and Rose 2008). Density-dependent growth is unlikely to be the sole cause of earlier maturation or increased fecundity. Key questions still remain: have northern cod evolved in response to past fishing (a genotypic response), or are they reacting solely to the low population state (a phenotypic response) and the environment, or to a combination of these factors? Under either scenario it is evident why there has been no net population growth in this stock since 1992 – mortality losses have trumped any possible population gains.

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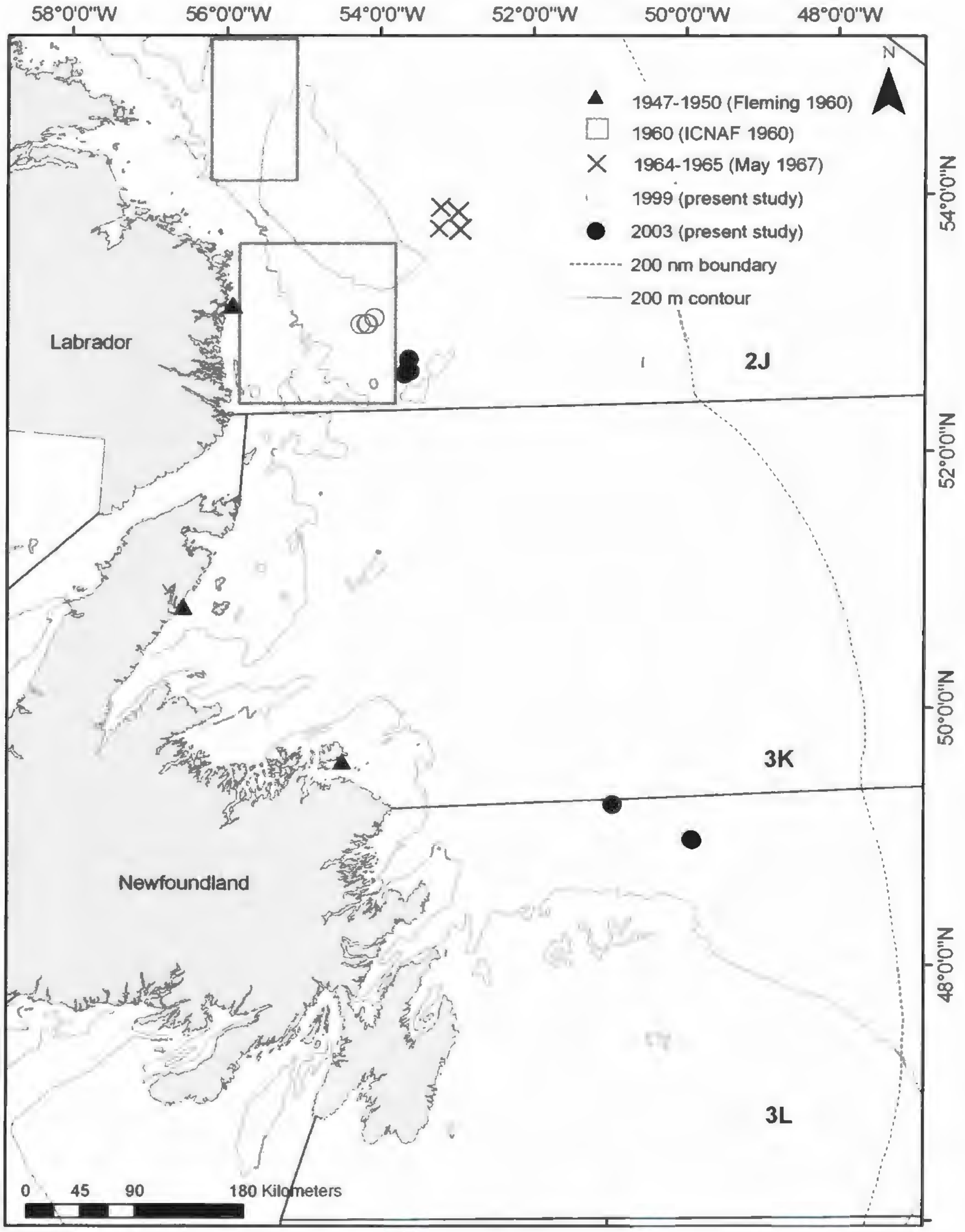

Figure 2.1 Sampling sites for pre-industrial (▲,□, x) and post-industrial (•, ○) data in NAFO subdivisions 2J3KL.

Table 2.1 Log_{10} regression parameters and significance results for cod fecundity-size relations. Female cod were sampled within NAFO sub-divisions 2J and 3L during 1999 and 2003. Results rounded to the nearest 0.01.

n = 62	Log_{10} Regression parameters				
	slope	intercept	R^2	p	F
Fecundity-Length	5.60	-3.61	0.36	<0.01	33.42
Fecundity - Age	3.65	3.33	0.29	<0.01	23.75
Fecundity - Weight	2.04	5.97	0.44	<0.01	45.47

Table 2.2 Summary of life history data and sources considered in present study.

Area	Year	Length (n)	Age (n)	Additional data	Source
2J3K	1947-1950	-	3-15 (1093)	maturities	Fleming 1960
2J	1960	-	2-16 (775)	-	ICNAF 1960
2J	1960/1962	-	2-17 (1536)	maturities	May 1960
2J	1964	-	-	fecundities (20)	May 1967
2J3KL	1999 - 2003	16-63(8723)	2-7 (8090)	fecundities (62)	Rose (unpublished); Fudge and Rose (in press)

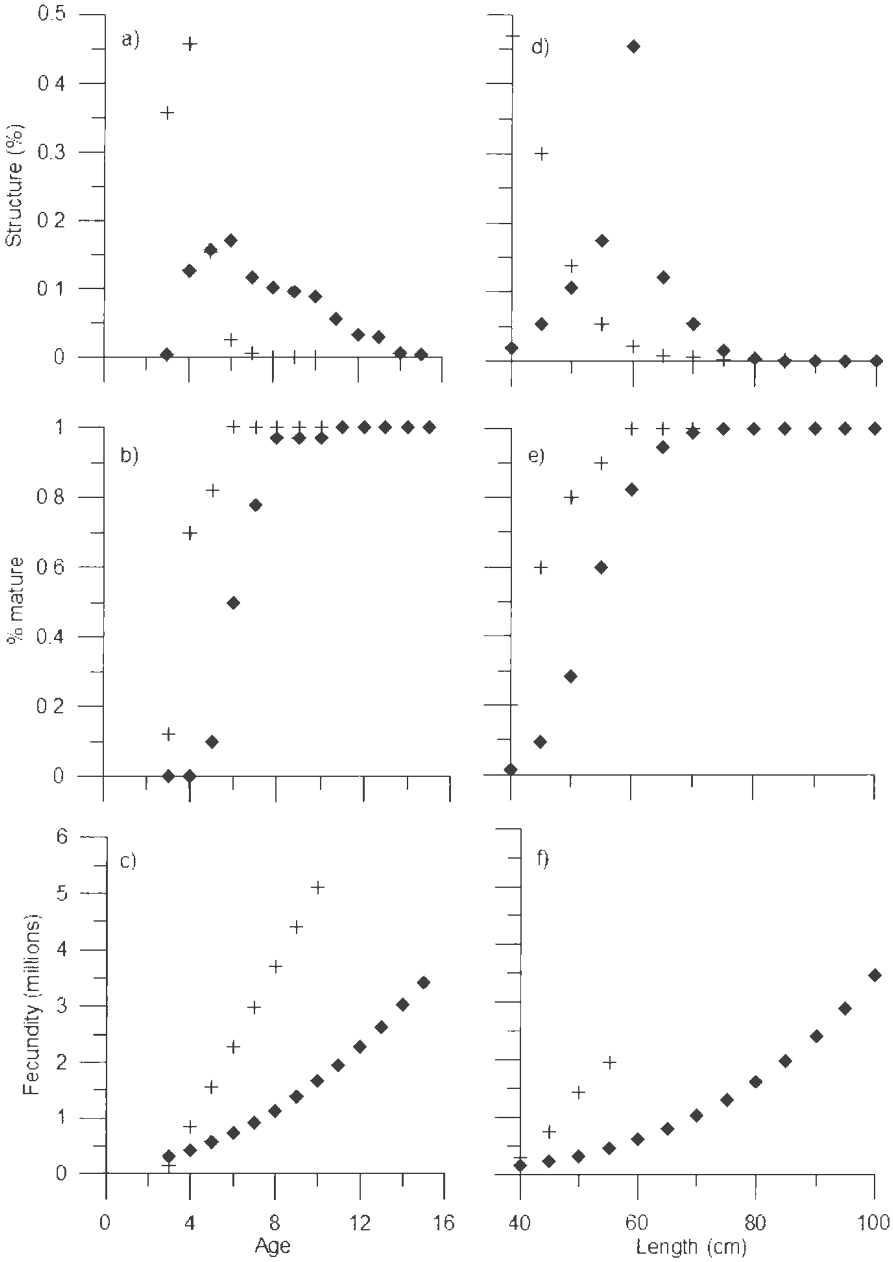

Figure 2.2 Life history information on northern cod (*Gadus morhua*) in relation to age and length. Pre-industrial data shown as solid diamonds, post-industrial data shown as crosses: structure (a) and (d) , percent maturity ogive (b) and (e) and fecundity at age (c) and (f).

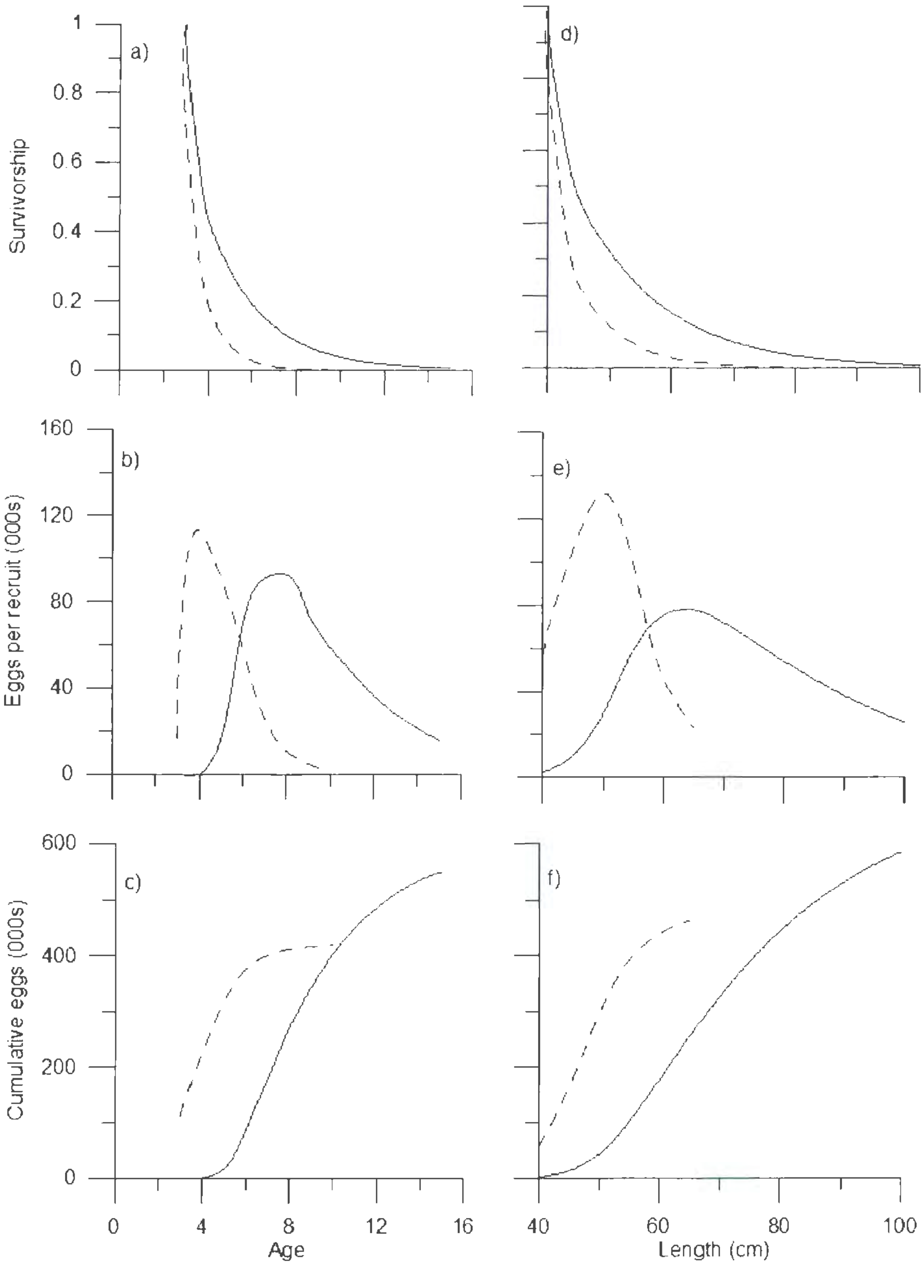

Figure 2.3 Life history EPR model outputs in relation to age and length for northern cod (*Gadus morhua*). Pre-industrial data shown as solid line, post-industrial data as dashed line: survivorship (a) and (d), eggs per recruit (b) and (e), and cumulative eggs per individual over life expectancy (c) and (f).

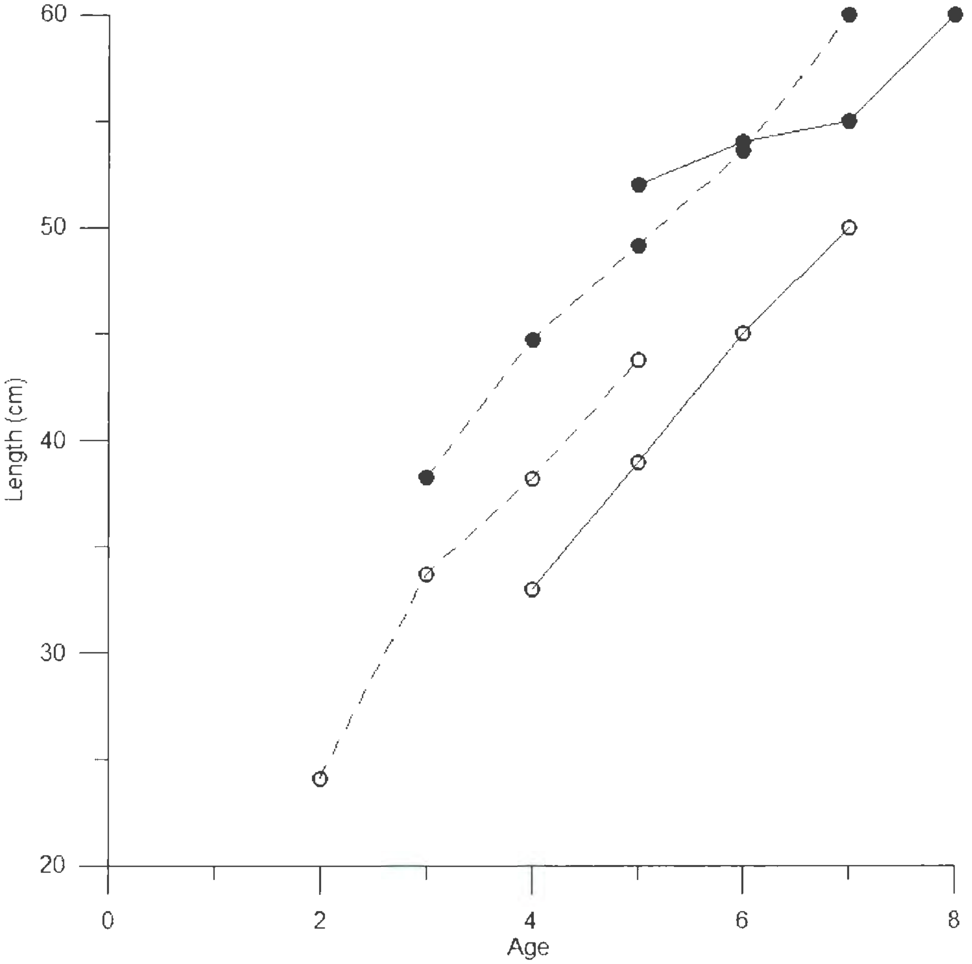

Figure 2.4 Length at age for mature (●) and immature (○) female northern cod. Pre-industrial data shown as solid line and post-industrial data as dashed lines.

3 CHAPTER 3: PASSIVE AND ACTIVE ACOUSTIC PROPERTIES OF A SPAWNING ATLANTIC COD (*GADUS MORHUA*) AGGREATION

3.1 Abstract

Passive and active acoustic properties of an Atlantic cod (*Gadus morhua*) spawning aggregation were observed at depths of 40-50 m at the Bar Haven grounds in Placentia Bay, Newfoundland in April 2003. A hydrophone was positioned on the seafloor beneath the aggregation while a 38 kHz split-beam transducer was mounted in a stationary mooring at the sea surface above the aggregation over a 24 hour period. Sounds were recorded in the sea and were similar to those recorded in the aquarium from captive spawning cod of the same stock. The sounds were short grunts with primary frequencies ranging from 30 to 250 Hz, and on average lasting 300ms. Sounds were less frequent than those recorded from the captive group of cod. From the surface-mounted transducer, cod were observed to undertake relatively rapid periodic vertical migrations approximately half way to the surface (20-25 m) which resulted in the formation of cod columns. This work is the first to demonstrate incidence coincidence of cod sound production and vertical movement resulting in column formations during spawning.

3.2 Introduction

The details of Atlantic cod (*Gadus morhua*) spawning behaviour have been observed in the laboratory and in the wild. In the aquarium cod show elaborate courtship behaviours (Brawn, 1961b; Rowe and Hutchings, 2006). Brawn (1961b) observed distinct courtship performed by males toward females, as well as territorial aggressive behaviour of males toward other males (Brawn, 1961a).

Observations of spawning behaviour, aggregation structures and pelagic behaviour have been made with echosounders and telemetry (following acoustically tagged fish). Males arrive first on a spawning ground (Robichaud and Rose, 2003) competing with other males in attempts to attract females (Hutchings et al., 1999; Nordeide and Folstad, 2000; Windle and Rose 2007). Spawning aggregations have been observed for many years in different parts of the range of cod (Sund, 1935; Rose, 1993, Lawson and Rose, 1999). Spawning aggregations involve vertical movements in the water column, with the extent of vertical migration depending on the depth of water.

Fish are known to produce low frequency sounds, especially members of the families Sciaenidae, Gadidae, Ictaluridae, Cyprinidae, Batrachoididae, Haemulidae, Lutjanidae, and Serranidae (Luczkovich et al., 2008). With cod, both sexes can produce sound, although it is the males whose sound production is thought to play an important role in spawning, by attracting females and enabling males to hold territories (Brawn, 1961c). A pair of drumming muscles attached to the swim bladder produce the sounds, and although not thoroughly demonstrated, drumming muscles mass has been suggested to relate to increased sound production (Rowe and Hutchings, 2006). Finstad and Nordeide (2004) provided a detailed study of the variation in acoustic repertoire of cod in captivity. Rowe and Hutchings (2006) further studied captive groups from two northwest Atlantic populations, quantifying temporal patterns and behavioural contexts. They found sound production occurred most frequently during peak spawning season, at the onset of darkness, and was positively associated with egg production. Only one previous *in situ* passive acoustic study of cod is known, Nordeide and Kjellsby (1999) showed an increase in ambient sound during spawning within the known frequency range of cod.

One of the largest spawning components of Atlantic cod in Newfoundland waters is located in Placentia Bay, on the south coast of Newfoundland (NAFO regulatory area 3Ps). During the spawning season, cod are found aggregated on shallow slopes within Placentia Bay. An area known as Bar Haven is the most consistently used spawning ground in the bay (Lawson and Rose, 2000; Brattey and Healey, 2003). The Bar Haven spawning grounds are located in the inner part of Placentia Bay, and are characterized by a series of islands separated by relatively shallow channels (> 90 m). During the spawning season (May-June), aggregations of cod are typically found on the shallow banks surrounding the islands, most notably the "Corner Bank" area off the northeast shore of Bar Haven Island (Rose et al. 2008). Sampling of cod in spawning aggregations have been conducted since 1997 at various locations in the area, and suggest that males arrive first, followed by females and immature individuals (Lawson and Rose, 2000). Although cod have been observed to migrate into and throughout the bay during the spawning season, retention on the spawning grounds has been observed at Bar Haven (Robichaud and Rose 2002;2003; Windle and Rose 2007).

This *in situ* study is one of the first attempts to document the sounds made during spawning and relate them to spawning behaviour, linking active and passive acoustic technologies in behavioural studies. The aim of the present study is to investigate the natural movements and behaviour of cod spawning as well as investigate the occurrence of cod sound production during spawning in the lab and in the wild.

3.3 Materials and Methods

During April 2003 an *in situ* study on cod spawning behaviour was carried out at Corner Bank of Bar Haven spawning grounds in Placentia Bay. The bottom depth ranged from 48 to 53m with the spring tides. *Ex situ* observations were conducted from February to April 2003 on spawning cod from the same sub-stock kept in the aquaculture facility of Memorial University of Newfoundland. Approximately 50 captive cod from NAFO division 3Ps, specifically Placentia

Bay were subjected to a four month phase shifted photoperiod, and fed frozen baitfish at the university's aquaculture facility. Cod were kept in a 4m diameter and 3 m high tank with a flow system of 100L/min, and water temperature kept at 6 °C.

Acoustic recordings

An acoustic survey of a cod spawning aggregation was conducted over Bar Haven grounds, Placentia Bay in 2003 using an echosounder with a transducer mounted in a towed body (Rose et al., 2008) on the "C.C.G.S. Shamook". The 2003 survey data were used to map spawning distribution in order to determine an optimal spot for a stationary experiment. To observe vertical distribution and densities of fish over time, *in situ* hydroacoustic data were recorded from 1430h on April 16 2003 to 0900h (NST) on April 17 2003, totalling 18.5 hours of data. The experiment fell short of twenty-four hours, due to the onset of winds, which prevented the vessel from holding its three-point mooring. Upon initial deployment of the hydrophone apparatus, fish were seen to scatter, returning approximately 10 minutes after equipment settled. Analyzed data were limited to times when cod echos were viewed on the sounder which appeared to occur with the onset of natural behaviour or return of the aggregation to the observation area.

The vessel was moored using a three point mooring with the towed body fixed to a boom with stabilizing lines. The towed body was positioned about 3m from the boat and 1m beneath the surface. A hydrophone was attached to a purpose built stand with a weighted bottom and positioned on the seafloor recording passive data along active recordings from the echosounder. In order to qualify and compare sounds from spawning cod, the same hydrophone and recording system was used in the *ex situ* observations of spawning cod.

All active acoustic data were collected using a Simrad EK500 split-beam echosounder (38 kHz, 7 ^{0} half-power beam width, pulse duration 1ms, 7.5 kHz digital sampling rate, pulse rate 1 ping s^{-1}). The echosounder was calibrated according to Foote et al. (1987). Vertical movement and densities were observed at high resolution (2min by 3m bins). Vertical movement and height of the spawning aggregation was derived from integration of active acoustic data using Echoview Fisheries Acoustic Software (Myriax). Height or distance from bottom of a spawning aggregation was measured from the start of the seabed to the average height of measured fish echos closest to the water surface. Fish densities were estimated according to Rose and Porter (1996):

$$TS = 20\log_{10}(L) - 66$$

where L was the mean total fish length (56 cm) obtained from sampling.

Passive data were recorded using a hydrophone (ITC 8212) with a Stanford Research System pre-amplifier (model SR560). Having the hydrophone mounted on the seabed during at sea recordings increased stability and decreased the recording of spurious signals resulting from movement of the hydrophone. The vessel switched to small gas generator to reduce noise. Data in the form of WAV files were collected, oscillograms and sounds characteristics were analyzed using Avisoft SASLab Pro software (Avisoft Bioacoustics). Pre-trigger setting was 0.03 sec (time before the start of the sound that triggers recorder), hold time equalled 3 seconds (minimum recording time; if another sound doesn't come). Preamplifier bandwith setting range was set at 3 Hz to 1KHz for captive and wild recordings.

Biological sampling

In situ cod were fished using hand lines. Total length and weight were measured, the fish were sexed, and otoliths were extracted for aging. Male cod were identified as either immature, in spawning condition, or spent. For females, individuals were classed as immature, spawning or spent. A total of 772 cod were sampled from Bar Haven bank prior to the stationary experiment. Maturity stages were determined by visual inspection of gonads according to Morrison (1990) and Templeman et al. (1978). Males in spawning condition had testes that were full of milt, while spent gonads were stringy and had little or no remaining milt. Mature females had either ripening or hydrated eggs present in gonads, spent females had little or no eggs with a deflated gonad appearance. For *ex situ* observations, spawning was verified by the presence of eggs, released eggs floated to surface water of the tank which was continuously filtered for eggs, separating eggs in separate holding tanks. Holding tanks were checked and eggs collected by aquaculture technicians at 0830h (NST) each day during spawning with volumes recorded. The sex ratio of the approximately fifty captive cod was unknown but suspected to be equally distributed according the technicians.

Statistical methods included a simple regression looking for a relation between egg production and sound production. An ANOVA was used to investigate the vertical height of spawning aggregation, while a Post-hoc Tukey test method looked at diel distribution of density within spawning aggregation. T-tests were used to investigate significant differences in the sound characteristics from *in situ* versus *ex situ* cod sound recordings. We hypothesize that cod sound production is associated with spawning behaviour and increased vertical movement with diel patterns for cod both in the wild and captivity.

3.4 Results

Ex situ

Over thirteen days (approximately 312 hrs) of recording during February 20 to March 26 2003, one hundred and ten cod sounds were recorded during the spawning period. Sounds may be described as grunts with average duration 300 ms, with peak frequencies ranging from 30 to 210

Hz (Table 3.1). Recordings existed of single grunts as well as double grunt cod sounds (Figure 3.1). Through the presence of eggs in the holding tanks, technicians noted spawning period began December 10 2002 and finished April 28 2003, therefore no recordings were made outside the spawning period. The maximum volume of eggs and number of grunts were recorded in March. Number of grunts observed peaked at 20/day on March 24 2003 and observed egg volume peaked at 2000 ml on March 9 2003. Using a regression analysis, there was a positive but non-significant correlation ($p > 0.05$) between egg volume and the number of sounds recorded. Of note, 85% of grunts were recorded during hours of darkness. Although no visual recordings of fish were possible, sounds indicative of fish bumping against hydrophone (which was hung just below the surface) were more frequent at night and suggest an increase in swimming movement or activity during spawning.

In situ

Sampled fish size ranged from 32-91 cm; ages 3 – 13 years. Only twenty-one percent of females and nine percent of males were classified as immature. The biomass of the spawning aggregation at Bar Haven bank observed in 2003 was estimated be 14000 t. These fish were in spawning condition with an almost equal distribution of males and females in the aggregation (Table 3.2).

Over 18.5 hours, a total of ten *in situ* cod sounds were recorded. Grunt durations ranged from 242 to 407 ms, peak frequency ranged from 30 to 250 Hz. The representative oscillogram of a double grunt sound in Figure 3.1A was recorded on April 16 2003, as with all double grunt recordings it is unknown if it came from a single cod. The oscillogram of a single grunt sound in Figure 3.1B was recorded *ex* situ. There were no significant differences between the physical characteristics (grunt duration, peak frequency) of the recorded sounds ($p > 0.05$ in all cases) *ex situ* vs. *in situ*.

During peak daylight hours cod were observed aggregated tight to the bottom (bottom five meters), at the onset of darkness (dusk), cod vertically migrated forming wave-like structures viewed on echograms when observed from the stationary platform (Figure 3.2). Wave-like formation height was measured in metres (distance from bottom) and varied over the experiment time period. Wave-like formation height (distance from bottom) was related to time of day (ANOVA, $p < 0.001$). Cod were distributed closer to the bottom during daylight hours (Post-hoc Tukey test; $p < 0.05$). Of note, the most demersal distribution occurred at dawn and dusk. Vertical diel migration was also seen in density distribution. During daylight, densities were concentrated in the bottom 10 m, with densities reaching above 0.8 kg/m^2. After the onset of darkness, densities were more evenly distributed throughout the water column (Figure 3.3).

3.5 Discussion

Atlantic cod spawning behaviour was observed in captivity and in the wild employing combined active and passive observations, at the well documented spawning grounds of Bar Haven, Placentia Bay. The comparisons between *in situ* and *ex situ* cod of the same sub-stock provide insight into the similarities and differences between wild and captive spawning behaviours.

Both in the lab and in the wild, spawning cod appear to have two behavioural phases one associated with daylight hours and one with hours of darkness. Cod were most active during darkness with greater observed vertical movement and production of sounds compared to daylight hours. Cod vertical migrations during darkness appeared as waves on echograms from our stationary platform, but would appear as stacks or columns (Figure 3.4) on echograms from a moving vessel (Rose, unpublished; Rose, 1993; Lawson and Rose 2000). Previous acoustic studies along with biological samples confirm peak spawning on Bar Haven bank from March to April (Lawson and Rose 2000). Diel vertical migration is common in many fish species suggesting that they follow zones of light intensity (Neilson and Perry, 1990). In the present study, vertical movements appear to relate to spawning behaviours. Pelagic formations of cod on spawning grounds was first observed with echosounders by Sund (1935) in the Loften area of coastal Norway and subsequently in Newfoundland waters by Rose (1993) and Lawson and Rose (2000). Rose (1993) suggested that columns may comprise of pairs of spawning fish, having paired near bottom then swim up to spawn. This observed behavior has been suggested to increase reproductive success, from a male perspective, in that columns may be a way the chosen male maximizes his reproductive success by reducing sperm competition from other males which try to sneak fertilization (Bekkevold et al. 2002). For the female, the vertical "escape" may be a way to ensure that her eggs are fertilized by the best sperm (Trippel et al. 2005). Along with echogram observations, measured densities at depth intervals showed the entire aggregation evenly migrating up in the water column after the onset on darkness. Also, the more elaborate movements along with additional mating tactics such as production of sounds may increase chances of mating successes in low light (Anthony, 1981). Other studies suggest that vertical migration and the formation of columns are not necessarily associated with cod spawning behavior (Hutchings et al. 1999; Nordeide 1998). Although our results provide further support that "columns" of cod are associated with spawning, it may be that varying spawning behaviours exist among different cod populations, a topic which requires further investigation.

In the laboratory component of my study, both cod sound production and increased swimming activity occurred during peak spawning. Egg volume was used to determine peak spawning time in situ, consistent with aquaculture practices (D. Boyce, pers.comm.). Gamete release was correlated with time of day being greater at night. Kjesbu (1989) documented a similar trend in one of two groups of captive cod, with cod held in outdoor tanks releasing the most eggs at night.

Rowe and Hutchings (2006) also observed a greater egg release at night. Sound production by cod was also greater at night during the spawning period.

Brawn (1961c) was the first to investigate sound production in cod. Sounds produced by drumming muscles vibrating on the swim bladder were described as low frequency grunts and associated with spawning behavior of courtship displays and ultimately ventral mounting. Males were observed to be territorial and aggressive towards other males, and the most vocal (Brawn, 1961a). However, Brawn's laboratory study did not relate behaviours temporally. Our data from captive observations collaborates Rowe and Hutchings (2006) observation of correlation of spawning behavior with egg production. Sound recordings in tanks are not ideal, however, as tank walls and the water surface may reflect and distort sounds limiting useful descriptive sound characteristics (Parvulescu, 1966; Rowe and Hutchings, 2006).

Single grunts and double grunts were recorded, although it is known that cod can produce a double grunt sound, it is unknown whether these "doubles" came from the same cod. Our study goes a step further than Nordeide and Kjellby (1999), with the simultaneous recording of single cod grunts with visual measures of spawning behaviours based on echo soundings at a fixed platform. Sounds recorded from wild populations allow for direct comparison of physical sound characteristics with captive data. We recorded five good quality single grunts from the wild. It has also been suggested that cod produce click-like sounds in the presence of predators (Vester et al., 2003), however, no such sounds were recorded during this study, but no predators were apparent in the area.

Observing wild cod behavior during spawning is not easy. We found both passive and active acoustics useful in assessing such behavior. Added visual observation, such as video recordings during *ex situ* observations would have provided additional behavioural data, such as courtship behavior as observed by Brawn (1961b). Video recordings were attempted *in situ*, but due to the poor quality of the underwater camera, no useful observations were acquired. More frequent egg sampling from captive cod would have provided additional information on sound production in relation to gamete release. Similarly, egg sampling *in situ* as well as more observation time would have provided additional support for peak spawning.

In conclusion we have shown that Atlantic cod produce sounds in the wild that are associated with increased vertical migration during the hours of peak spawning time *in situ*, and are at a minimum associated with increased swimming activity *ex situ*. This work using combined acoustic approaches is the first to demonstrate the simultaneous incidence of cod sounding and vertical behaviours and support the formations of columns during spawning.

3.6

3.7 References

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Table 3.1 Physical characteristics of cod sound *in situ* and *ex situ*. No significant differences were apparent between any of the statistics between groups (t-tests, $p > 0.05$)

	Statistic	Grunt duration (ms)	# Pulses	Peak Frequency (Hz)	Peak Amplitude (mV)
In situ	Mean	303.0	11.2	61.6	403.2
n = 5	S.D.	71.6	3.0	65.0	73.0
	Min	242.3	9.0	30.0	309.7
	Max	407.2	16.0	250.0	469.3
Ex situ	Mean	294.4	8.6	92.4	398.6
n = 76	S.D	184.4	2.2	43.3	211.4
	Min	117.0	3.0	30.0	130.4
	Max	1000.0	16.0	210.0	1000.0

* results rounded to the nearest 0.1

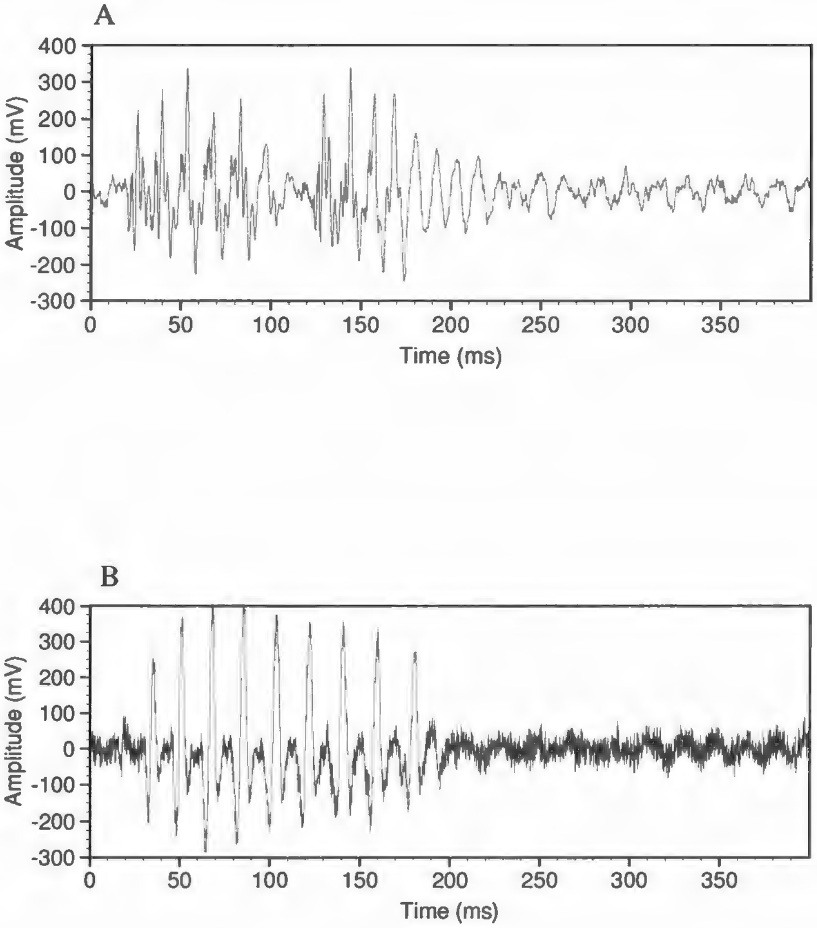

Figure 3.1: Oscillograms of *in situ* double cod grunt (A) and *ex situ* (B) single cod grunt.

Table 3.2 Biological sampling data (sample number followed by % of sex)

	N	Mature	Immature	Partly spent	Spent present	Spent last	Size (cm)	Age
Females	365(47)	245(67)	76(21)	-	1(< 1)	42(< 3)	35-91	3-12
Males	407(53)	325(80)	37(9)	18(3)	8(< 2)	19(< 1)	32-74	3-13
Total	772	570	113	18	9	61	32-91	3-13

* one female maturity undetermined

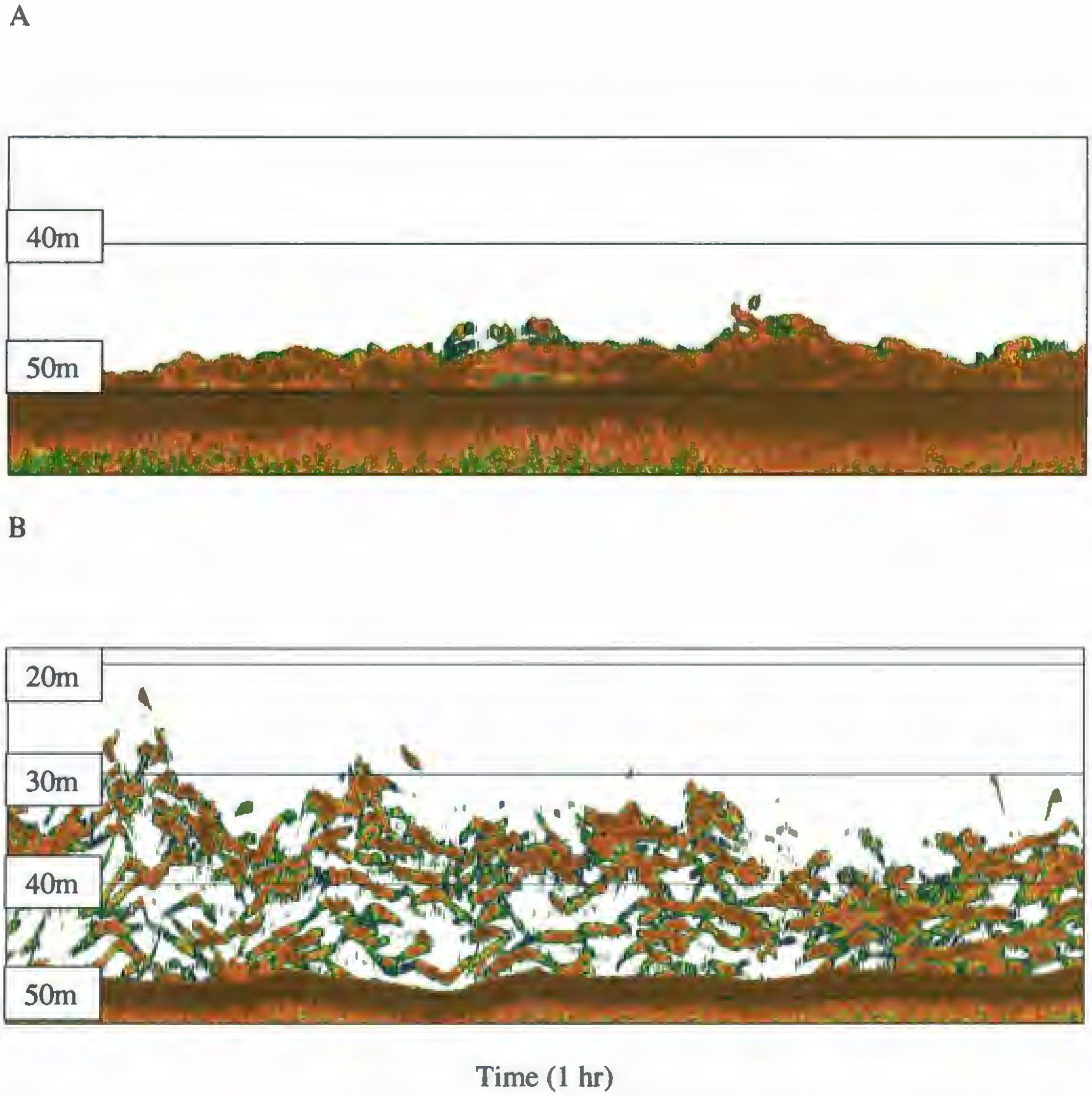

Figure 3.2: S_V echograms at 38 kHz of spawning cod during day light (A) recorded at 1448h and night time/darkness (B) recorded at 2114h on April 16 2003.

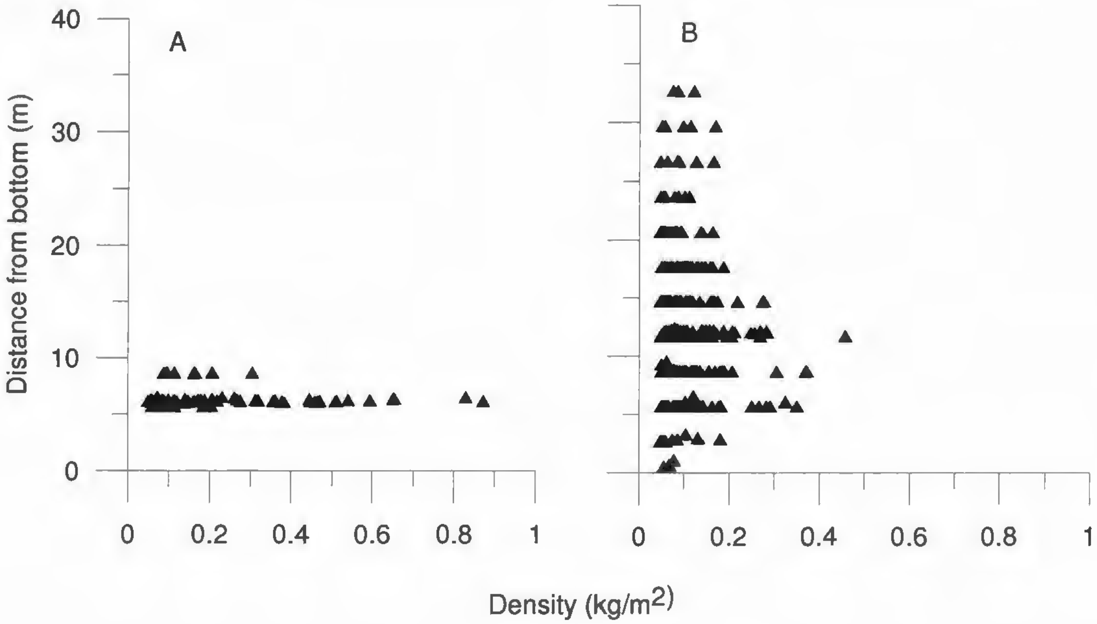

Figure 3.3 Density of cod versus distance from bottom during daylight (A) and darkness (B). Data limited to ≥ 0.1 kg/m^2

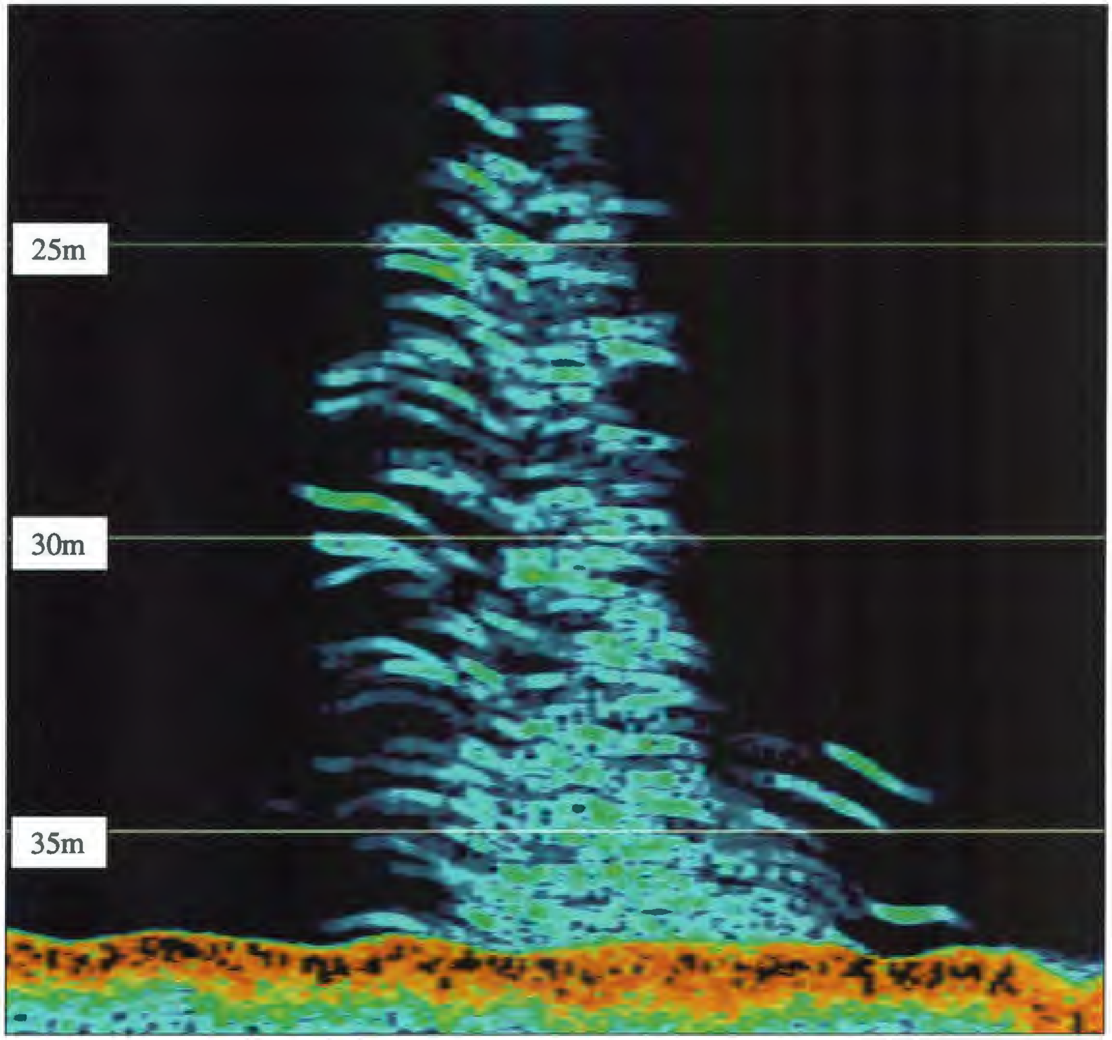

Figure 3.4: S_V echogram at 38 kHz of a spawning cod column. Data recorded from a moving vessel during spring 1997 in Placentia Bay. Total water depth 40m

SUMMARY

In the first part of my thesis I provide contemporary data on cod fecundity in the northwest Atlantic. It was found that southern cod populations have fecundity schedules similar to historical norms, but the formerly dominant northern fish are maturing at earlier ages and smaller sizes and dying young. I have indicated that potential fecundity of Atlantic cod is strongly correlated with weight, length, and age and less so with somatic and liver conditions. Spatial variations in cod fecundity were shown to be evident in all three management areas sampled (NAFO divisions 2J, 3KL, and 3Ps) as well as between offshore and inshore sampling locations. Cod life histories in the northern offshore areas bear little resemblance to historical norms. Offshore cod were shown to be maturing earlier and at smaller sizes than cod inhabiting southern waters (Fleming 1960, May 1967). I also compared the fecundity-weight relation across the north Atlantic. May (1967) noted that the relatively high fecundity from the western Baltic and Norway might result from the low age and small size at maturation, and was not necessarily representative of the northeast Atlantic as a whole. My research has shown that not only are offshore northern cod maturing at earlier ages and sizes but they are producing a higher number of eggs at equivalent sizes and ages than in any other reported stock. Early maturation, early mortality, and high fecundity are likely to be linked to life history responses to environmental, population or genetic changes. I further investigated these changes by examining the co-variation and growth hypotheses by comparing life history traits (age and size at maturity, mortality rates and fecundity) for the northern cod stock in the pre-industrial and post-industrial fishery eras. In addition, to

show the co-variation of these traits, I compare the total potential fecundity for these periods using an egg-per-recruit model. Few fish in the post-industrial fisheries era reached 6 years of age or > 60cm (formally many reached > 12 years and > 80cm), but fecundity at size in the early maturing fish was higher than ever recorded in any cod stock. Post-industrial cod at 4 years of age had a potential fecundity of 0.5 million eggs, which did not occur until age 6 in pre-industrial times. Mortality was low during the pre-industrial periods but increased dramatically in the post-industrial period. Using an egg-per recruit model, fit to age and length structure data, I show how reduced survivorship, earlier age at maturity and increased fecundity resulted in a compensated fecundity per recruit that was > 75% of pre-industrial levels. The cause of these changes in life history, whether they represent traits selected for by the fishery, responses to reduced densities, or a combination of these factors is discussed.

In the final section of my thesis I report on the observed acoustic properties of spawning cod from the same stock from experiments conducted both *in situ* (wild cod) and *ex situ* (lab cod). The comparisons between *in situ* and *ex situ* observations provided insight into the similarities and differences between wild and captive spawning behaviours. Both in the lab and in the wild cod appeared to have two behavioural phases associated with daylight hours and hours of darkness. Cod were most active during darkness with greater observed vertical movement and production of sounds compared to daylight hours. My results provide further evidence that columns of cod, first reported by Rose (1993), are associated with spawning and is the first to show the simultaneous incidence of vertical behaviours that result in the formation of such columns with cod sounding during spawning.

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APPENDICES

Appendix 1- Observation data for *ex situ* passive recordings taken from 2003 at the Oceans Science Centre, MUN.

DATA RECORD SHEET

ID	filename	# grunts	day	month	year	time	light cat
1	64_030803_002125	1	8	3	2003	00:21:25	0
2	54_030703_003034	1	7	3	2003	00:30:34	0
3	55_030703_005924	1	7	3	2003	00:59:24	0
4	35_022403_010129	3	24	2	2003	01:01:29	0
5	36_022403_010133	1	24	2	2003	01:01:33	0
6	90_032503_011007	2	25	3	2003	01:10:07	0
7	86_031003_011029	2	10	3	2003	01:10:29	0
8	91_032503_011453	1	25	3	2003	01:14:53	0
9	87_031003_012249	2	10	3	2003	01:22:49	0
10	88_031003_012256	1	10	3	2003	01:22:56	0
11	92_032503_014527	1	25	3	2003	01:45:27	0
12	65_030803_015103	1	8	3	2003	01:51:03	0
13	17_022203_015624	3	22	2	2003	01:56:24	0
14	66_030803_015657	1	8	3	2003	01:56:57	0
15	8_022103_020703	3	21	2	2003	02:07:03	0
16	56_030703_022123	1	7	3	2003	02:21:23	0

17	67_030803_022218	1	8	3	2003	02:22:18	0
18	27_022303_022359	1	23	2	2003	02:23:59	0
19	18_022203_024606	1	22	2	2003	02:46:06	0

ID	filename	# grunts	day	month	year	time	light cat
20	68_030803_024652	1	8	3	2003	02:46:52	0
21	80_030803_025046	2	8	3	2003	02:50:46	0
22	37_022403_025235	1	24	2	2003	02:52:35	0
23	19_022203_025953	1	22	2	2003	02:59:53	0
24	14_022203_003346	2	22	2	2003	03:34:06	0
25	15_022203_003350	1	22	2	2003	03:35:00	0
26	69_030803_033559	1	8	3	2003	03:35:59	0
27	57_030703_033745	1	7	3	2003	03:37:45	0
28	70_030803_033942	1	8	3	2003	03:39:42	0
29	96_032503_035251	2	25	3	2003	03:52:51	0
30	81_030803_051948	.	8	3	2003	05:19:48	0
31	71_030803_052021	1	8	3	2003	05:20:21	0
32	16_022203_005405	1	22	2	2003	05:40:05	0
33	89_032403_061548	1	24	3	2003	06:15:48	1

ID	filename	# grunts	day	month	year	time	light cat
34	82_030903_064804	1	9	3	2003	06:48:04	1
35	93_032503_083611	2	25	3	2003	08:36:11	1
36	94_032503_085726	1	25	3	2003	08:57:26	1
37	20_022203_095636	1	22	2	2003	09:56:36	1
38	83_030903_114132	1	9	3	2003	11:41:32	1
39	72_030803_134943	1	8	3	2003	13:49:43	1
40	41_030603_154908	1	6	3	2003	15:49:08	1
41	73_030803_162522	1	8	3	2003	16:25:22	1
42	9_022103_173103	1	21	2	2003	17:31:03	1
43	84_030903_181724	1	9	3	2003	18:17:24	0
44	60_030703_185502	2	7	3	2003	18:55:02	0
45	74_030803_191749	1	8	3	2003	19:17:49	0
46	61_030703_192311	1	7	3	2003	19:23:11	0
47	85_030903_192934	1	9	3	2003	19:29:34	0
48	45_030603_193900	2	6	3	2003	19:39:00	0
49	75_030803_194853	1	8	3	2003	19:48:53	0
50	76_030803_195355	2	8	3	2003	19:53:55	0

51	46_030603_202035	1	6	3	2003	20:20:35	0
52	10_022103_203110	4	21	2	2003	20:31:10	0
53	1_022003_203132	1	20	2	2003	20:31:32	0
54	2_022003_ 203139	1	20	2	2003	20:31:39	0
55	48_030603_203310	1	6	3	2003	20:33:10	0
56	3_022003_203913	6	20	2	2003	20:39:13	0
57	4_022003_203920	1	20	2	2003	20:39:20	0
58	5_022003_204134	1	20	2	2003	20:41:34	0
59	77_030803_204332	2	8	3	2003	20:43:32	0
60	50_030603_210452	1	6	3	2003	21:04:52	0
61	95_032503_211350	2	25	3	2003	21:13:50	0
62	78_030803_212109	2	8	3	2003	21:21:09	0
63	62_030703_212328	1	7	3	2003	21:23:28	0
64	24_022203_212459	1	22	2	2003	21:24:59	0
65	6_022003_212820	1	20	2	2003	21:28:20	0
66	51_030603_213256	1	6	3	2003	21:32:56	0
67	22_022203_213454	3	22	2	2003	21:34:54	0

ID	filename	# grunts	day	month	year	time	light cat

68	79_030803_214227	1	8	3	2003	21:42:27	0
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70	63_030703_215413	1	7	3	2003	21:54:13	0
71	25_022203_220457	1	22	2	2003	22:04:57	0
72	30_022303_220700	1	23	2	2003	22:07:00	0
73	7_022003_221625	1	20	2	2003	22:16:25	0
74	31_022303_221707	1	23	2	2003	22:17:07	0
75	32_022303_223833	1	23	2	2003	22:38:33	0
76	33_022303_231131	1	23	2	2003	23:11:31	0
77	26_022203_231526	1	22	2	2003	23:15:26	0
78	11_022103_231537	1	21	2	2003	23:15:37	0
79	53_030603_232044	.	6	3	2003	23:20:44	0
80	12_022103_232429	1	21	2	2003	23:24:29	0
81	13_022103_235302	2	21	2	2003	23:53:02	0
82	34_022303_235607	1	23	2	2003	23:56:07	0

Appendix 2 - Observation data for *in situ* passive recordings taken from 2003 at Bar Haven, Placentia Bay.

DATA RECORD SHEET

ID	filename	# grunts	day	month	year	time	light cat
83	a_041603_165804	1	16	4	2003	16:58:04	1
84	b_041603_165811	1	16	4	2003	16:58:11	1
85	c_041603_165823	2	16	4	2003	16:58:23	1
86	d_041603_165829	1	16	4	2003	16:58:29	1
87	i_041603_173405	1	16	4	2003	17:34:05	1